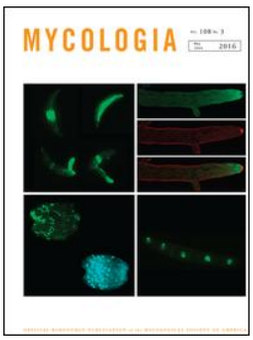

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A systematic revision of the ectomycorrhizal genus *Laccaria* from Korea

Hae Jin Cho [a], Myung Soo Park[a], Hyun Lee[a], Seung-Yoon Oh [a], Andrew W. Wilson[b], Gregory M. Mueller[c], and Young Woon Lim [a]

[a]School of Biological Sciences and Institute of Microbiology, Seoul National University, Seoul 08826, Republic of Korea; [b]Sam Mitchel Herbarium of Fungi, Denver Botanic Gardens, 909 York Street, Denver, Colorado 80206; [c]Plant Science and Conservation, Chicago Botanic Garden, 1000 Lake Cook Road, Glencoe, Illinois 60022

ABSTRACT

Species of *Laccaria* (Hydnangiaceae, Basidiomycota) are important in forest ecosystems as ectomycorrhizal fungi. Nine of the 75 described *Laccaria* species worldwide been reported from Korea. Most of these have European and North American names, and their identities are based solely on morphological features. To evaluate the taxonomy of Korean *Laccaria*, we used 443 specimens collected between 1981 and 2016 in a phylogenetic analysis based on sequence data from nuc rDNA internal transcribed spacer ITS1-5.8S-ITS2 rDNA (ITS) region, nuc 28S rDNA (28S), RNA polymerase II subunit 2 (*rpb2*), and translation elongation factor 1-α (*tef1*). Ten *Laccaria* species were identified. Three of these were previously reported from Korea: *L. bicolor, L. tortilis*, and *L. vinaceoavellanea*. *Laccaria alba, L. japonica*, and *L. murina* are confirmed as new reports from Korea. Lastly, four new *Laccaria* species are described: *L. araneosa, L. parva, L. torosa*, and *L. versiforma*. This study supports the general contention that Asian species of ectomycorrhizal fungi may not be conspecific with morphologically similar species from Europe and North America. Furthermore, identification based on morphology alone is often unreliable in *Laccaria* due to considerable overlap of characters among species. Thus, use of molecular methods is necessary for effective identification. Illustrations of the four newly described species and a taxonomic key to species of *Laccaria* in Korea are provided.

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KEYWORDS
Agaricales; Hydnangiaceae; new species; taxonomy; 4 new taxa

INTRODUCTION

The genus *Laccaria* (Hydnangiaceae, Agaricales) contains over 75 recognized species worldwide (Kirk et al. 2008). It has been reported from temperate and tropical areas and is an important constituent in alpine ecosystems (Mueller 1992; Kropp and Mueller 1999; Osmundson et al. 2005; Wilson et al. 2013; Popa et al. 2014). *Laccaria* species are root mutualists with a variety of vascular plant families, such as Betulaceae, Fagaceae, Myrtaceae, Pinaceae, and Salicaceae. Being ectomycorrhizal (ECM) fungi, they facilitate effective nutrient acquisition for their plant partners (Smith and Read 2008), thereby providing benefits of growth and survival to its associated plants. Thus, studies of *Laccaria* diversity contribute to an effective understanding of terrestrial ecosystems and forest management. In addition, two species of *Laccaria, L. bicolor* and *L. amethystina*, serve as model species for studying the genetics and life history of ECM fungi (Bastide et al. 1995; Martin et al. 2008; Vincenot et al. 2012; Kohler et al. 2015).

Laccaria is characterized morphologically by globose to oblong, echinulate, multinucleate basidiospores and brown-, orange-, or purple-colored basidiomes (Berkeley and Broome 1883; Singer 1986; Mueller 1991). Some species can be distinguished using a combination of morphological characters, such as basidiome color, basidiospore shape and size, and number of sterigmata per basidium (Mueller 1992). However, accurate identification using morphological data alone is difficult because of the overlap of similar character states (Mueller 1992; Sheedy et al. 2013).

Molecular analysis has become an increasingly important tool for accurate identification of fungal species (Bruns et al. 1991; Gardes and Bruns 1993; Taylor et al. 2000). In *Laccaria*, Mueller (1991) used restriction fragment length polymorphisms (RFLPs) of mitochondrial and ribosomal DNA to differentiate species within the *L. laccata* and *L. bicolor* complexes. Analysis of sequences from the nuc rDNA internal transcribed spacer ITS1-5.8S-ITS2 (ITS) region has improved the accuracy of identification of fungal species and led to the recognition of new *Laccaria* species (Wilson et al. 2013; Popa et al. 2014, 2016). Even so, the ITS is limited in its ability to resolve closely related species within the genus (Wilson et al. 2017b). The use of multigene sequence data has increased the accuracy

CONTACT Young Woon Lim ywlim@snu.ac.kr
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of phylogenetic relationships in *Laccaria* (Wilson et al. 2017b). In addition to the ITS, other loci used in *Laccaria* studies include nuc 28S rDNA (28S), the most variable region of RNA polymerase II subunit 2 (*rpb2*), and translation elongation factor 1-α (*tef1*) (Sheedy et al. 2013; Wilson et al. 2017a). Sheedy et al. (2013) showed that *rpb2* and *tef1* provided better species-level resolution than the ITS region in Australian *Laccaria*.

Since *Laccaria laccata* was first reported in Korea in 1940 (as *Clitocybe laccata*), nine species have been reported (Kaburagi 1940; Lee et al. 2015). These were identified based on phenotypic similarities to European, North American, and Japanese *Laccaria* but without detailed descriptions. Recently, several studies found that Asian members of fungal genera, e.g., *Laccaria, Russula*, and *Sparassis*, are divergent from their European and North American counterparts, and many specimens were reported as new species (Vincenot et al. 2012, 2017; Zhao et al. 2013; Lee et al. 2017; Wilson et al. 2017a). Thus, it is likely that the diversity of Korean *Laccaria* taxa is different from what is currently described. Here, we investigate Korean *Laccaria* using morphological data and phylogenetic analyses of sequences from four nuclear markers and provide detailed descriptions and illustrations of four new species.

MATERIALS AND METHODS

Specimen collections.—A total of 443 *Laccaria* specimens were examined in this study. These were obtained from the Kangwon National University (TPML), Korea National Arboretum (KA), Rural Development Administration (ASIS), and Seoul National University Fungus Collection (SFC). Specimens were collected throughout South Korea between 1981 and 2016 (SUPPLEMENTARY TABLE 1). Some were labeled as *L. fraterna, L. pumila*, and *L. tetraspora*, species not previously recorded in Korea. Most of the specimens were well preserved and in good condition, whereas a few were in too poor of a condition for molecular study. Ecological information for most of these specimens is unclear because they lack host and habitat metadata.

A total of 389 specimens were examined and reannotated using ITS sequences and morphological analysis. Forty-six representatives of each species were then included in a multilocus phylogenetic analysis using ITS, 28S, *rpb2*, and *tef1* loci.

Morphological observations.—Gross morphological features of fresh basidiomes were compared with published treatments (Breitenbach and Kränzlin 1991; Mueller 1991) and photographic illustrations (http://archive.fieldmuseum.org). All color names and alphanumeric codes follow the Methuen Handbook of Colour (Kornerup and Wanscher 1963). "L" refers to the number of complete lamellae; "l" refers to the number of lamellulae.

Sections of dried basidiomes were rehydrated in 3% KOH, stained in Congo red solution, Melzer's reagent (Largent et al. 1977), and observed under an 80i compound light microscope (Nikon, Tokyo, Japan) at either 400× or 1000× magnification. Two or three specimens (except for a single sample of *L. tortilis*) were used for measurements. At least 40 basidiospores, 40 basidia, and 10 cystidia (if possible) were measured per specimen. Measurements, rounded to the nearest integer or half micrometer, are indicated as minimum to maximum length or width, excluding individual extremes or outliers, with the mean values provided in italics between the range sizes. "Q" refers to the length/width ratio of an individual basidiospore.

For scanning electron microscope imaging (SEM), dried pieces of lamellae with basidiospores were attached to aluminum stubs using double-sided adhesive tape, coated with platinum in a sputter coater (Bal-Tec/SCD 005; Leica Microsystems, Wetzlar, Germany) and then examined with a SEM at 10000× magnification (SUPRA 55VP; Carl Zeiss, Oberkochen, Germany). Basidiospore size and echinulae were measured using SEM to the nearest 0.1 μm.

DNA extraction, PCR, and sequencing.—A small piece of fungal tissue from each dried specimen was placed in a 1.5-mL tube containing cetyltrimethylammonium bromide (CTAB) buffer and ground with a plastic pestle. Genomic DNA was extracted with a modified CTAB extraction protocol (Rogers and Bendich 1994).

The ITS region was amplified using primers ITS1F and ITS4B (Gardes and Bruns 1993), the 28S using LROR (Moncalvo et al. 2000) and LR5 (Vilgalys and Hester 1990), *rpb2* using fRPB2-5f (Liu et al. 1999) and fRPB2-8.2R (Matheny et al. 2007), and *tef1* using EF1-983F or EF1-altertative-3f and EF1-1567R or EF1-alternative-3r (Rehner and Buckley 2005; Stielow et al. 2015). Polymerase chain reaction (PCR) amplifications were performed on a thermal cycler (C1000TM; Bio-Rad, Richmond, California) using the AccuPower PCR premix (Bioneer, Daejeon, South Korea) following instructions as outlined in Park et al. (2013). PCR products were visualized on a 1% agarose gel and purified using the Expin PCR purification kit (GeneAll Biotechnology, Seoul, South Korea). Sanger sequencing was performed at Macrogen (Seoul) on an

automated DNA sequencer (ABI Prism 3730XL analyzer; Applied Biosystems, Foster City, California) using the aforementioned PCR primers.

DNA sequences were proofread using MEGA5 (Tamura et al. 2011) and deposited in GenBank. All sequences of four loci were individually aligned with *Laccaria* reference sequences from GenBank and UNITE using MAFFT (Katoh and Standley 2013) (SUPPLEMENTARY TABLE 2). Southern Hemisphere *Laccaria* form a grade, from which Northern Hemisphere lineages are derived (Wilson et al. 2017a) and thus excluded. Alignments were also checked by eye, and ambiguous positions were adjusted manually. Some sequences were treated with gaps due to missing data.

All phylogenetic analyses were performed based on maximum likelihood (ML) analysis in RAxML 8.0.2 (Stamatakis 2014) implemented on the CIPRES Web portal (Miller et al. 2010) using a GTRCAT model with 1000 bootstrap replicates (Stamatakis 2006). In the multigene analysis, alignments of four genes were concatenated and partitioned by gene regions, codon positions, and intron regions. *Laccaria acanthospora*, a basal taxon of the Northern Hemisphere, was chosen as the outgroup (Wilson et al. 2017a). Alignments and phylogenetic trees have been deposited at TreeBASE (S22078).

RESULTS

A total of 150 new sequences (46 ITS, 34 28S, 38 *rpb2*, 32 *tef1*) of *Laccaria* were produced from the 46 specimens analyzed. These are deposited in GenBank under accession numbers MG519517–MG519562 for ITS, MG519565–MG519598 for 28S, MG551594–MG551631 for *rpb2*, and MG551632–MG551636/ MG551638–MG551664 for *tef1* (TABLE 1). The concatenated alignment contained 46 taxa, of which sequences from the four loci were present. The alignments consisted of 660 characters for ITS, 920 for 28S, 580 for *rpb2*, and 613 for *tef1*.

Among the 443 Korean *Laccaria* specimens investigated, 389 were categorized into 10 taxa according to morphological features (color of basidiomes and lamellae, basidia and basidiospore sizes, number of sterigmata, presence or absence of cheilocystidia) and ITS sequence analysis (FIG. 1). The other 54 specimens were excluded from further sequencing and microscopy due to missing information or poor condition. Phylogenetic analyses based on individual loci (ITS, 28S, *rpb2*, and *tef1*) also separate the 10 Korean taxa, but their relationships are unclear (SUPPLEMENTARY FIGS. 1–4).

The multigene phylogenetic analysis supports the conclusion that six taxa are known species (*L. alba, L. bicolor, L. japonica, L. murina, L. tortilis*, and *L. vinaceoavellanea*) and four are new (FIG. 2). Among the four new species, *L. araneosa* is sister to *L. bicolor* with strong support and *L. versiforma* is sister to *L. salmonicolor* with strong support (FIG. 2). Asian *L. laccata* clustered separately from the European clade of *L. laccata* in all trees. We propose that the Korean *Laccaria* previously identified as *L. laccata* is a new species, which we describe as *L. parva* (FIGS. 1–2; SUPPLEMENTARY FIG. 1). The precise phylogenetic positions of *L. parva* and *L. torosa* are unclear due to low support values (FIG. 2).

Many of the herbarium specimens previously identified using morphological criteria were determined to be different species. Only three species (*L. bicolor, L. tortilis*, and *L. vinaceoavellanea*) matched recorded species in Korea. Three *Laccaria* species are reported for the first time in Korea (*L. alba, L. japonica*, and *L. murina*), and four are described as new. Most specimens labeled as *L. amethystina, L. laccata*, and *L. vinaceoavellanea* (over 80% of the collections) matched these species names morphologically, whereas phylogenetic analyses further clarified specimens previously labeled "*L. amethystina*" and "*L. laccata*" to represent the taxa *L. japonica* and *L. parva*, respectively (FIG. 3).

TAXONOMY

Laccaria araneosa H.J. Cho & Y.W. Lim, sp. nov. FIGS. 4A–B, 5

MycoBank MB823887

Typification: REPUBLIC OF KOREA. JEOLLABUK-DO: Muju-gun, Mt. Deogyu, 35°45′1.19″N, 127°40′32.10″ E, 770 m, 12 Sep 2012, *N.K. Kim* (**holotype** TPML20120912-40). GenBank: ITS = MG519548; 28S = MG519588; *rpb2* = MG551621; *tef1* = MG551654.

Etymology: *araneosa* (Greek), cobwebby, in reference to the pileus center covered with hyphal mat similar to a spider's web.

Diagnosis: Laccaria araneosa is characterized by hyphal mat on the center of orange-brown-colored pileus and absence of cystidia.

Pileus 10–18(–25) mm diam, convex to plane, with shallow central depression, covered with hyphal mat, orange-brown (5B5–7) or light brown (5A5), hygrophanous, fading to pale orange buff (5C5); margin involute to decurved, entire, sometimes crenate. Lamellae adnate to subdecurrent, thick, distant, orange-brown (5B5–7), L 20–28, l 1–4. Stipe 30–70 × 2.5–6.0 mm, cylindrical, solid, becoming hollow in age, minutely fibrillose; concolorous with pileus, sometimes darker; basal tomentum white, scant to moderately dense. Context thin, concolorous with stipe. Odor and taste unknown.

Basidiospores 8–*8.4*–9 × 7.5–*8.2*–9 µm, Q = 0.96–*1.03*–1.10, globose to subglobose, hyaline, echinulate; echinulae 1–1.2 µm in length, 0.6–0.8 µm wide at base. Basidia 42–

Table 1. Collection information and GenBank accession numbers of Korean *Laccaria* species used in this study.

Species	Specimen code	Forest type	Locality	GenBank accession numbers			
				ITS	28S	*rpb2*	*tef1*
Laccaria alba[a]	ASIS14694	—	Wonju-si, Gangwon-do	MG519545	MG519586	MG551619	—
	ASIS18039	—	Pyeongchang-gun, Gangwon-do	MG519546	—	MG551620	MG551652
	TPML20120807-69	Broadleaf (*Quercus*)	Muju-gun, Jeollabuk-do	MG519542	MG519583	MG551616	MG551649
	TPML20130628-14	Mixed	Bonghwa-gun, Gyeongsangbuk-do	MG519543	MG519584	MG551617	MG551650
	TPML20130628-19	Broadleaf	Bonghwa-gun, Gyeongsangbuk-do	MG519544	MG519585	MG551618	MG551651
	SFC20150903-58	Broadleaf	Gurye-gun, Jeollanam-do	MG519541	MG519582	MG551615	MG551648
	SFC20160907-38	Conifer (*Pinus*)	Yangyang-gun, Gangwon-do	MG519547	MG519587	—	MG551653
L. araneosa[b]	KA13-0940	—	—	MG519551	MG519591	MG551624	MG551657
	TPML20120912-25	Broadleaf (*Quercus*)	Muju-gun, Jeollabuk-do	MG519550	MG519590	MG551623	MG551656
	TPML20120912-40	Broadleaf (*Quercus*)	Muju-gun, Jeollabuk-do	MG519548	MG519588	MG551621	MG551654
	SFC20130917-21	Broadleaf	Yecheon-gun, Gyeongsangbuk-do	MG519549	MG519589	MG551622	MG551655
L. bicolor	ASIS9757	—	Jeju-si, Jeju-do	MG519523	—	—	MG551635
	KA13-0253	—	Geochang-gun, Gyeongsangnam-do	MG519524	MG519570	MG551599	MG551636
L. japonica[a]	TPML20120914-18	Conifer (*Pinus*)	Inje-gun, Gangwon-do	MG519522	MG519569	—	—
	SFC20130928-07	Broadleaf	Sangju-si, Gyeongsangbuk-do	MG519517	MG519565	MG551594	MG551632
	SFC20120722-12	Broadleaf	Gimpo-si, Gyeonggi-do	MG519518	MG519566	MG551595	MG551633
	SFC20110921-34	Broadleaf	Wonju-si, Gangwon-do	MG519519	—	MG551596	—
	SFC20120726-28	Mixed	Gongju-si, Chungcheongnam-do	MG519520	MG519567	MG551597	MG551634
	SFC20130704-34	Mixed	Yecheon-gun, Gyeongsangbuk-do	MG519521	MG519568	MG551598	—
L. murina[a]	ASIS24249	—	Seogwipo-si, Jeju-do	MG519552	MG519592	MG551625	MG551658
	ASIS216	—	—	MG519553	—	—	—
	ASIS2021	—	Hongcheon-gun, Gangwon-do	MG519554	—	—	—
L. parva[b]	ASIS19814	—	Hwaseong-si, Gyeonggi-do	MG519531	MG519575	MG551606	MG551642
	ASIS21282	—	Hwaseong-si, Gyeonggi-do	MG519526	MG519571	MG551601	MG551638
	ASIS21290	—	Hwaseong-si, Gyeonggi-do	MG519532	—	MG551607	MG551643
	SFC20120906-01	Broadleaf (*Quercus*)	Daehak-dong, Gwanak-gu	MG519527	MG519572	MG551602	MG551639
	SFC20120919-05	Broadleaf (*Quercus*)	Daehak-dong, Gwanak-gu, Seoul	MG519529	MG519573	MG551604	MG551640
	SFC20120919-40	Broadleaf	Daehak-dong, Gwanak-gu, Seoul	MG519525	—	MG551600	—
	SFC20121001-08	Broadleaf	Yuseong-gu, Daejeon	MG519530	MG519574	MG551605	MG551641
	SFC20130730-85	—	Guri-si, Gyeonggi-do	MG519528	—	MG551603	—
L. torosa[b]	SFC20150902-17	Mixed	Ulleung-gun, Gyeongsangbuk-do	MG519561	MG519598	MG551631	MG551664
	KA12-1306	Mixed	Ulleung-gun, Gyeongsangbuk-do	MG519562	—	—	—
L. tortillis	ASIS22273	—	Cheoin-gu, Gyeonggi-do	MG519533	MG519576	MG551608	MG551644
L. vinaceoavellanea	ASIS23860	—	—	MG519538	MG519579	MG551613	MG551645
	SFC20120907-18	Broadleaf	Seogwipo-si, Jeju-do	MG519536	MG519578	MG551611	—
	SFC20120922-02	Broadleaf (*Quercus*)	Dongdaemun-gu, Seoul	MG519535	—	MG551610	—
	SFC20120919-81	Broadleaf	Gongju-si, Chungcheongnam-do	MG519534	MG519577	MG551609	—
	SFC20130730-01	Broadleaf	Guri-si, Gyeonggi-do	MG519537	—	MG551612	—
	SFC20150810-10	Broadleaf	Daehak-dong, Gwanak-gu, Seoul	MG519539	MG519580	MG551614	MG551646
	SFC20160713-41	Broadleaf	Jeju-si, Jeju-do	MG519540	MG519581	—	MG551647
L. versiforma[b]	ASIS11	—	Yangyang-gun, Gangwon-do	MG519558	—	—	—
	ASIS20939	—	Pyeongchang-gun, Gangwon-do	MG519557	MG519595	MG551628	MG551661
	TPML20120924-82	Conifer (*Larix*)	Goesan-gun, Chungcheongbuk-do	MG519559	MG519596	MG551629	MG551662
	TPML20121008-03	Broadleaf	Chungju-si, Chungcheongbuk-do	MG519560	MG519597	MG551630	MG551663
	SFC20120926-01	Mixed	Gongju-si, Chungcheongnam-do	MG519556	MG519594	MG551627	MG551660
	SFC20121010-51	Broadleaf	Seosan-si, Chungcheongnam-do	MG519555	MG519593	MG551626	MG551659

[a]Newly recorded species to Korea.
[b]New species.

46–52 × 11–*12*–14 µm, 4-spored, sterigmata 8–10 µm long, clavate, hyaline. Pleurocystidia and cheilocystidia absent. Stipitipellis of parallel, cylindrical, repent, hyaline hyphae, caulocystidia absent. Pileipellis of interwoven, cylindrical, mostly repent hyphae, hyaline. Lamellar trama of subparallel to interwoven, cylindrical, repent, hyaline hyphae; subhymenium undifferentiated. All tissues inamyloid. Clamp connections present in all tissues.

Habitat and phenology: Scattered on ground in temperate forests including *Quercus*, Sep.

Sample of other specimens examined: REPUBLIC OF KOREA. JEOLLABUK-DO: Muju-gun, Mt. Deogyu, on ground of broadleaf forest, 12 Sep 2012, *N.K. Kim* (TPML20120912-25); GYEONGSANGBUK-DO: Yecheon-gun, Mt. Maebong, on ground of broadleaf forest, 17 Sep 2013, *H. Lee* (SFC20130917-21).

Notes: Laccaria araneosa closely resembles *L. acanthospora* and *L. alba* in basidiome size and color. However, *L. acanthospora* has longer basidiospore echinulae (2–6 µm in length × 1–2 µm in width) than *L. araneosa* (Wilson et al. 2013). *Laccaria araneosa* lacks cheilocystidia, whereas *L. alba* has filamentous to narrowly clavate cheilocystidia (Wang et al. 2004).

Laccaria parva H.J. Cho & Y.W. Lim, sp. nov.
FIGS. 4C–D, 6

MycoBank MB823888

Typification: REPUBLIC OF KOREA. SEOUL: Daehak-dong, Seoul National University, 37°27′29.16″ N, 126°56′57.45″E, 90 m, 19 Sep 2012, *H. Lee* (**holotype** SFC20120919-40). GenBank: ITS = MG519525; *rpb2* = MG551600.

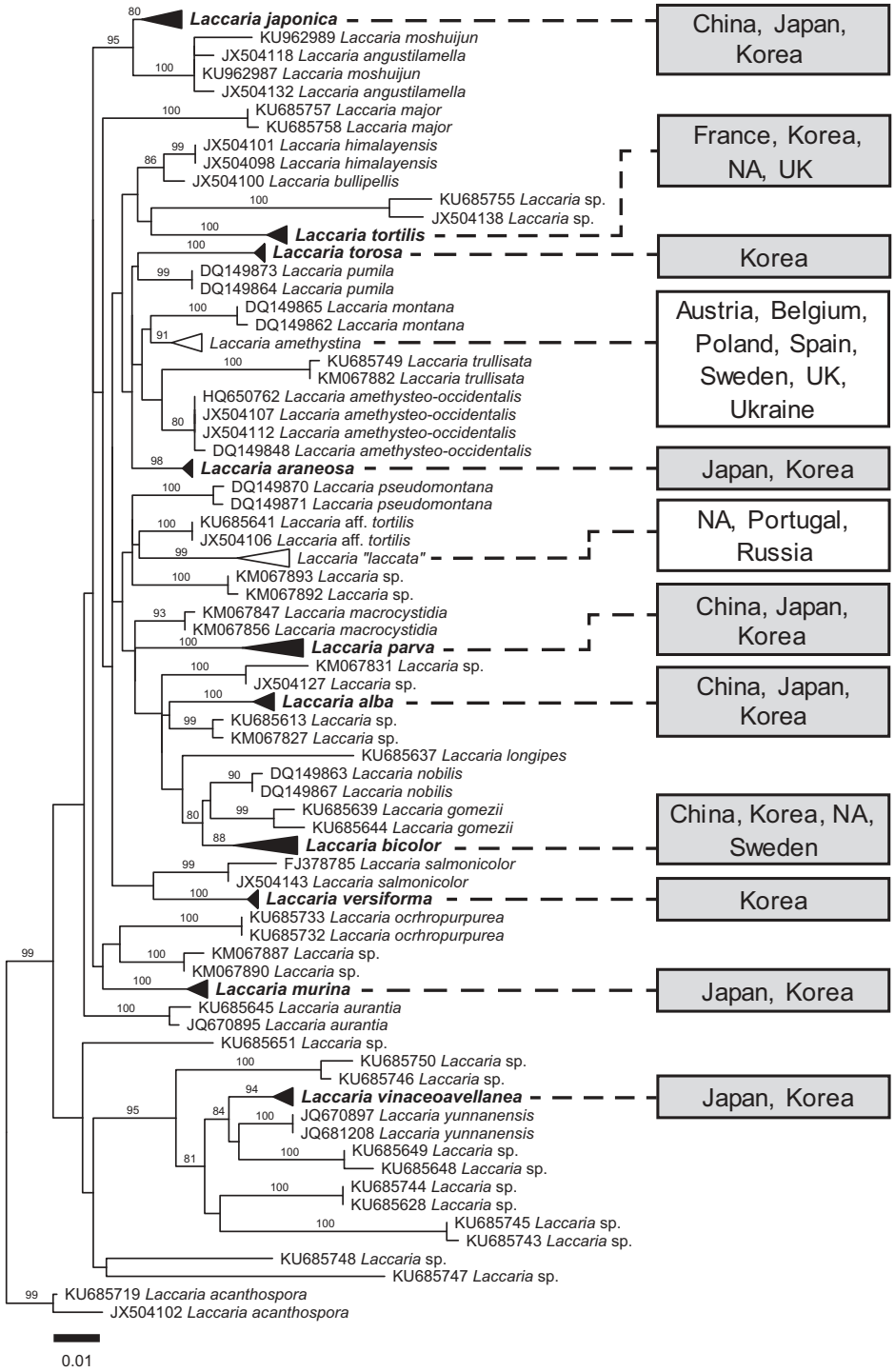

Figure 1. Phylogeny of *Laccaria* species based on ML analysis of the ITS region. Bootstrap values >70% are indicated. The scale bar indicates the number of expected nucleotide substitutions per site. New *Laccaria* species are represented in bold with gray fill. Boxes summarize the geographical distribution of specimens. Species from Korea are identified by gray boxes. NA = North America; UK = United Kingdom.

Etymology: parva (Latin), little, in reference to the small size of the basidiomes.

Diagnosis: Laccaria parva is morphologically similar to *L. alba* and *L. laccata*. However, caulocystidia are found only in *L. alba*. *Laccaria parva* differs from *L. laccata* by the presence of pleurocystidia.

Pileus 5–25 mm diam, broadly convex to flat, often slightly depressed at center; glabrous, sometimes finely hairy to scaly, slightly lined at maturity, sometimes wavy; bright brown (5B5), orange-brown (6B5–7), or reddish brown (7C7–8), hygrophanous, fading to light brown (5A5) or pale buff (6B4–6C6). Lamellae adnexed,

Figure 2. Phylogeny of *Laccaria* species based on ML analysis of a concatenated data set of ITS, 28S, *rpb2*, and *tef1* sequences. Bootstrap values >70% are presented at nodes. The scale bar indicates the number of expected nucleotide substitutions per site. Specimens from Korea are indicated in bold. New species are indicated by gray-shaded clades.

concolorous with pileus, powdery, pinkish brown (6B6–6C5) when dried, subdistant to distant, L 16–24, l 1–3. Stipe 20–40 × 3–5 mm, subcylindrical, glabrous to fibrillose, usually darker than pileus but sometimes concolorous; basal tomentum white. Context thin, concolorous with stipe. Odor and taste unknown.

Basidiospores 8–*9*–10 × 8.5–*9.2*–10 μm, Q = 0.90–*0.98*–1.05, globose to subglobose, hyaline, echinulate; echinulae 1–1.2 μm in length, 0.8–1 μm wide at base. Basidia 44–*50*–56 × 12–*14*–15 μm, 4-spored, sterigmata 8–10 μm long, clavate, hyaline. Cheilocystidia 19–40 × 3.5–6 μm, filamentous, sometimes irregular, thin-walled, hyaline. Pleurocystidia 25–33 × 4.5–5.5 μm, filamentous, hyaline. Stipitipellis of parallel, cylindrical, repent, hyaline hyphae, caulocystidia absent. Pileipellis of interwoven, cylindrical, hyaline, thin-walled hyphae. Lamellar trama of subparallel to interwoven, cylindrical, repent, hyaline hyphae; subhymenium undifferentiated. All tissues inamyloid. Clamp connections present in all tissues.

Habitat and phenology: Scattered on ground in temperate forests of *Quercus* and *Carpinus*, Sep and Oct.

Sample of other specimens examined: REPUBLIC OF KOREA. DAEJEON: Hagi-dong, Mt. Geumbyeong, on ground of broadleaf forest, 1 Oct 2012, *M.S. Park* (SFC20121001-08).

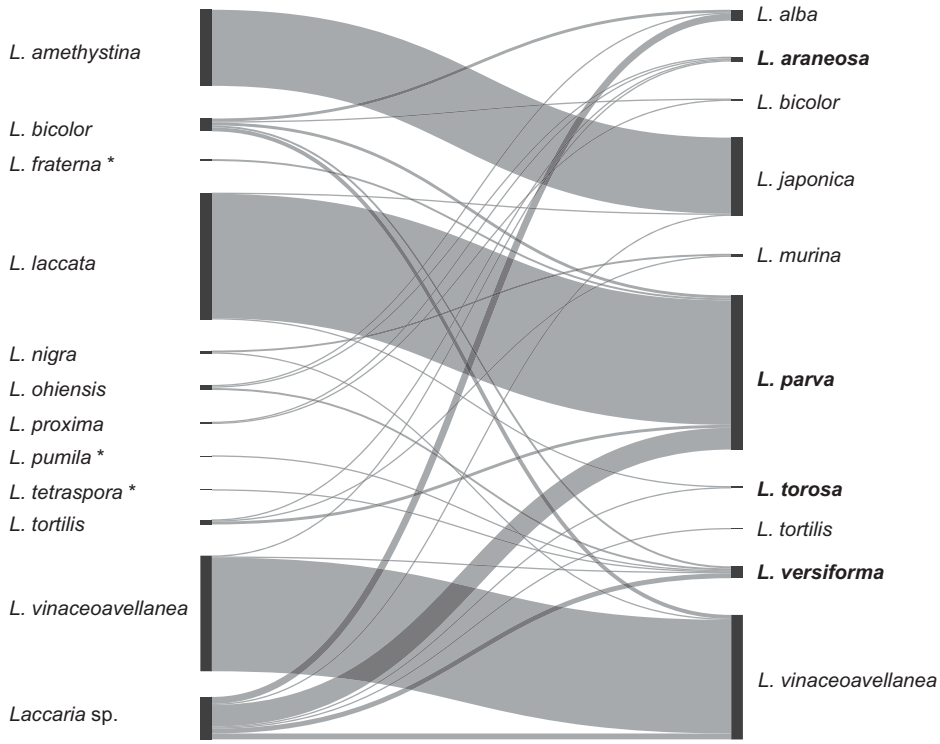

Figure 3. Flow plot of Korean *Laccaria* taxonomic revision. Morphological identification of specimens used in this study is on the left, with revised species identifications on the right. New species are indicated in bold. Names with asterisks (*) indicate specimens that have been used but are not confirmed as occurring in Korea in the present study.

Notes: Previously *Laccaria parva* was identified as *L. laccata* in Korea. However, *Laccaria parva* differs from *L. laccata* by the presence of pleurocystidia (Mueller and Vellinga 1986; Mueller 1992), and molecular data clearly distinguish them (FIGS. 1–2).

Laccaria torosa H.J. Cho & Y.W. Lim, sp. nov.
FIGS. 4E–F, 7

MycoBank MB823889

Typification: REPUBLIC OF KOREA. GYEONGSANGBUK-DO: Ulleung-gun, Buk-myeon, Nari Basin, 37°31′07.44″N, 130°52′47.13″E, 550 m, 2 Sep 2015, *N.K. Kim & J.Y. Park* (**holotype** SFC20150902-17). GenBank: ITS = MG519561; 28S = MG519598; *rpb2* = MG551631; *tef1* = MG551664.

Etymology: torosa (Latin), cylindrical with bulges, in reference to the thick stipe base.

Diagnosis: Laccaria torosa closely resembles *L. bicolor* in both macro- and micromorphology. However, the basidiospores of *L. torosa* have longer echinulae than *L. bicolor* (0.5 µm in length). Also, the conspicuous blue- or lilac-violaceous tomentum covering the lower part of stipe is found in *L. bicolor* but not in *L. torosa*.

Pileus 10–70 mm diam, convex to plane, with shallow central depression; orange-brown (6B5–7) or brown (6C8), hygrophanous, fading to pale orange buff (5C5); prominently pectinate-striate inwards from the edge; margin involute to decurved, entire or crenate. Lamellae subdecurrent or sinuate, thick, distant, powdery, orange-brown (5A4–6A3) or brown (6C6), L 20–28, l 1–3. Stipe 35–95 × 5–13 mm, thickened at base, solid, becoming hollow in age, sinewy fibrillose-striate; light brown or pale buff (6B4–6C6). Context thin, concolorous with stipe. Odor and taste unknown.

Basidiospores 8–*8.3*–9 × 8–*8.6*–9.5 µm, Q = 0.87–*0.97*–1.01, globose to subglobose, hyaline, echinulate; echinulae 1.2–1.4 µm in length, 1–1.2 µm wide at base. Basidia 39–*43*–47 × 12.5–*14.5*–16.5 µm, 4-spored, sterigmata 6–10 µm long, clavate, hyaline. Pleurocystidia 55–75 × 7–13 µm, filamentous to subclavate, sometimes irregular, thin-walled, hyaline. Cheilocystidia 54–94 × 5–8.5 µm, filamentous to subclavate, thin-walled, hyaline. Stipitipellis of parallel, cylindrical, repent, hyaline hyphae, caulocystidia 30–40 × 7.5–9 µm, clavate, thin-walled, hyaline. Pileipellis of interwoven, cylindrical, mostly repent hyphae, some hyaline but many clusters containing a yellow-brown pigmentation in 3% KOH. Lamellar trama of subparallel to interwoven, cylindrical, repent, hyaline hyphae; subhymenium undifferentiated. All tissues inamyloid. Clamp connections present in all tissues.

Figure 4. Basidiomes of four new *Laccaria* species from Korea. A–B. *L. araneosa* (TPML20120912-40, holotype; SFC20130917-21). C–D. *L. parva* (SFC20120919-40, holotype; SFC20121001-08). E–F. *L. torosa* (SFC20150902-17, holotype; KA12-1306). G–I. *L. versiforma* (SFC20120926-01, holotype; SFC20121010-51, TPML20120924-82). Bars = 10 mm.

Habitat and phenology: Scattered on ground in temperate forest dominated by *Pinus densiflora, Acer takesimense*, and *Acer okamotoanum*, Sep.

Sample of other specimens examined: REPUBLIC OF KOREA. GYEONGSANGBUK-DO: Ulleung-gun, Buk-myeon, Nari Basin, on ground of mixed forest, 5 Sep 2012, *S.K. Han* & *J.W. Jo* (KA12-1306).

Notes: Laccaria torosa was collected from only Ulleung Island, which is located in the East Sea. The bulging and thick stipe of *L. torosa* is similar to that of *L. bicolor* (Orton 1960). In a phylogenetic analysis, *L. torosa* formed a distinct clade with strong support (100%) and was clearly separated from *L. bicolor* (FIGS. 1–2).

Laccaria versiforma H.J. Cho & Y.W. Lim, sp. nov.
FIGS. 4G–I, 8

MycoBank MB823890

Typification: REPUBLIC OF KOREA. CHUNGCHEONGNAM-DO: Jeongan-myeon, Mt.

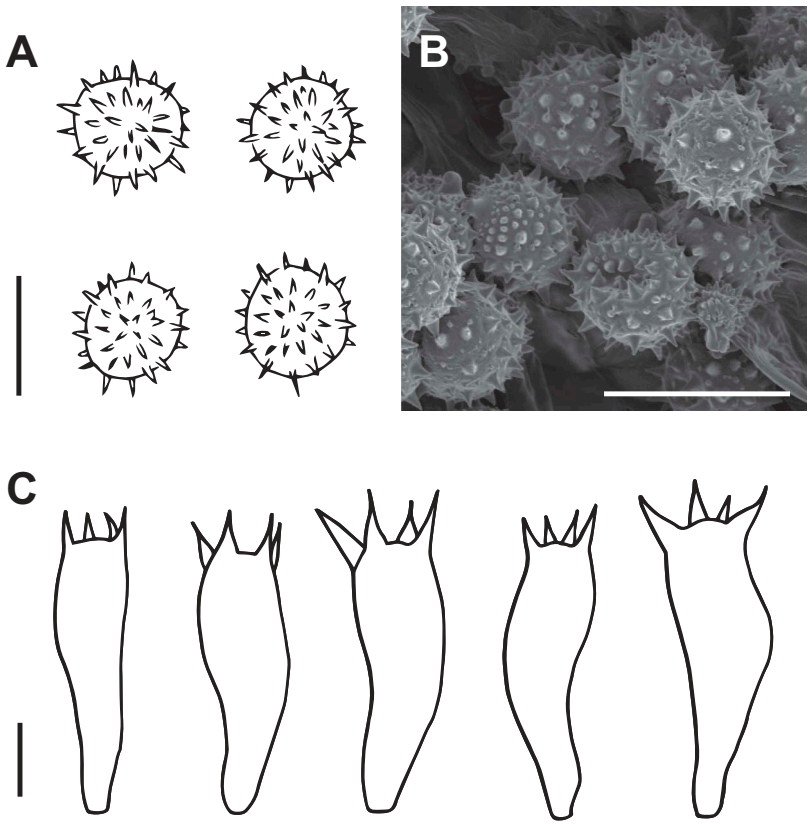

Figure 5. Micromorphological features of *Laccaria araneosa* (TPML20120912-40, holotype). A. Basidiospores. B. Basidiospores under SEM. C. Basidia. Bars = 10 mm.

Museong, 36°32′43.17″N, 127°04′06.75″E, 290 m, 26 Sep 2012, *H. Lee* (**holotype** SFC20120926-01). GenBank: ITS = MG519556; 28S = MG519594; *rpb2* = MG551627; *tef1* = MG551660.

Etymology: versiforma (Latin), of different shapes, in reference to the various forms and color of the pileus.

Diagnosis: Laccaria versiforma can be confused with *L. bicolor* because both species share a brown pileus color and pinkish-colored lamellae. However, *L. versiforma* has larger basidia and basidiospores than *L. bicolor*.

Pileus 10–35 mm diam, convex to plane, with shallow central depression; pale brown (5C5–6) or brown (6B8), hygrophanous, pale orange buff (5C5) or pale buff (6B4–6C6); margin involute to decurved, entire, sometimes crenate. Lamellae adnexed or sinuate, thick, distant to subdistant, pinkish brown (6B6–6C5), L 20–28, l 1–3. Stipe 30–35 × 2–4 mm, cylindrical, solid becoming hollow in age, sometimes minutely fibrillose, sometimes mottled; brown to pale brown or concolorous with the pileus; basal tomentum pale, sometimes white. Context thin, concolorous with stipe. Odor and taste unknown.

Basidiospores 7.5–*8.2*–10 × 7.5–*8.3*–9.5 µm, Q = 0.91–*0.99*–1.05, globose to subglobose, hyaline, echinulate; echinulae 1 µm in length, 0.8–1 µm wide at base. Basidia 41–*47*–55 × 10–*12*–14 µm, 4-spored, sterigmata 7–9 µm long, clavate, hyaline. Pleurocystidia 42–65 × 6.5–8.5 µm, filamentous to subclavate, hyaline. Cheilocystidia 42–54 × 6–8 µm, filamentous to subclavate, thin-walled, hyaline. Stipitipellis of parallel, cylindrical, hyaline hyphae, caulocystidia absent. Pileipellis of interwoven, cylindrical, mostly repent hyphae, hyaline. Lamellar trama of subparallel to interwoven, cylindrical, repent, hyaline hyphae; subhymenium undifferentiated. All tissues inamyloid. Clamp connections present in all tissues.

Habitat and phenology: Scattered on ground in temperate forests of *Quercus* and *Pinus densiflora*, Sep and Oct.

Sample of other specimens examined: REPUBLIC OF KOREA. CHUNGCHEONGNAM-DO: Seosan-si, Mt. Gaya, on ground of broadleaf forest, 10 Oct 2012, *H. Lee* (SFC20121010-51); CHUNGCHEONGBUK-DO: Goesan-gun, Mt. Bakdal, on ground of broadleaf forest, 24 Sep 2012, *N.K. Kim* (TPML20120924-82).

Notes: Laccaria versiforma is phylogenetically and morphologically similar to *L. salmonicolor* (FIGS. 1–2). However, compared with *L. salmonicolor, L. versiforma* has less reddish pigmentation in the basidiomes (Wilson

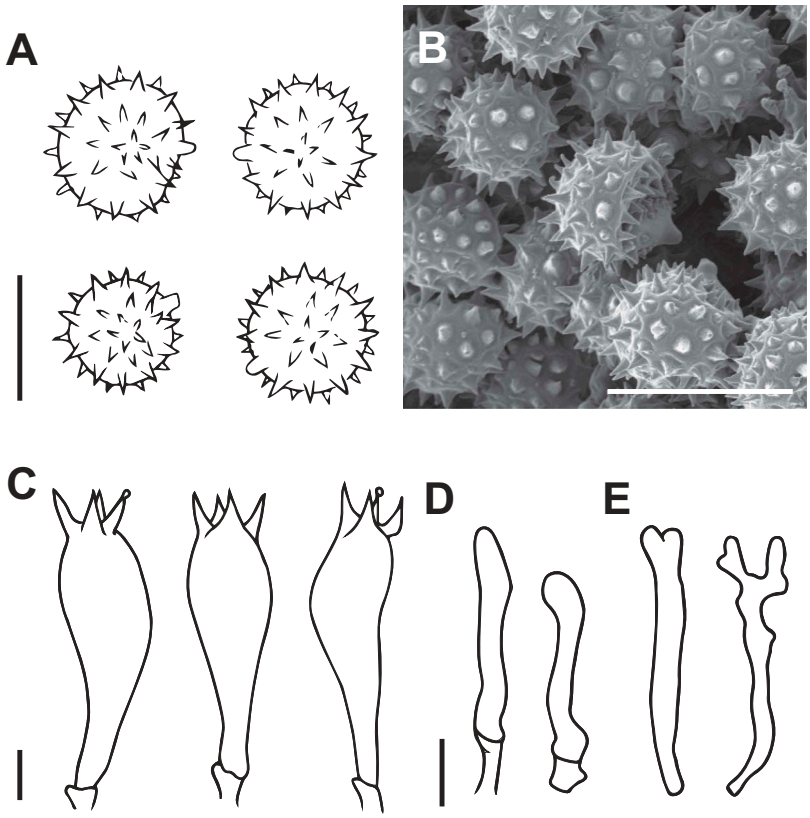

Figure 6. Micromorphological features of *Laccaria parva* (SFC20120919-40, holotype). A. Basidiospores. B. Basidiospores under SEM. C. Basidia. D. Pleurocystidia. E. Cheilocystidia. Bars = 10 μm.

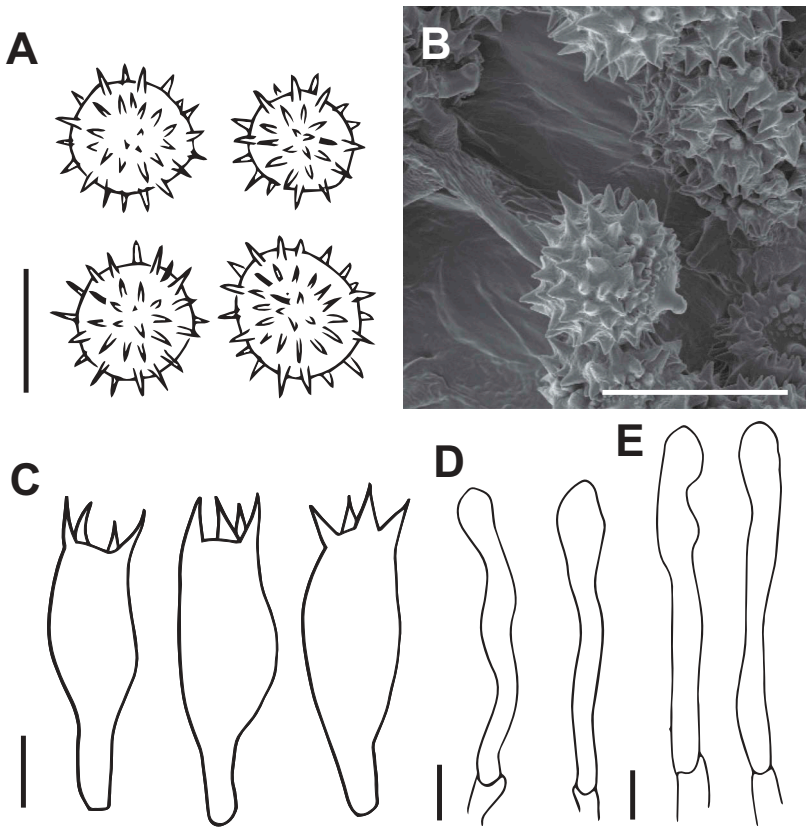

Figure 7. Micromorphological features of *Laccaria torosa* (SFC20150902-17, holotype). A. Basidiospores. B. Basidiospores under SEM. C. Basidia. D. Pleurocystidia. E. Cheilocystidia. Bars = 10 μm.

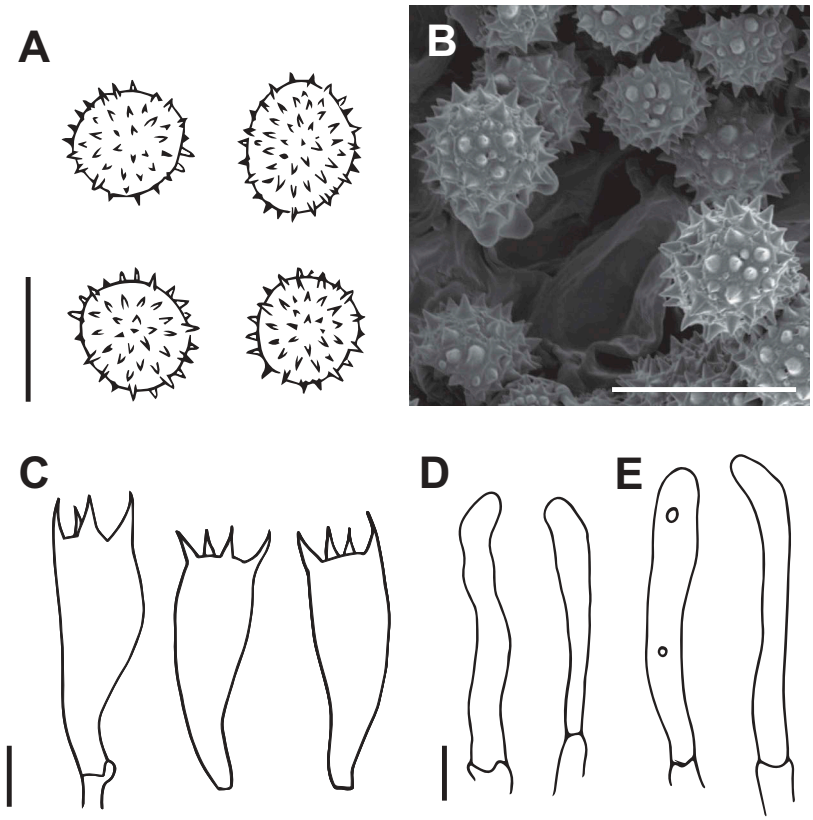

Figure 8. Micromorphological features of *Laccaria versiforma* (SFC20120926-01, holotype). A. Basidiospores. B. Basidiospores under SEM. C. Basidia. D. Pleurocystidia. E. Cheilocystidia. Bars = 10 µm.

et al. 2013). Pleurocystidia were found only in *L. versiforma*.

KEY TO KOREAN *LACCARIA* SPECIES

1. Basidiomes gray or purple 2
1′. Basidiomes buff or orange-brown 4
2. Basidiomes light gray to dark gray, basidia with 2 sterigmata ..... *L. murina*
2′. Basidiomes lavender-purple, basidia with 4 sterigmata 3
3. Pileus large at maturity (40–60 mm wide), basidiomes light grayish lavender when fresh, grayish buff in age or upon drying; basidiospores globose (Q = 1) ..... *L. vinaceoavellanea*
3′. Pileus small at maturity (10–30 mm wide), basidiomes deep purple when fresh, grayish brown in age or when dry; basidiospores subglobose (Q > 1) ..... *L. japonica*
4. Basidia with 2 sterigmata ..... *L. tortilis*
4′. Basidia with 4 sterigmata 5
5. Lamellae pinkish or light vinaceous 6
5′. Lamellae orange-brown 7
6. Basidia 32–42 µm long; basidiospores on average 7.5 × 7.4 µm ..... *L. bicolor*
6′. Basidia 41–56 µm long; basidiospores on average 8.2 × 8.3 µm ..... *L. versiforma*
7. Cheilocystidia absent ..... *L. araneosa*
7′. Cheilocystidia present 8
8. Pleurocystidia absent ..... *L. alba*
8′. Pleurocystidia present 9
9. Caulocystidia absent ..... *L. parva*
9′. Caulocystidia present ..... *L. torosa*

DISCUSSION

Many *Laccaria* species in Korea were previously interpreted based on broad morphological species concepts. Some specimens lacked detailed descriptions and used misapplied European and North American names, hindering estimates of *Laccaria* diversity and species composition in Korea. This study uses molecular phylogenetic analyses to evaluate the taxonomy of Korean *Laccaria* and identifies 10 species from Korea, of which only three matched previously recorded species: *L. bicolor, L. tortilis*, and *L. vinaceoavellanea*. Three species, *L. alba, L. japonica*, and *L. murina*, are reported from Korea for the first time. Their morphological features are identical to previous descriptions (Imai 1938;

Wang et al. 2004; Vincenot et al. 2017), and their phylogenetic identities are well supported by molecular analysis. Four new *Laccaria* species are described in this study: *L. araneosa, L. parva, L. torosa*, and *L. versiforma*. All of these lack distinctive macromorphological characters, resulting in previous misidentification (FIG. 3). However, these four species form unique species-level clades.

Laccaria amethystina and *L. laccata* have been reported from Korea (Kaburagi 1940; Lee et al. 1959); however, these are European names that have been misapplied to morphologically similar but phylogenetically distinct East Asian species. Recent phylogenetic analysis shows that Asian purple-toned *Laccaria* specimens were distinct from European ones and were described as two new species: *L. japonica* and *L. moshuijun* (Vincenot et al. 2017). Korean specimens labeled as *L. amethystina* were identified as *L. japonica. Laccaria laccata* was originally described from Sweden (Cooke 1884). Recent multigene phylogenetic analysis shows that *L. laccata* is polyphyletic (Wilson et al. 2017a). In the absence of a type specimen for *L. laccata*, it is difficult to evaluate the taxonomy of this species. Korean specimens of *L. laccata* formed a clade with reference sequences reported from China and Japan (FIGS. 1 and 2), but these are distantly related to European *L. laccata*. Although morphology did not distinguish Korean *L. laccata* from other *L. laccata* sensu lato, phylogenetic support based on four loci indicates that this is a new species, described here as *L. parva* (FIGS. 1–2). Similar to the case of *L. japonica* and *L. parva*, Asian species form a distinct clade with European-North American species, even though they share many morphological characters.

Four species previously reported from Korea were not confirmed in this study: *L. galerinoides, L. nigra, L. ohiensis*, and *L. proxima. Laccaria galerinoides* was originally reported from Chile (Singer and Moser 1965) and is phylogenetically related to *Laccaria* species in the Southern Hemisphere (Wilson et al. 2017a). This species has not been reported in Korea since 1979 (Cho and Lee 1979), and the name was likely misapplied. Two other species originally described from North America and Europe, respectively—*L. ohiensis* (Montagne 1856) and *L. proxima* (Boudier 1881)—were also reported from Korea but without detailed descriptions (Committee for the Suggestions on Standard Korean Name of Mushrooms 1978; Cho 1996). Sequence data from North American and European specimens of *L. ohiensis* and *L. proxima* did not match those of our specimens. Korean specimens of *L. ohiensis* have been revised here as *L. alba, L. araneosa*, and *L. versiforma*, and specimens of *L. proxima* have been revised as *L. araneosa* and *L. bicolor* (FIG. 3). *Laccaria nigra* was first described from Japan (Hongo 1959) and later used to name Korean specimens by the Committee for the Suggestions on Standard Korean Name of Mushrooms (1978). Korean specimens of *L. nigra* have been reidentified here as *L. murina* and *L. vinaceoavellanea* (FIG. 3). Previous determinations of *L. fraterna, L. pumila*, and *L. tetraspora* to Korean specimens were also not supported by this study. *Laccaria fraterna* and *L. pumila* are similar to *L. tortilis* in having two sterigmata, and *L. teteraspora* has often been confused as *L. laccata* because of their similar gross morphology (Singer and Moser 1965; Mueller and Vellinga 1986).

In conclusion, we can confirm 10 species of *Laccaria* from Korea, including four new species, based on morphological and molecular methods. Our results show that identification of *Laccaria* species using morphological data alone is risky. Because this issue is not likely to be limited to *Laccaria*, we suggest that study of Asian specimens in other taxa be performed to evaluate the actual diversity in Asian macrofungi.

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ORCID

Hae Jin Cho http://orcid.org/0000-0003-3041-5824
Seung-Yoon Oh http://orcid.org/0000-0002-9745-1849
Young Woon Lim http://orcid.org/0000-0003-2864-3449

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