




Taxonomic revision of the genus *Lactarius* (Russulales, Basidiomycota) in Korea

Hyun Lee¹ · Komsit Wissitrassameewong¹ · Myung Soo Park¹ · Annemieke Verbeken² · John Eimes³ · Young Woon Lim¹ 

Received: 1 October 2018 / Accepted: 13 April 2019 / Published online: 10 May 2019
© The Author(s) 2019

Abstract

The genus *Lactarius* Pers. (Russulales) is a cosmopolitan group of Basidiomycota that forms ectomycorrhizal relationships primarily with both deciduous and coniferous trees. Although the genus has been well-studied in Europe and North America, only fragmentary researches have been carried out on Asian species. In particular, the distribution of *Lactarius* species in South Korea is poorly understood due to insufficient morphological descriptions and a lack of DNA sequence data. In addition, the misuse of European and North American names has added to confusion regarding the taxonomy of Asian *Lactarius* species. In this study, the diversity of *Lactarius* in South Korea was evaluated by employing both morphological and phylogenetic approaches. A multi-locus phylogenetic analysis of 729 *Lactarius* specimens collected between 1960 and 2017 was performed using the internal transcribed spacer (ITS) region, partial nuclear ribosomal large subunit (nrLSU), partial second largest subunit of RNA polymerase II (*rpb2*), and minichromosome maintenance complex component 7 (*mcm7*). 49 *Lactarius* species were identified in three *Lactarius* subgenera: *L.* subg. *Russularia* (17 spp.), *L.* subg. *Lactarius* (22 spp.), and *L.* subg. *Plinthogalus* (10 spp.). Among them, 28 *Lactarius* species were identified as new to science, while just 17 were previously described *Lactarius* species. Four of the taxa remain un-named due to paucity of materials. A key to Korean *Lactarius* species, molecular phylogenies, a summary of diversity, and detailed description are provided.

Keywords Intercontinental conspecificity · *mcm7* · Milkcaps · Multi-locus phylogeny · Species delimitation

Introduction

Lactarius Pers. is a well known ectomycorrhizal genus that is characterized by the presence of latex (Persoon 1797), hence the common name milkcaps. The genus has long

been recognized as one of two major groups (together with the larger genus *Russula* Pers.) in the family Russulaceae. A recent multi-locus study revealed that species identified as *Lactarius* spp. actually represent three genera: *Multifurca* Buyck & V. Hofst (Buyck et al. 2008), *Lactarius*, and *Lactifluus* (Pers.) Roussel (Buyck et al. 2010; Verbeken et al. 2011, 2012; Stubbe et al. 2012).

Microscopically, all *Lactarius* species have basidiospores with an amyloid ornamentation, sphaerocytes (rounded cells) in the trama, and pseudocystidia in the hymenium (Hesler and Smith 1979; Heilmann-Clausen et al. 1998). *Lactarius* species are distributed in all terrestrial ecosystems (Hesler and Smith 1979; Montoya and Bandala 1996, 2003; Heilmann-Clausen et al. 1998; Basso 1999; Verbeken and Horak 1999, 2000; Verbeken et al. 2002; Nuytinck et al. 2006; Le et al. 2007a, b; Yamin-Pasternak 2008; Verbeken and Walley 2010; Wisitrassameewong et al. 2014a, b, 2015, 2016; Wang 2016, 2017a, b, 2018; Das et al. 2017, Herrera et al. 2018;

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s13225-019-00425-6>) contains supplementary material, which is available to authorized users.

✉ Young Woon Lim
ywlim@snu.ac.kr

¹ School of Biological Sciences and Institute of Microbiology, Seoul National University, 1 Gwanak-ro, Gwanak-gu, Seoul 08826, Korea

² Department of Biology, Research Group Mycology, Ghent University, K.L. Ledeganckstraat 35, 9000 Ghent, Belgium

³ University College, Sungkyunkwan University, 2066 Seoburo, Jangan-gu, Suwon 16419, Korea

Shi et al. 2018; Unipal et al. 2018; Wang et al. 2015, 2018a, b). To date, 583 *Lactarius* species have been recorded globally (Kirk et al. 2008, <http://www.catalogueoflife.org/col/browse/tree>). While most milkcaps are edible and popular as food in certain areas (e.g. *L. deliciosus* (L.) Gray, *L. indigo* (Schwein.) Fr., and *L. sanguifluus* (Paulet) Fr.) (Singer 1986; Sanmee et al. 2003), others produce mutagenic compounds (e.g. *L. helvius* (Fr.) Fr. and *L. necator* (Bull.) Pers.) (Von Wright et al. 1982; Suortti et al. 1983).

Until recently, species identification of *Lactarius* was based on morphological characters such as latex colour and colour change, pileus features, spore ornamentation, the presence/absence of cystidia and pileipellis structures (Hesler and Smith 1979; Heilmann-Clausen et al. 1998). Classification of *Lactarius* species has historically been problematic, as mycologists often use different morphological characters for infrageneric classification. Pileipellis structure has been the most frequently used character for infrageneric classification in *Lactarius*. However, Neuhoﬀ (1956) divided the milkcaps into two subgenera based on pileipellis structure, while Hesler and Smith (1979) classified North American species of *Lactarius* s.l. into six subgenera using pileus and latex features. For European *Lactarius*, Heilmann-Clausen et al. (1998) described six subgenera using pileipellis structure as well as features of cystidia, while Basso (1999) proposed six subgenera based on the pileipellis structure and ecological complements.

While some *Lactarius* species are easily identified to the species level using only morphological characters, most *Lactarius* species are difficult to distinguish due to subtle morphological differences between species (Heilmann-Clausen et al. 1998; Stubbe et al. 2010; Nuytinck and Ammirati 2014). As the sequence data available in public nucleotide databases such as GenBank and UNITE have increased in recent years, the combination of morphological, molecular, and ecological data has greatly improved the accuracy of species identification in the *Lactarius* (Nuytinck and Verbeken 2003; Lee et al. 2015a). The internal transcribed spacer (ITS) region is commonly used as a fungal barcode (Schoch et al. 2012) and has been instrumental in identifying new *Lactarius* species (Verbeken et al. 2001; Das et al. 2015). The accuracy of phylogenies has been further enhanced through the use of a multi-locus approach, for example the partial nuclear ribosomal large subunit 28S (nrLSU) and the conserved region between domain 6 and 7 of the second largest subunit of RNA polymerase II (*rpb2*) (Stubbe 2012; Verbeken et al. 2014; Wisitrassameewong et al. 2016).

Based on recent molecular studies, three *Lactarius* subgenera are currently recognized: *Lactarius* subgenus *Lactarius*, *L.* subg. *Russularia* (Fr. ex Burl.) Kauffman, and *L.* subg. *Plinthogalus* (Burl.) Hesler & A.H. Sm. (Verbeken

and Nuytinck 2013; Wisitrassameewong et al. 2014a). Only *L.* subg. *Plinthogalus* is well-supported by molecular data in the most recent global phylogeny (Eberhardt and Verbeken 2004). Before the twenty-first century, the taxonomy of *Lactarius* was well-studied in Europe and North America (Hesler and Smith 1979; Heilmann-Clausen et al. 1998). As a result, European and North American nomenclature was applied to *Lactarius* species found in other continents or relatively distant geographical regions (e.g. Central and South America) (Pegler and Fiard 1979; Singer et al. 1983) and East Asia (Tanaka 1890; Imai 1935; Hongo 1957a, b, 1971, 1979). Recent studies based on molecular analysis demonstrated that most *Lactarius* species are not cosmopolitan and certain species are distributed to specific geographical regions (Le et al. 2007a; Nuytinck et al. 2007; Wisitrassameewong et al. 2016). Consequently, many Asian *Lactarius* species have been misidentified, often using European and American species names. Similar situations have been reported in South Korea (Lee et al. 2014, 2015a; Kim et al. 2015). Thus a re-evaluation of Korean *Lactarius* species is warranted.

Uyeki (1936) identified the first three *Lactarius* species in Korea: *L. akahatsu* Nobuj. Tanaka, *L. hatsudake* Nobuj. Tanaka and *L. piperatus* (L.) Pers. (now *Lactifluus piperatus* (L.) Roussel). Since then 64 additional *Lactarius* species have been recorded in South Korea, with 49 of these belonging to the *Lactarius* s. str. (Bok and Shin 1985; Lee et al. 2015b, 2018). These species were identified based on phenotypic similarities to European and North American *Lactarius* and lacked detailed descriptions and molecular data. Recently, several studies found that Asian members of many fungal genera, e.g., *Amanita* Pers., *Laccaria* Berk. & Broome, *Russula*, and *Sparassis* Fr. as well as *Lactarius*, are divergent from their European and North American counterparts, and many specimens were reported as new species (Zhao et al. 2013; Lee et al. 2017; Vincenot et al. 2017; Cho et al. 2018; Cui et al. 2018). Thus, it is likely that the diversity of Korean *Lactarius* taxa is different from what is currently described. Here, we investigated 729 Korean *Lactarius* specimens collected from 1960 to 2017 using morphological data and phylogenetic analyses of sequences from four markers: the ITS, nrLSU, *rpb2* and minichromosome maintenance complex component 7 (*mcm7*).

Materials and methods

Sampling

A total of 729 *Lactarius* specimens were obtained from five herbaria in South Korea: Seoul National University (SFC), Kangwon National University (TPML), National Institute

of Agricultural Sciences (HCCN), National Institute of Biological Resources (NIBR), and Korea National Arboretum (KA). Samples were collected in South Korea from 1960 to 2017. All specimens were initially identified using morphological characters and collection information was obtained from each herbarium where available.

Morphology

Newly collected specimens were preliminary identified using field guides (Romagnesi 1985; Heilmann-Clausen et al. 1998; Kränzlin 2005; Park and Lee 2011) and the Russulales news website (<http://www.mtsn.tn.it/russulales-news/>) in order to have a provisional working name. The terminology of macro-morphology is in accordance with Verbeken and Walley (2010). We observed latex colour when it was exuded from basidiocarps and colour changes when exposed to the air. The Methuen Handbook of Colour (Kornerup and Wanscher 1978) was used for colour indications.

Microscopic characters were studied and illustrated from dried specimens using an Eclipse 80i light microscope (Nikon, Tokyo, Japan). Specimens were mounted in 3–5% (w/v) KOH and 1% (w/v) phloxine (Largent et al. 1977) to observe hyphae contents. To compare with other published data, we measured at least 20 basidia and cystidia per specimen. All elements on the hymenium and pileal structure were observed using 5% (w/v) Congo red solution (Cléménçon 1973) to observe cell walls and to measure the size of elements. The amyloidity of the plage on basidiospores was observed using Melzer's reagent (Largent et al. 1977). The length and width of basidiospores were measured in lateral size using scanning electron microscope (SEM). Pieces of dried lamellae were attached to aluminum stubs using double sided adhesive tape, coated with platinum in a sputter coater (EM ACE200, Leica, Austria), and then examined with a SEM (SUPRA 55VP, Carl Zeiss, Germany). Pileipellis was observed from the middle part of pileus. Twenty basidiospores were measured per collection. Basidiospore size and shape are calculated as $(\text{MIN} -)[\text{AVa} - 2 \times \text{SD}] - \text{AVa} - \text{AVb} - [\text{AVb} + 2 \times \text{SD}](- \text{MAX})$, in which MIN = the minimum value, MAX = the maximum value, AVa = lowest mean value for the measured collection, AVb = highest mean value for the measured collection and SD = standard deviation. Q value represents basidiospore "length/width ratio which corresponds to basidiospore shape and is reported as $\text{MIN} - \text{QAVa} - \text{QAVb} - \text{MAX}$, where QAVa and QAVb are the lowest and the highest mean ratio for a measured specimen, respectively. For species with only one sample, the size and shape are calculated as $(\text{MIN} -)[\text{AV} - 2 \times \text{SD}] - \text{AV} - [\text{AV} + 2 \times \text{SD}](- \text{MAX})$ and $\text{MIN} - \text{QAV} -$

MAX, in which AV = mean value for the measured collection and QAV = mean ratio for a measured specimen. All average values are in italics. The size of hymenial elements and pileal structure were presented as MIN–MAX and rounded up up to 0.5 μm .

DNA extraction, PCR amplification, and sequencing

Genomic DNA was extracted from fresh or dried material using a modified CTAB extraction protocol of Rogers and Bendich (1994) (Park et al. 2013). Four loci were amplified and sequenced: the ITS, nrLSU, *mcm7*, and *rpb2*. PCR amplification and sequencing were conducted in two steps. First, we amplified and sequenced the ITS region from all specimens. Second, we sequenced the nrLSU, *mcm7*, and *rpb2* loci from the representative specimens of each putative species, which was delimited by the ITS phylogeny and morphological features.

PCR amplifications were conducted using AccuPower[®] PCR premix (Bioneer Co., Daejeon, Korea) in a C1000 thermal cycler (Bio-Rad, Hercules, CA, USA). The ITS region was amplified using two primer sets: forward primers ITS1F or ITS5 (White et al. 1990; Gardes and Bruns 1993) and reverse primers ITS4B or Russ3R (Gardes and Bruns 1993; Park et al. 2013). PCR conditions for the ITS are described in Park et al. (2013). The nrLSU region was amplified using ITS3 and LR5 primers (Vilgalys and Hester 1990; White et al. 1990). The PCR conditions for the nrLSU locus were: 5 min initial denaturation at 95 °C followed by 35 cycles of 40 s at 95 °C, 40 s at 55 °C and 60 s at 72 °C with a final extension step for 7 min at 72 °C. The partial *rpb2* locus was amplified using two sets of primers. The first amplification was conducted using the fRPB2-5F and bRPB2-8.2R primers (Liu et al. 1999; Matheny et al. 2007) under the following amplification conditions: 5 min initial denaturation step at 95 °C, followed by 35 cycles of 1 min at 95 °C, 1 min at 50 °C with 0.3 °C ramp per s to 72 °C and 1 min at 72 °C, and a final extension for 10 min at 72 °C. The primers bRPB2-6F and bRPB2-7.1R or bRPB2-7R (Matheny 2005) were used to amplify domain 6 to 7 of the *rpb2* in the second amplification. The PCR program consisted of an initial 5 min denaturation step at 95 °C, followed by 35 cycles of 40 s at 95 °C, 40 s at 58 °C and 60 s at 72 °C, and a final extension 7 min at 72 °C. We developed four Russulaceae-specific *mcm7* primers using Primer3 (Rozen and Skaletsky 2000): *mcm7*-Russ1F (GRA ARG AGT TYA CBC CYA TT), *mcm7*-Russ2F (GAC TGY CAG AAY GAG AAC GA), *mcm7*-Russ1R (TGA KAT CSC CAC GRA TYY TCA T), and *mcm7*-Russ2R (GCT TTC TTS ACG TCR AYR TG). The first amplification of the *mcm7* locus was conducted using either the primers *mcm7*-Russ1F/*mcm7*-

Russ1R or mcm7-Russ2F/mcm7-Russ2R with the same amplification conditions previously described for nrLSU.

All PCR amplicons were checked on a 1% agarose gel stained with EcoDye DNA staining solution (SolGent Co., Daejeon, Korea). PCR products were purified with the Expin PCR Purification Kit (GeneAll Biotechnology, Seoul, Korea) according to the manufacturer's instructions. DNA sequencing was performed by Macrogen (Seoul, South Korea), using the same set of primers for each locus on an ABI3730 automated DNA Sequencer. Forward and reverse sequences were checked and edited when necessary using FinchTV 1.4.0 (Geospiza, Inc.; <http://www.geospiza.com/finchtv>) and assembled in Mega 6 (Tamura et al. 2013). Sequences of all DNA regions generated in this study were deposited in GenBank (Supplementary Table 1).

Phylogenetic analyses

ITS sequences were aligned with *Lactarius* reference sequences from GenBank and UNITE using MAFFT v. 7.380 (Kato and Standley 2013). Ambiguously aligned positions were determined using Gblock (Castresana 2000) and excluded from further analyses. Maximum likelihood (ML) analyses were performed using RAxML v. 7.03 (Stamatakis 2006) and the GTR + G model with 1000 bootstrap replicates. A jModelTest 2.1.7 (Darriba et al. 2012) was used to determine the model of character evolution. Bayesian inference (BI) analyses were executed with MrBayes v. 3.2.6 (Ronquist and Huelsenbeck 2003) using the model K80 + I + G. The BI analyses were performed with four independent runs in which each run had four chains. Each run had 20 million generations at a sampling frequency of 1000. All analyses were done on the CIPRES Science Gateway (Miller et al. 2010).

Phylogenetic relationships among Korean *Lactarius* species were determined using sequences of the four loci. Phylogenetic tree was constructed using only sequences from Korean *Lactarius* species because no reference sequences of the *mcm7* locus were available. Sequences of each locus were aligned and analyzed separately. Sequence

Fig. 1 Phylogram generated from Maximum Likelihood (RAxML) analysis based on ITS sequence data of *Lactarius*. ML bootstrap support values/Bayesian posterior probability greater than 70%/0.95 are indicated. Korean specimens are marked in bold. Names of the species in red, and green represent new species and previously described species in South Korea, respectively. The names in blue are potentially new species but not be presented as new in this study because they lack morphological data or photographs of basidiomata

alignments were performed using the same method as that of the ITS described above. Alignment properties of each gene were analyzed using MEGA v. 6 (Tamura et al. 2013). ML and BI analyses were performed on the CIPRES Science Gateway with the same criteria used for the ITS. The BI analysis models for the nrLSU, *mcm7*, and *rpb2* loci were K80 + I + G, HKY + I + G, and SYM + I + G, respectively. Finally, a combined analysis of the ITS, nrLSU, *mcm7*, and *rpb2* sequences was conducted using the same methods and models previously assigned for each gene. Clades were considered to be independent evolutionary lineages when strongly supported (bootstrap support exceeding 70 and the posterior probability exceeding 0.95).

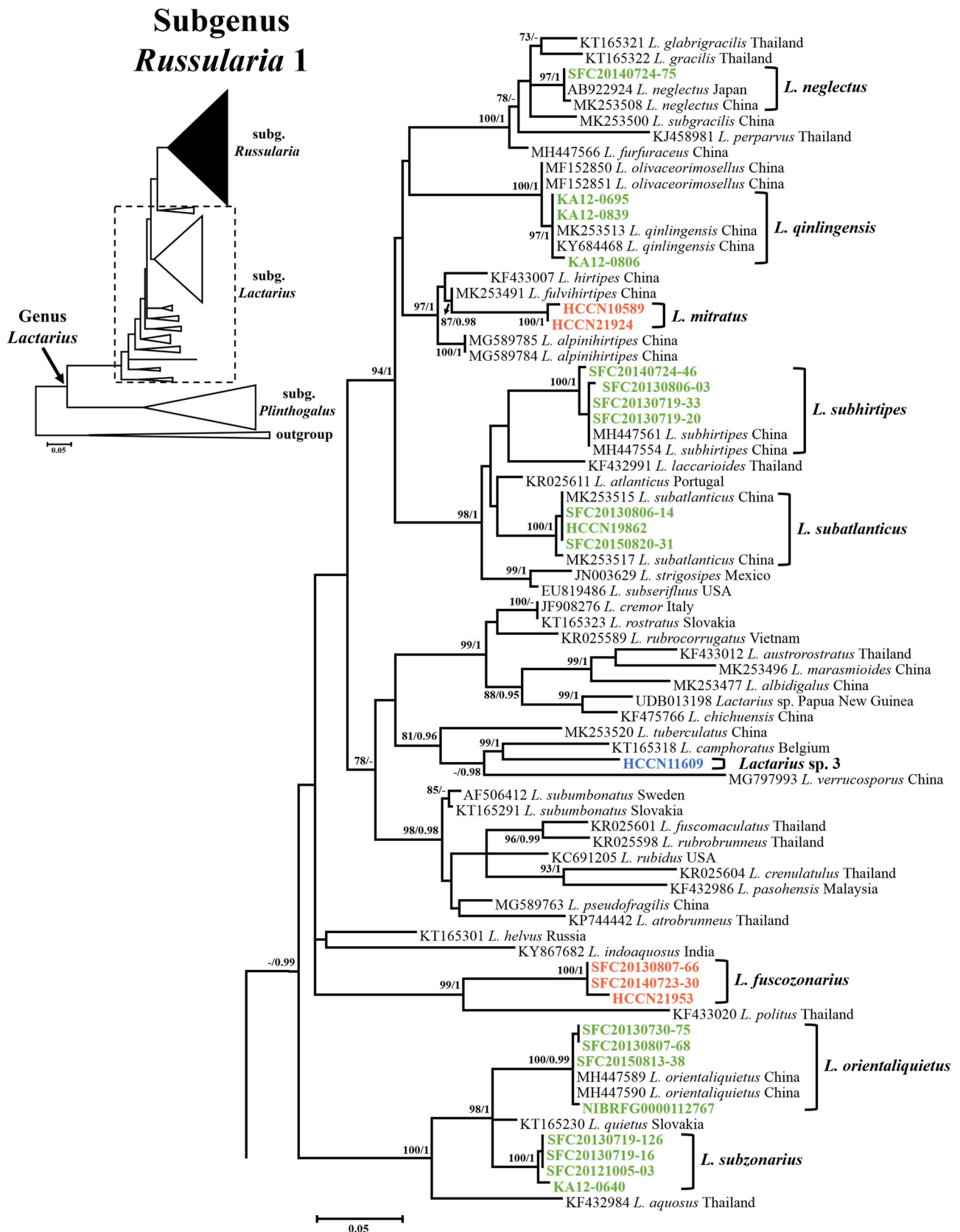
Results

Diversity of *Lactarius* in South Korea

Among 729 Korean *Lactarius* specimens examined, ITS fragments of 650–700 bp were successfully sequenced from 525 specimens. The other 204 specimens were excluded from the study due to missing information or poor condition. ITS sequences from 525 specimens in Korea was analyzed with 238 reference ITS sequences and found to represent 49 species (Fig. 1). To confirm species identity and infer the phylogenetic relationships of Korean *Lactarius*, three additional loci were amplified and sequenced for 128 specimens representing the 49 species: nrLSU (540–550 bp), *rpb2* (630–670 bp), and *mcm7* (420–440 bp). The ITS, nrLSU, *rpb2*, and *mcm7* sequence

Table 1 Alignment properties and nucleotide substitution models

	ITS	nrLSU	<i>rpb2</i>	<i>mcm7</i>	Combined 4 loci
Characters included (with gaps)	1068	554	656	453	2731
Invariable positions	693	451	400	254	1798
Parsimony informative positions (%)	327 (31)	92 (17)	231 (35)	184 (41)	834 (30)
Uninformative variable positions	48	11	25	15	99
Number of branches > 70% bootstrap ML analysis	11	5	14	18	22
Nucleotide substitution models	K80 + I + G	K80 + I + G	SYM + I + G	HKY + I + G	



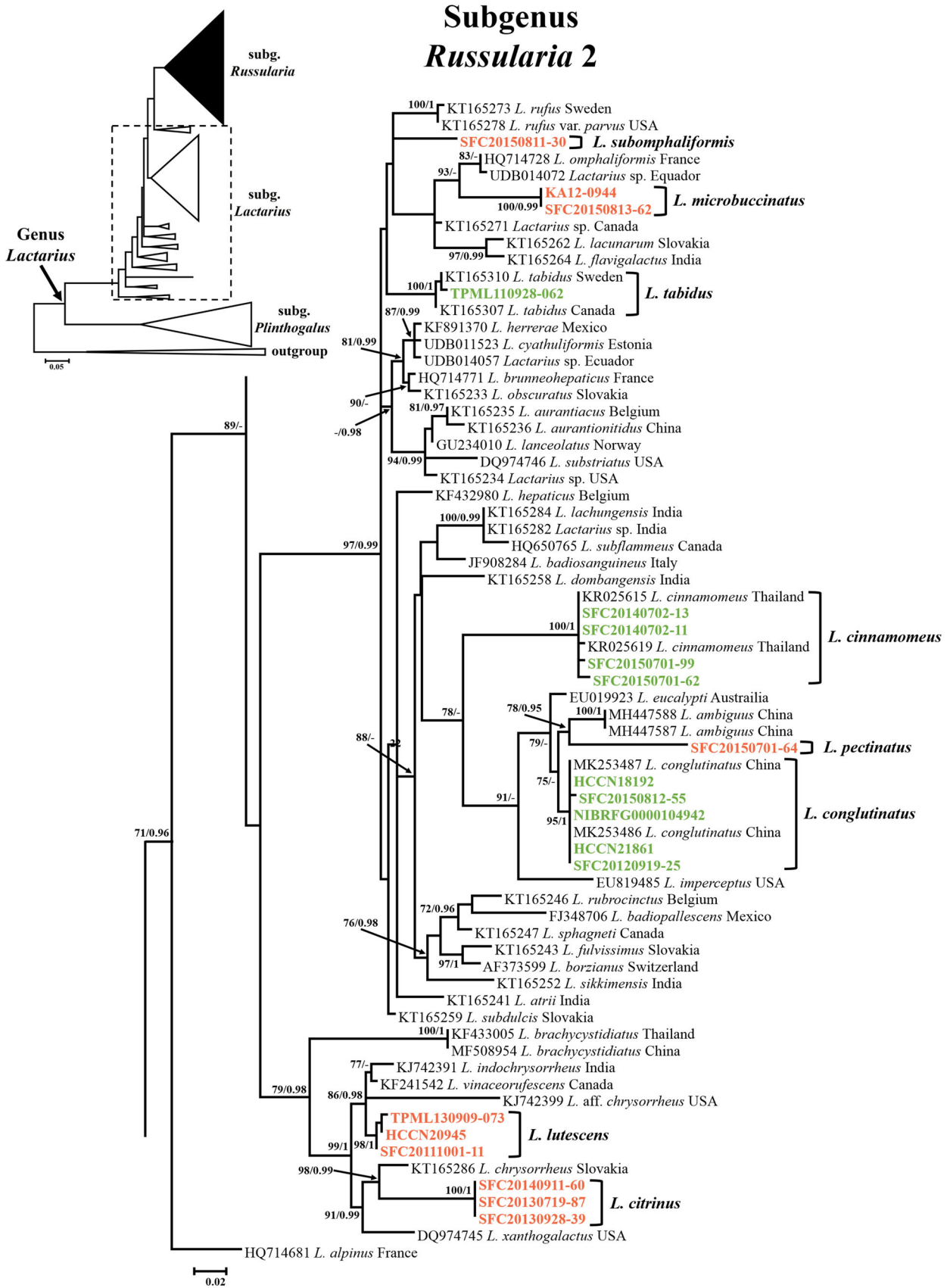


Fig. 1 continued

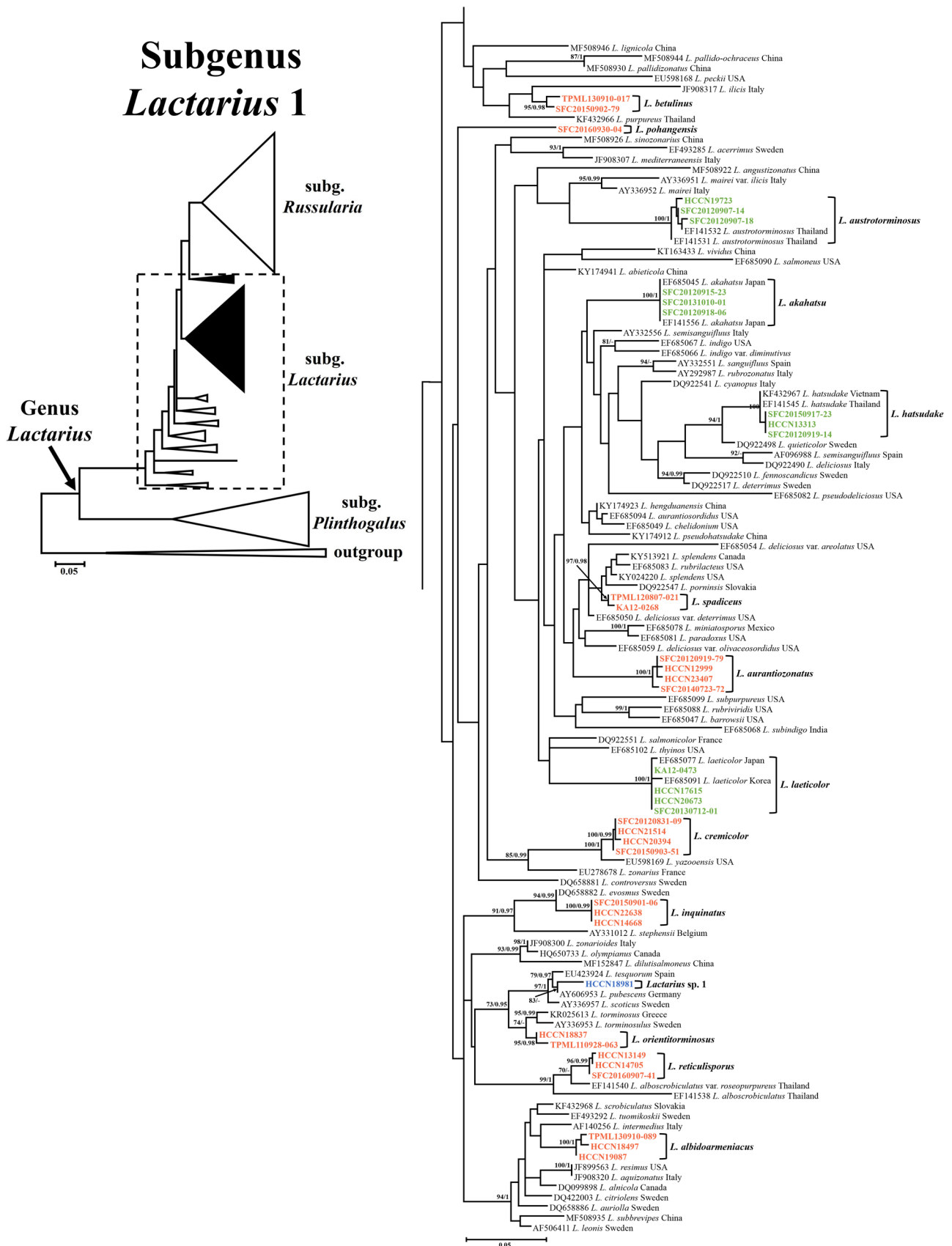


Fig. 1 continued

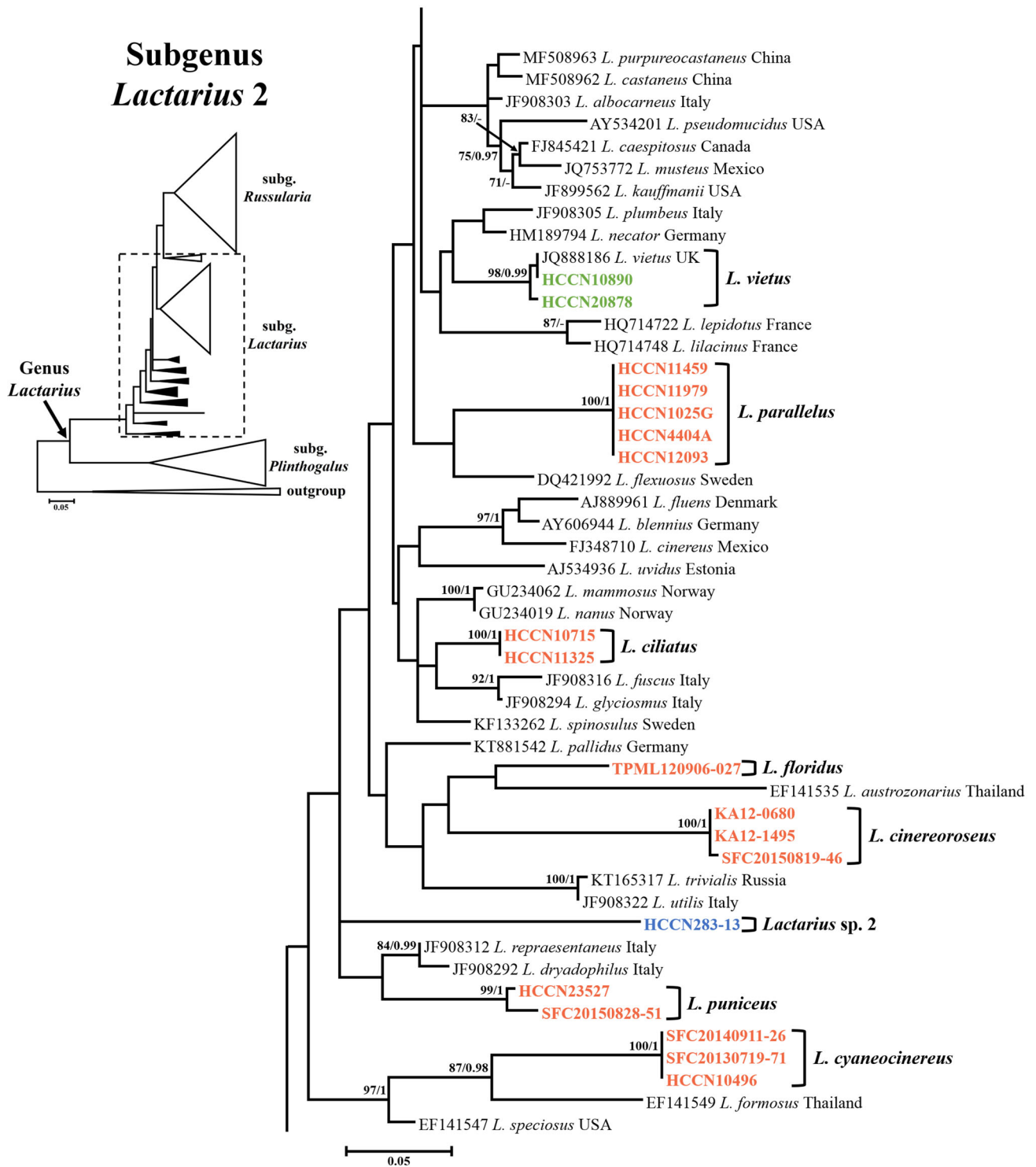


Fig. 1 continued

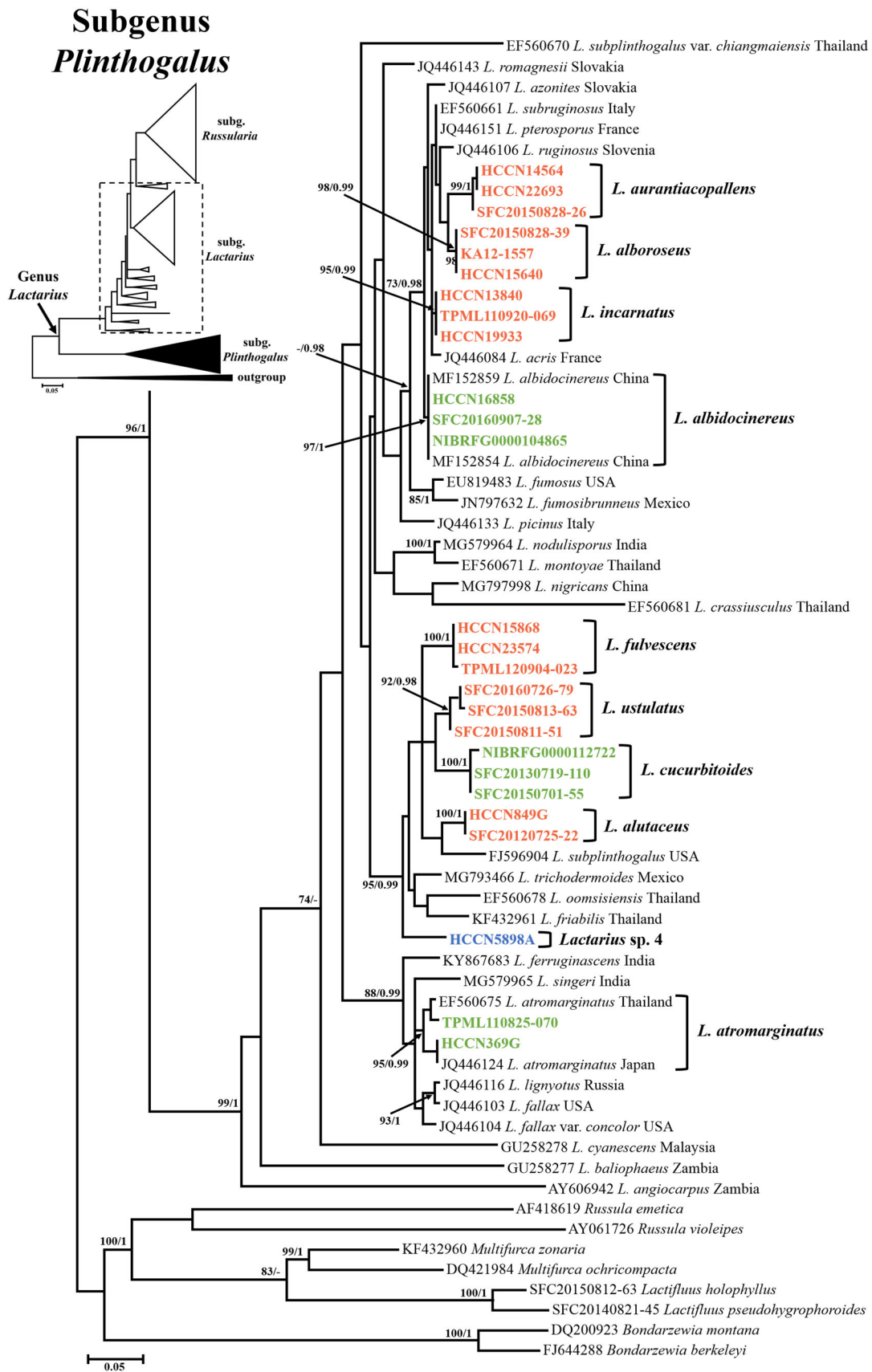


Fig. 1 continued

alignments consisted of 1068, 554, 656, and 453 characters including gaps, variable sites (375, 103, 256, and 199), and informative sites (327, 92, 231 and 184), respectively (Table 1). The ratio of parsimony informative characters of the *mcm7* locus (41%) was the highest among the four loci (Table 1). All species branches were well supported on the *mcm7* and *rpb2* trees, and the phylogenies were consistent with the ITS tree (data not shown). The nrLSU phylogeny, while largely consistent with the other loci, lacked sufficient bootstrap support for some species (ML bootstrap value/BI posterior probability < 70/0.95) (data not shown). Branch numbers representing ML/BI exceeding 70/0.95 were 11, 5, 14, and 18 in the phylograms of ITS, nrLSU, *rpb2*, and *mcm7*, respectively (Table 1). In the combined dataset, the aligned four loci matrix contained 2,734 bases. Of these aligned bases, 2416 positions were retained using Gblocks. The ML and BI analyses generated nearly identical tree topologies with minimal variation in statistical support values. A ML tree is presented in Fig. 2.

A total 17 taxa were identified as previously described species: *Lactarius akahatsu*, *L. albidocinereus* X.H. Wang et al., *L. atromarginatus* Verbeken & E. Horak, *L. austrotorminosus* H.T. Le & Verbeken, *L. cinnamomeus* W.F. Chiu, *L. conglutinatus* X.H. Wang, *L. cucurbitoides* H. Lee & Y.W. Lim, *L. hatsudake*, *L. laeticolor* (S. Imai) Imazeki ex Hongo, *L. neglectus* X.H. Wang, *L. orientaliquietus* X.H. Wang, *L. qinlingensis* X.H. Wang, *L. subatlanticus* X.H. Wang, *L. subhirtipes* X.H. Wang, *L. subzonarius* Hongo, *L. tabidus* Fr., and *L. vietus* (Fr.) Fr. The other 32 taxa formed distinct branches not corresponding to any of the described species. Four of these taxa lack morphological data or photographs of basidiomata, and thus remain un-named until additional data are collected. The other 28 species were confirmed as new to science after morphological comparison with closely related species.

While two subgenera, *Lactarius* subg. *Russularia* and *L.* subg. *Plinthogalus*, form monophyletic clades with strong support, *L.* subg. *Lactarius* appears to be paraphyletic (Figs. 1 and 2). The 49 Korean species belong to the three different subgenera in *Lactarius*: 17 in *L.* subg. *Russularia*, 22 species in *L.* subg. *Lactarius*, and 10 in *L.* subg. *Plinthogalus* (Fig. 1). *Lactarius* subg. *Russularia* includes seven new species, one undetermined species and nine previously described species (*L. cinnamomeus*, *L. conglutinatus*, *L. neglectus*, *L. orientaliquietus*, *L. qinlingensis*, *L. subatlanticus*, *L. subhirtipes*, *L. subzonarius*, and *L. tabidus*). *Lactarius* subg. *Lactarius* appears to be the most diverse in South Korea, with 15 new species, two undetermined species and five previously described species (*L. akahatsu*, *L. austrotorminosus*, *L. hatsudake*, *L. laeticolor*, and *L. vietus*). The smallest subgenus is *Lactarius* subg. *Plinthogalus*, with six new species, one undetermined

species and three previously described species (*L. albidocinereus*, *L. atromarginatus* and *L. cucurbitoides*).

Morphological characters of Korean *Lactarius* species

Lactarius subg. *Russularia* contains four well supported clades and two unclustered species (Fig. 2). Most species in this subgenus have transparent to watery white or white latex and show no discoloration. A few species have white latex turning pale yellow or strong yellow. Some species have an orange brown pileus or a hispid stipe. Microscopically, the presence of cheilo- and pleuro-macrocyttidia and pileipellis structure are variable among species. In this subgenus, clade 1 consists of *L. citrinus* and *L. lutescens*, which is part of the “*chrysorrhoeus* group”. They have common characters such as a zonate and dry pileus, white latex which turns lemon yellow, and a cutis as pileipellis structure (Fig. 2). Five species (*L. mitratus*, for description see below, *L. neglectus*, *L. qinlingensis*, *L. subatlanticus*, and *L. subhirtipes*) in clade 2 have an orange-brown pileus and slender or small basidiomata. *Lactarius* sp. 3 and *L. fuscozonarius*, see below, form an unsupported clade with long branches which is sister to clade 2 (Fig. 2). Clade 3 contains six species (*L. cinnamomeus*, *L. conglutinatus*, *L. tabidus* and the new taxa described below, namely *L. microbuccinatus*, *L. pectinatus* and *L. subomphaliformis*). Species in this clade are characterized by an azonate pileus, a striate pileus margin and incompletely reticulate spore ornamentation with plage inamyloid to slightly amyloid in the distal part. *L. orientaliquietus* and *L. subzonarius* in clade 4 are placed at the base of this subgenus and belong to the “*quietus* group” (Figs. 1 and 2). Both species have a zonate pileus and white to watery pale cream latex (Fig. 2).

Lactarius subg. *Lactarius* contains three clades and seven unclustered species (Fig. 2). These species have a zonate pileus, scrobiculate pileus and stipe, hispid pileus margins, viscid to slimy pileus, and ixocutis to ixotrichoderm pileipellis. Relationships within this subgenus are unclear because of paraphyly and low branch support. Phylogenetic placement of *L. betulinus* (see taxonomic part) is unclear, but morphologically this species fits well in *L.* subg. *Lactarius* because of the sticky pileus surface with inconspicuous zonation and an ixotrichoderm type pileipellis. Eight species in clade 5 have a variety of morphological features. *Lactarius* species with lilac, violet, and olive discoloration of latex were included in this clade (Fig. 2). Five species in clade 6 are classified as *L.* section *Deliciosi* (Fr.) Redeuilh et al. All species have orange or reddish latex, except for *L. spadiceus* and *L. aurantiozonatus* (see taxonomic part below) with white and unchanging latex (Fig. 2). These species are associated with conifers such as *Pinus* and *Abies*. *Lactarius*

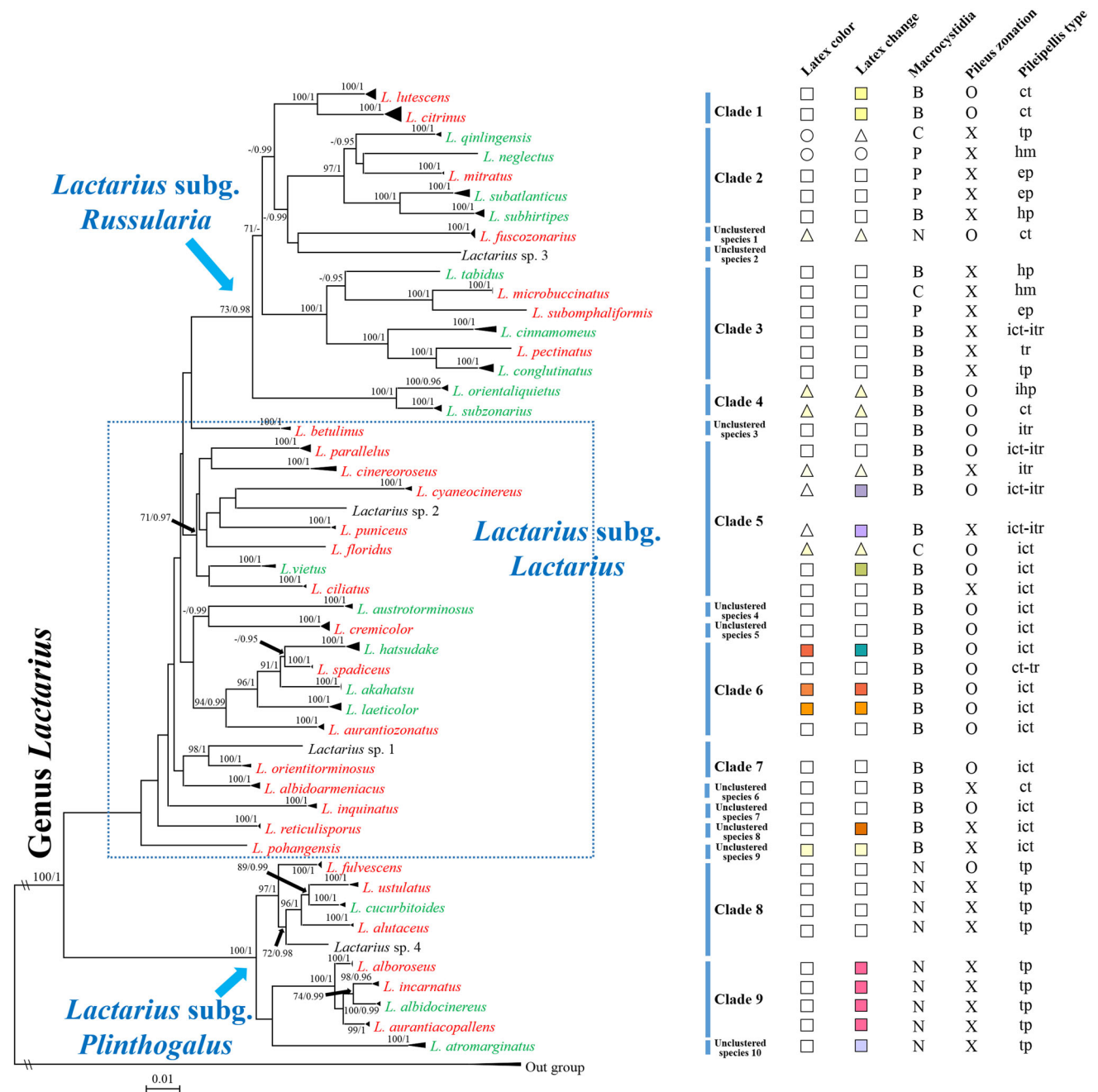


Fig. 2 Phylogram generated from Maximum Likelihood (RAxML) analysis based on combined sequence data of ITS, nrLSU, *rpb2*, and *mcm7* of Korean *Lactarius*. ML bootstrap support values/Bayesian posterior probability greater than 70%/0.95 are indicated. Names of the species in red, and green represent new species and previously described species in South Korea, respectively. **Abbreviations in Latex color:** open square opaque, open triangle translucent, open

circle transparent latex. **Abbreviations in macrocyctidia:** B both of pleuromacrocyctidia and cheilocystidia present, C only cheilomacrocyctidia present, P only pleuromacrocyctidia present, N no macrocyctidia. **Abbreviations in pileipellis type:** ct cutis, ep epithelium, hm hymenoepithelium, hp hyphoepithelium, ict ixocutis, ihp ixohyphoepithelium, itr ixotrichoderm, tp trichopalisaded, tr trichoderm

austrotorminosus and *L. cremicolor* (see below) are weakly supported by share characters such as a fibrillose to hispid pileus and white latex. Clade 7 contains two species (*L. orientitorminosus*, see below, and *Lactarius* sp. 1). They have a common character such as hispid pileus. *L.*

albidoarmeniacus (see below) has a slightly tomentose pileus and is a sister to clade 7. The other unclustered new species *L. inquinatus*, *L. pohangensis*, and *L. reticulisporus* (see below) are placed at the base of the major clade of subg. *Lactarius/Russularia*.



Fig. 3 Fruiting bodies of Korean species of *Lactarius* subg. *Russularia*. **a** *L. cinnamomeus*, **b** *L. citrinus*, **c** *L. conglutinatus*, **d** *L. fuscozonarius*, **e** *L. lutescens*, **f** *L. microbuccinatus*, **g** *L. mitratus*, **h** *L. neglectus*, **i** *L. orientaliquietus*, **j** *L. pectinatus*, **k** *L. qinlingensis*, **l** *L.*

subatlanticus, **m** *L. subhirtipes*, **n** *L. subomphaliformis*, **o** *L. subzonarius*, **p** *L. tabidus*. Scale bar = 1 cm. **a** and **p** are reproduced from Lee et al. (2018)

Lactarius subg. *Plinthogalus* has two supported clades and one unclustered species (Fig. 2). The dry, velvety and azonate pileus (typical for the subgenus) are shown in all species except *L. fulvescens* (see taxonomic part). Microscopically, Korean species of *L.* subg. *Plinthogalus* share a winged spore ornamentation, a trichopalisade, presence of cheiloleptocystidia, and absence of macrocystidia. Clade 8 contains five taxa that are characterized by unchanging white latex (Fig. 2). Clade 9 consists of four species (*L. albidocinereus*, *L. incarnatus*, and the other two new taxa, namely *L. alboroseus* and *L. aurantiacopallens*) which have pinkish discolouring latex. Finally, *L. atromarginatus*, which exhibits white latex with lilac discolouration, is placed at the basal position of clade 9 (Figs. 2, 3, 4).

Taxonomy

Taxonomic keys to species in South Korea and the full descriptions of the new species are provided below. Abbreviations in Figs. 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23, 24, 25, 26, 27, 28, 29, 30, 31, 32, 33, 34, 35, and 36 are as follows: **ba** basidia, **clc** cheiloleptocystidia, **cmc** cheilomacrocystidia, **mc** marginal cells, **pc** pseudocystidia, **pmc** pleuromacrocystidia, **pp** pileipellis. All scale bars = 10 μ m. Horizontal scale bars are for pileipellis and vertical scale bars are for other microscopic features.

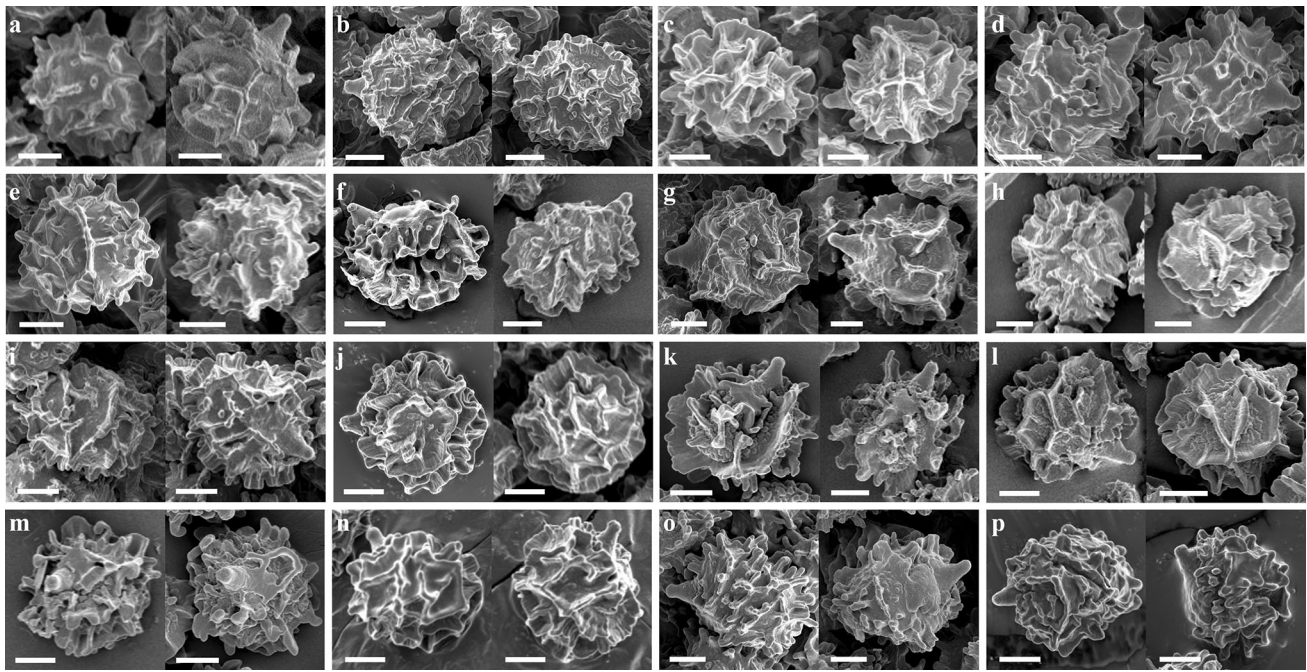


Fig. 4 Basidiospores (SEM) of Korean species of *Lactarius* subg. *Russularia*. **a** *L. cinnamomeus*, **b** *L. citrinus*, **c** *L. conglutinatus*, **d** *L. fuscozonarius*, **e** *L. lutescens*, **f** *L. microbuccinatus*, **g** *L. mitratus*, **h** *L. neglectus*, **i** *L. orientaliquietus*, **j** *L. pectinatus*, **k** *L. qinlingensis*, **l** *L.*

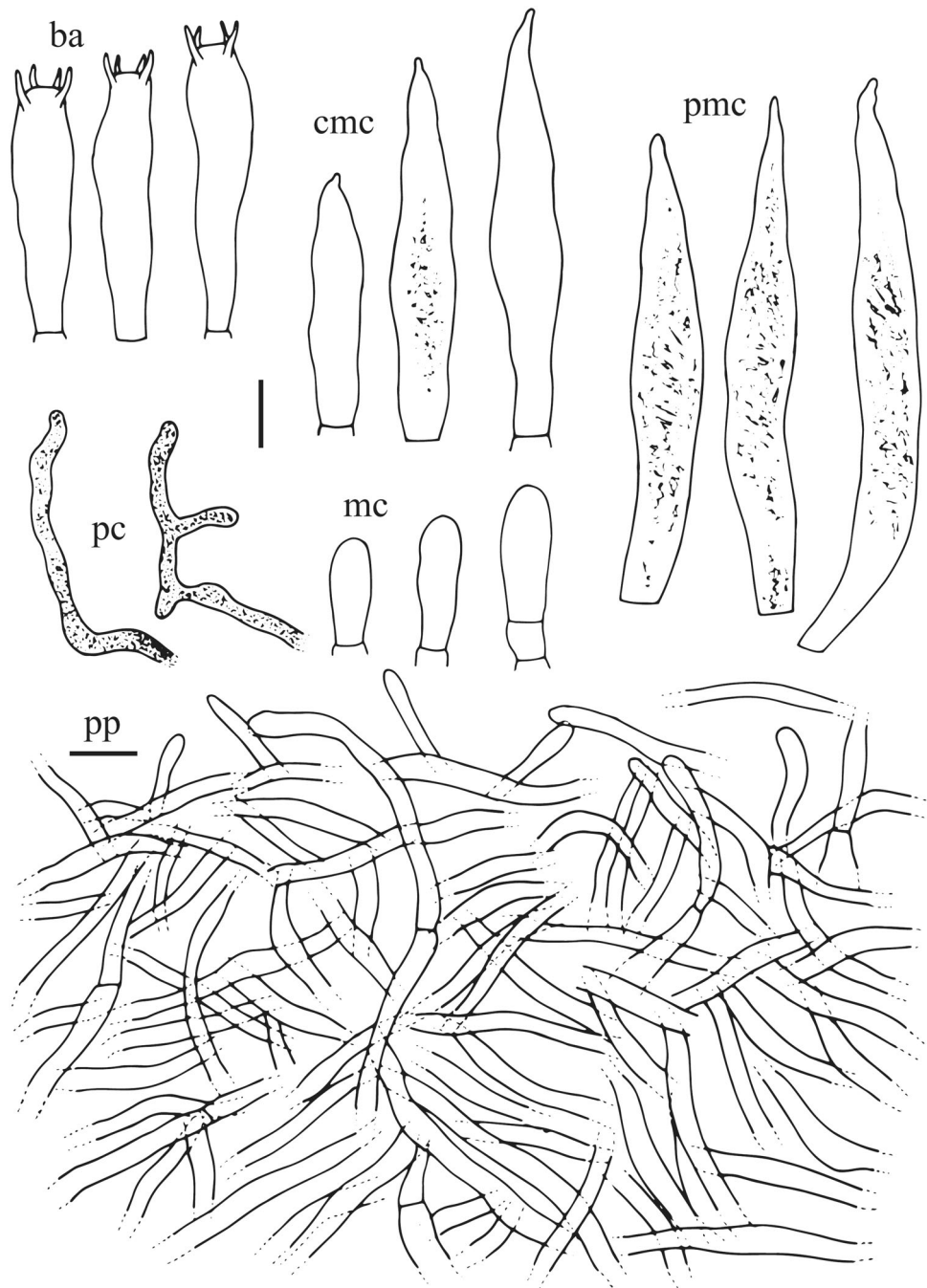
subatlanticus, **m** *L. subhirtipes*, **n** *L. subomphaliformis*, **o** *L. subzonarius*, **p** *L. tabidus*. Scale bar = 2 μm. **a** and **p** are adapted from Lee et al. (2018)

Key to the species of *Lactarius* subgenus *Russularia* in South Korea

- 1. Completely transparent latex; small-sized basidiomata; pileus colour of full grown specimen dark brown to violet brown; pileipellis a trichopalisade *L. qinlingensis*
- 1. Latex white or cream 2
- 2. White latex turning lemon yellow quickly on exposure; pileipellis a cutis..... 3
- 2. Latex unchanging or slowly turning pale yellow on exposure; pileipellis not a cutis 4
- 3. Associated with *Pinus*; pleurocystidia with moniliform apex *L. lutescens*
- 3. Associated with *Quercus*; pleurocystidia with obtuse apex..... *L. citrinus*
- 4. Latex turning slowly pale yellow, turning pale on white cotton tissue, associated with *Betula* *L. tabidus*
- 4. Latex unchanging 5
- 5. Pileus size smaller than 25 mm diam. 6
- 5. Pileus size larger than 25 mm diam. 8
- 6. Distant lamellae; pleurocystidia with distinctively acuminate to rostrate apex; pileipellis a hymenopithelium *L. neglectus*
- 6. Crowded lamellae 7
- 7. Spore ornamentation up to 0.6 μm high; pileipellis a trichopalisade *L. microbuccinatus*

- 7. Spore ornamentation minimum up to 1.1 μm high; pileipellis an epithelium *L. subomphaliformis*
- 8. Macrocystidia absent; basidiospores almost reticulate *L. fuscozonarius*
- 8. Macrocystidia present..... 9
- 9. Pileus often viscid in moist condition, pileipellis gelatinized 10
- 9. Pileus dry; pileipellis never with gelatinous layer..... 11
- 10. Pileus zonate; basidiomata pinkish buff; pileipellis an ixohyphoepithelium of approximately 85–120 μm thick *L. orientaliquietus*
- 10. Pileus azonate; basidiomata grayish yellow to reddish blond; pileipellis an ixocutis to ixotrichoderm of approximately 150–200 μm thick *L. cinnamomeus*
- 11. Relatively thick and short stipe..... 12
- 11. Thin and long stipe 13
- 12. Zonate pileus with reddish brown colour..... *L. subzonarius*
- 12. Azonate pileus with light orange colour, pileus margin distinctively pectinate *L. pectinatus*
- 13. Long stipe with strigose base, pileus colour of full grown specimens warm orange brown to reddish brown 14
- 13. Long stipe without strigose base, pileus colour of full grown specimen pale orange brown 15

Fig. 5 Microscopic features of *Lactarius citrinus*



14. Pileipellis a hyphoepithelium, often thinner than 100 μm , terminal cells covered by parallel cylindrical hyphae *L. subhirtipes*
 14. Pileipellis an epithelium, often thicker than 100 μm , terminal cells globose *L. subatlanticus*
 15. Pileipellis an epithelium, 90–150 μm thick; pleurocystidia with capitate apex *L. mitratus*
 15. Pileipellis a trichopalisade, 130–210 μm thick; pleurocystidia with mucronate to moniliform apex *L. conglutinatus*

Lactarius* subgenus *Russularia

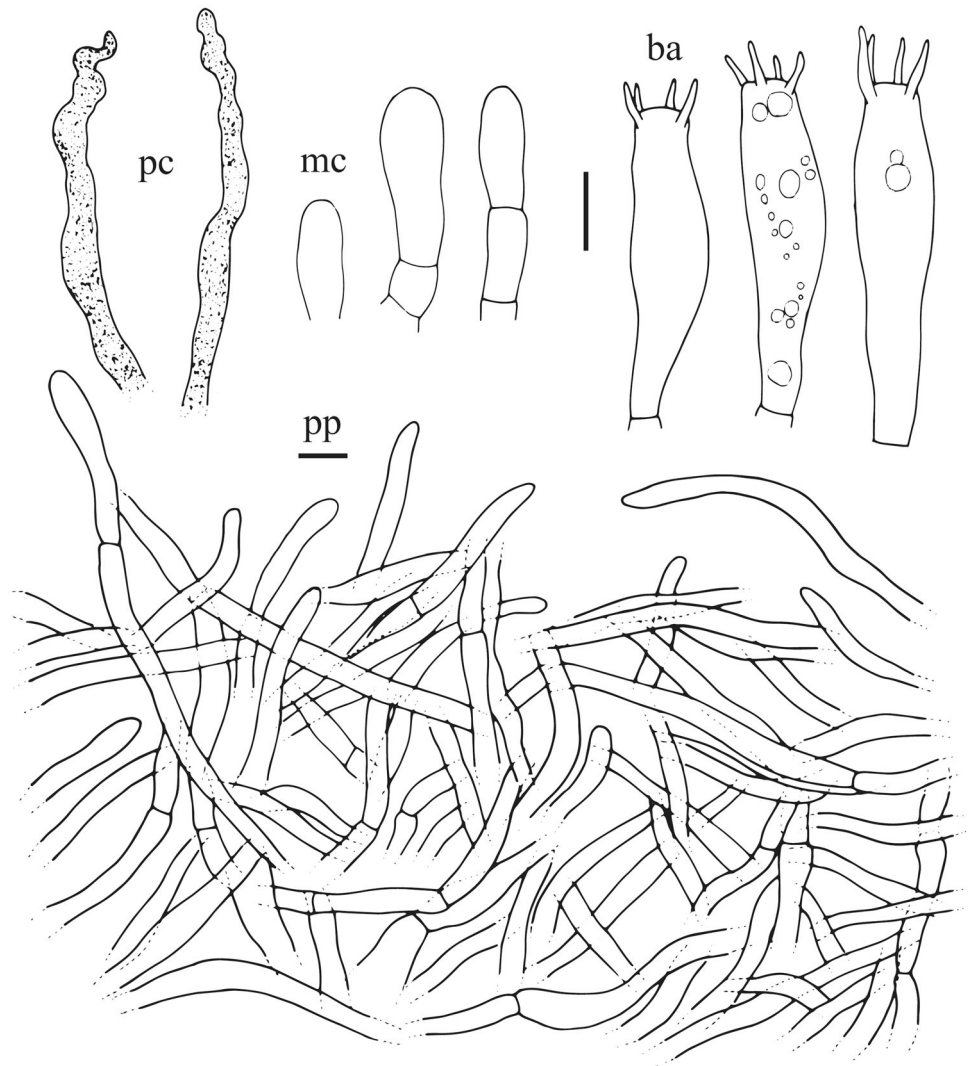
Lactarius citrinus H. Lee, Wisitr. & Y.W. Lim, **sp. nov.**

Mycobank: MB 827895

Etymology: ‘citrinus’ means lemon-coloured referring to the lemon yellow discolouration of latex.

Holotypus: SOUTH KOREA, Jeollabuk-do, Jinan-gun, Unjangan Natural Recreation Forest, alt. 464 m, N35°53'56" E127°25'05", 11 Sep 2014 (SFC20140911-60)

Fig. 6 Microscopic features of *Lactarius fuscozonarius*



Pileus 30–70 mm diam., convex then appanate to infundibuliform; margin first inrolled, in age expanded, uneven; surface orange white (5A2) to pale red (7A3), often with yellowish tinges, smooth, fibrillose, rugulose when young, often inconspicuously zonate, sometimes distinctly zonate, with pale orange brown spots in the zonation. *Lamellae* adnate to slightly decurrent, rather crowded, sometimes forked, with abundant lamellulae, up to 5 mm broad, white to pale apricot when young, cream to pale orange brown in age, staining pale greyish brown when bruised. *Stipe* 35 – 80 × 10 – 25 mm, cylindrical, fistulose in age; surface whitish grey when young, con-colourous with lamellae or darker in age, sometimes slightly longitudinally striated, sometimes with white mycelia at the base. *Odour* unremarkable. *Taste* mild, sometimes slightly acrid. *Latex* rather abundant, white quickly changing to lemon yellow, drying pale yellowish ocher.

Basidiospores (n = 40), (6.4 –)6.6 – 7.8 – 7.9 –9.0 × 5.7 – 6.4 – 6.6 – 7.5 μm, Q = 1.03 – 1.14 – 1.17 – 1.29, mostly subglobose to broadly ellipsoid, few globose; ornamentation amyloid, composed of up to 0.8 μm high, irregular and branched short ridges and isolated warts, connected by fine lines, forming an incomplete reticulum; plage inamyloid. *Basidia* 34 – 51 × 7.5 – 10 μm, 4-spored, cylindrical to narrowly clavate. *Pleuromacrocystidia* numerous, 68.5 – 87 × 10 – 11.5 μm, narrowly fusiform to lanceolate, mostly emergent beyond the hymenium; apex mucronate to slightly acute. *Lamellar edges* consisting of marginal cells, cheilomacrocystidia and basidia; marginal cells cylindrical to narrowly clavate; cheilomacrocystidia numerous, 35 – 61 × 7.5 – 11 μm, narrowly fusiform to cylindrical, apex slightly acute to obtuse. *Pseudocystidia* numerous, aseptate, mostly embedded, sometimes inconspicuously emergent, irregular, 2–5 μm broad, sometimes multiple branched near apex; apex rounded, sometimes slightly broader. *Pileipellis* a cutis, 110–190 μm thick,

composed of parallel to intricate cylindrical hyphae; terminal cells $15 - 70 \times 3 - 6 \mu\text{m}$.

Habitat: Scattered to gregarious on soil in forests dominated by *Quercus*.

Additional studied material: SOUTH KOREA, Gyeongsangbuk-do, Sangju-si, Seongjubong Natural Recreation Forest, alt. 269 m, N36°31'58" E128°02'24", 19 Jul 2013 (SFC20130719-87); *ibid.*, alt. 179 m, N37°18'38" E127°18'42", 6 Aug 2013 (SFC20130806-14).

Comments: *Lactarius citrinus* is phylogenetically related to *L. chrysorrhoeus* Fr. (Europe), *L. lutescens* (see below), *L. indochrysothecus* K. Das & Verbeken (India), *L. vinaceorufescens* A.H. Sm. (North America), *L. xanthogalactus* Peck (North America), and *L. xanthogalus* Verbeken & E. Horak (Papua New Guinea). These species have common characters such as quickly changing latex, distinct pileus zonation, and (\pm) ixocutis. *Lactarius chrysorrhoeus* has smaller cheilomacrocytidia ($25 - 50 \times 5 - 9 \mu\text{m}$) than *L. citrinus* (Heilmann-Clausen et al. 1998). The host tree and the more greyish lamellae distinguish *L. lutescens* from *L. citrinus*. *Lactarius vinaceorufescens* and *L. indochrysothecus* can be distinguished from *L. citrinus* by the gelatinous pileipellis (Hesler and Smith 1979, Das et al. 2015). *L. xanthogalactus* has globose spores and darker pileus (pinkish cinnamon to reddish brown) than *L. citrinus* (Hesler and Smith 1979). The basidiospore ornamentation of *L. xanthogalus* is distinguished from the other species by its zebroid ornamentation (Verbeken and Horak 2000).

Lactarius fuscozonarius H. Lee, Wisitr. & Y.W. Lim, **sp. nov.**

Mycobank: MB 827899

Etymology: ‘fusco’ means dark brown, ‘zonarius’ means zonation. It refers to the dark brown zonation on the pileus.

Holotypus: SOUTH KOREA, Jeollabuk-do, Jinan-gun, Unjangan Natural Recreation Forest, alt. 520 m, N35°54'45" E127°24'10", 23 Jul 2014 (SFC20140723-30) **Pileus** 30–100 mm diam., convex then applanate to infundibuliform; margin first decurved, in age expanded, uneven to crenate, striated; surface orange white (6A2) to pastel red (9A4), with brown to dark brown zonation dry, minutely fibrillose, inconspicuously zonate to distinctly zonate. **Lamellae** slightly decurrent to decurrent, rather crowded, often forked near the stipe, rarely multifurcate, with abundant lamellulae, up to 3 mm broad, pale cream when young, concolourous to pileus in age. **Stipe** 20 – 80 \times 8 – 15 mm, cylindrical, sometimes tapering downwards, fistulose; surface pale brown when young, dark brown in age, sometimes slightly longitudinally striated. **Odour** unremarkable to slightly fruity. **Taste** mild,

sometimes slightly acrid. **Latex** rather abundant, translucent cream to watery white, unchanging.

Basidiospores (n = 40), $6.3 - 7.1 - 7.5 - 8.2 \times 5.6 - 6.3 - 6.5 - 7.1(-7.2) \mu\text{m}$, Q = 1.00 – 1.13 – 1.15 – 1.28, globose to broadly ellipsoid; ornamentation amyloid, composed of up to 0.7 μm high, irregular and branched long ridges and isolated small warts, forming almost complete reticulum, connected by fine lines; plage inamyloid to weakly amyloid in the distal part. **Basidia** $38.5 - 47 \times 8.5 - 11 \mu\text{m}$, 4-spored, mostly cylindrical to narrowly clavate, sometimes ventricose. **Macrocytidia** absent. **Lamellar edges** consisting of marginal cells and basidia; marginal cells mostly cylindrical, sometimes cylindrical to narrowly clavate, **Pseudocyttidia** numerous, aseptate, mostly conspicuous emergent, sometimes embedded, irregular, 2–4 μm broad, multiple branched near apex; apex rounded, sometimes moniliform. **Pileipellis** 90–160 μm thick, a cutis, composed of parallel to intricate cylindrical hyphae; terminal cells $35 - 85 \times 2 - 7 \mu\text{m}$.

Habitat: Scattered to gregarious on moss covered soil in mixed forests dominated by *Pinus*.

Additional studied material: SOUTH KOREA: Gangwon-do, Pyeongchang-gun, Mt. Odae, alt. 1155 m, 37°45'30" E128°35'44", 26 Aug 2011 (HCCN21953); Gyeongsangbuk-do, Yecheon-gun, Mt. Maebong, alt. 538 m, N36°44'03" E128°21'54", 7 Aug 2013 (SFC20130807-66).

Comments: *Lactarius fuscozonarius* is characterized by the orange white to pastel red coloured, zonate and fibrillose pileus surface, and watery white to milky latex. This species is distinguished from other species of *L. subg. Russularia* in Korea by the absence of macrocytidia and the almost completely reticulate basidiospore. *Lactarius politus* Wisitr. & K.D. Hyde from Thailand is the phylogenetically closest species to *L. fuscozonarius* (Fig. 1). However, the Thai species has much darker colour and heavier basidiospore ornamentation (up to 2.5 μm) than *L. fuscozonarius* (Wisitrassameewong et al. 2015).

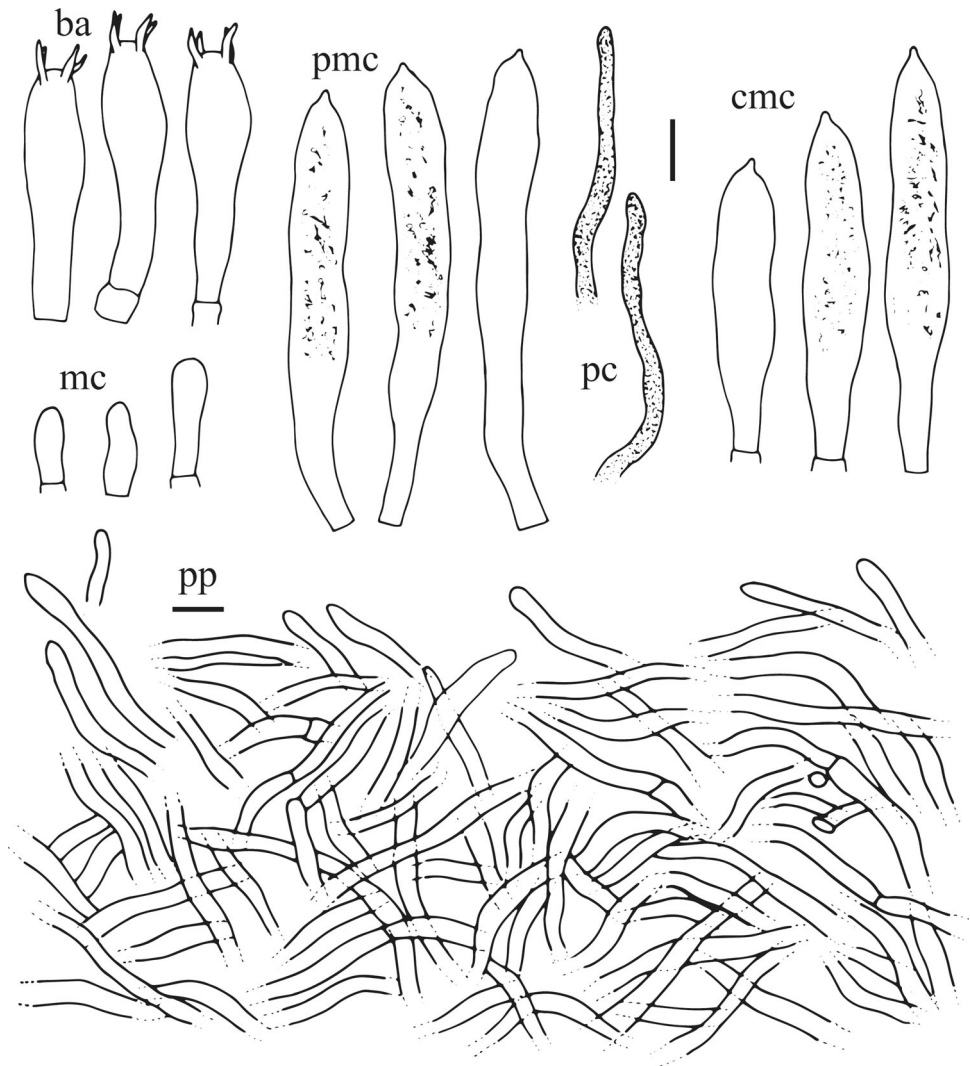
Lactarius lutescens H. Lee, Wisitr. & Y.W. Lim, **sp. nov.**

Mycobank: MB 827901

Etymology: ‘lutescens’ means becoming yellow which refers to the yellowing milk of the species.

Holotypus: SOUTH KOREA, Gangwon-do, Wonju-si, Mt. Chiak, alt. 494 m, N37°24'51" E128°03'34", 1 Oct 2011 (SFC20111001-11)

Pileus 30–60 mm diam., convex then applanate to infundibuliform; margin first decurved, in age expanded, sometimes uneven; surface orange white (6A2) to pale red (8C3), often with yellowish tinge, with greyish red

Fig. 7 Microscopic features of *Lactarius lutescens*

zonation, often with red brown spots, with distinct zonation, sometimes inconspicuous zonate, smooth, fibrillose, rugulose when young. *Lamellae* adnate, rather crowded, very rarely forked near the stipe, with abundant lamellulae, up to 5 mm broad, white to pale apricot when young, cream to pale greyish brown in age. *Stipe* 30–50 × 8–15 mm, cylindrical, fistulose; surface whitish grey when young, concolourous with lamellae, with pale greyish brown tinge, sometimes with white mycelia at the base. *Odour* unremarkable to faintly fruity. *Taste* slightly acrid. *Latex* rather abundant, white rapidly turning to lemon yellow.

Basidiospores (n = 40), 5.9–6.8–6.9–8.0 × (5.0–)5.1–6.0–6.2–7.0 μm, Q = 1.06–1.15–1.30, subglobose to broadly ellipsoid; ornamentation amyloid, composed of up to 0.7 μm high, irregular and branched short ridges and isolated warts, forming an incomplete reticulum, connected by fine lines; plage amyloid in the distal part. *Basidia*

36–48.5 × 8.5–11 μm, 4-spored, cylindrical to narrowly clavate. *Pleuromacrocystidia* numerous, 65.5–82 × 8.5–10 μm, narrowly fusiform to lanceolate, mostly emergent beyond the hymenium, apex obtuse. *Lamellar edges* consisting of marginal cells, cheilomacrocystidia and basidia; marginal cells cylindrical to narrowly clavate; cheilomacrocystidia numerous, 45–78 × 8.5–11.5 μm, cylindrical to fusiform. *Pseudocystidia* numerous, aseptate, mostly embedded, sometimes inconspicuous emergent, irregular, 2–5 μm broad, branched near apex; apex rounded, sometimes slightly broader. *Pileipellis* 130–250 μm thick, a cutis, comprised of parallel to intricate cylindrical hyphae; terminal cells 35–110 × 1.5–4 μm, underlying layer of isodiametric cells 6–28 μm broad.

Habitat: Scattered to gregarious on soil in forests dominated by *Pinus*.

Additional studied material: SOUTH KOREA, Gangwon-do, Pyeongchang-gun, Mt. Odae, alt. 985 m, N37°45'39" E128°35'10", 18 Oct 2010 (HCCN20945); *ibid.*, alt. 888 m, N37°45'07" E128°34'59", 9 Sep 2013 (TPML130909-073).

Comments: *Lactarius citrinus* (see above) and *L. lutescens* are members of the *chryssorheus* group. They are distinguished by their host trees; the former is associated with *Quercus* and the latter with *Pinus*. For a comparison with other species of the *chryssorheus* group, refer the comments of *L. citrinus* mentioned above.

Lactarius microbuccinatus H. Lee, Wisitr. & Y.W. Lim, **sp. nov.**

Mycobank: MB 827902

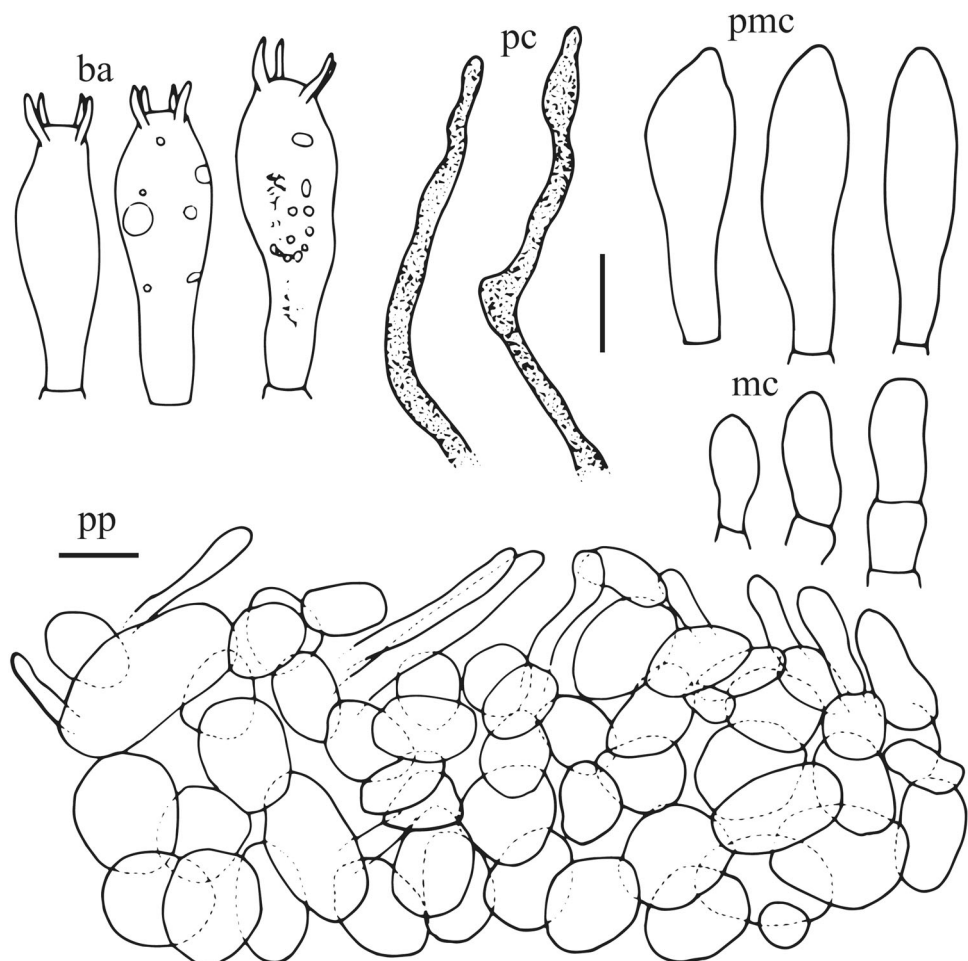
Etymology: ‘microbuccinatus’ means small and trumpet-shaped which refers to small-sized and funnel-shaped like trumpet of the basidiomata.

Holotypus: SOUTH KOREA, Gyeonggi-do, Goyang-si, Seo-o-reung Royal Tombs, alt. 147 m, N37°37'60" E126°54'19", 13 Aug 2015 (SFC20150813-62)

Pileus 8–25 mm diam., convex then appanate to infundibuliform with obtuse umbo; margin first decurved, in age expanded, often rugose to crenate; surface orange (6A6) to brownish orange (7C6), dry, smooth, radially rugulose to striated, pruinose when young. *Lamellae* decurrent, rather crowded, rarely forked near the stipe, with abundant lamellulae, up to 2 mm broad, pale cream to pale orange brown, staining greyish brown when bruised. *Stipe* 10–40 × 2–4 mm, cylindrical, fistulose in age; surface concolourous with pileus or darker, pruinose to slightly tomentose, with pale cream to orange brown hairs at the base, sometimes fasciculate with stipes of 2–3 basidiomata. *Odour* unremarkable. *Taste* bitter. *Latex* rather scarce, white, unchanging on exposure.

Basidiospores (n = 40), 5.9–6.6–6.8–7.8(–8.0) × 4.8–5.7–5.8–6.8(–7.0) μm, Q = 1.00–1.19–1.42, globose to ellipsoid; ornamentation amyloid, composed of up to 0.6 μm high, irregular and branched short ridges and isolated warts, forming an incomplete reticulum, connected by fine lines, joined by fine lines; plage inamyloid. *Basidia* 30.1–38.9 × 8.4–10.4 μm, 4-spored, narrowly clavate to clavate. *Pleuromacrocystidia* absent. *Lamellar*

Fig. 8 Microscopic features of *Lactarius microbuccinatus*



edges consisting of marginal cells, cheilomacrocytidia and basidia; marginal cells cylindrical to clavate; cheilomacrocytidia abundant, $18.5 - 29.5 \times 7.5 - 9.5 \mu\text{m}$, fusiform to ventricose, apex obtuse to slightly acute. *Pseudocystidia* numerous, aseptate, embedded, rarely inconspicuous emergent, irregular, sometimes branched near apex, apex rounded, often slightly broader, $2-5 \mu\text{m}$ broad. *Pileipellis* $50-110 \mu\text{m}$ thick, a trichopalisade; terminal cells $7.5 - 21 \times 4.5 - 8.5 \mu\text{m}$, cylindrical; subpellis comprised of globose to isodiametric cells, up to $25 \mu\text{m}$ broad.

Habitat: Solitary or scattered on soil in mixed forests dominated by *Quercus*.

Additional studied material: SOUTH KOREA, Gyeonggi-do, Pocheon-si, Korean Arboretum, alt. 121 m, $37^{\circ}44'55''$ E127 $^{\circ}09'55''$, 8 Aug 2012 (KA12-0944).

Comments: *Lactarius microbuccinatus* is characterized by its small size and the funnel-shaped pileus in mature specimens, the hispid stipe, incompletely reticulate basidiospores, and hymenoepithelium pileipellis. This species can be distinguished from the other small-sized species in South Korea by the series of lamellulae and absence of pleurocystidia. This species is phylogenetically closely

related to the European *L. omphaliformis* Romagn (Fig. 1). However, *L. omphaliformis* has pleuromacrocytidia and larger basidiospores ($6.9 - 9.6 \times 5.5 - 7.8 \mu\text{m}$) (Heilmann-Clausen et al. 1998).

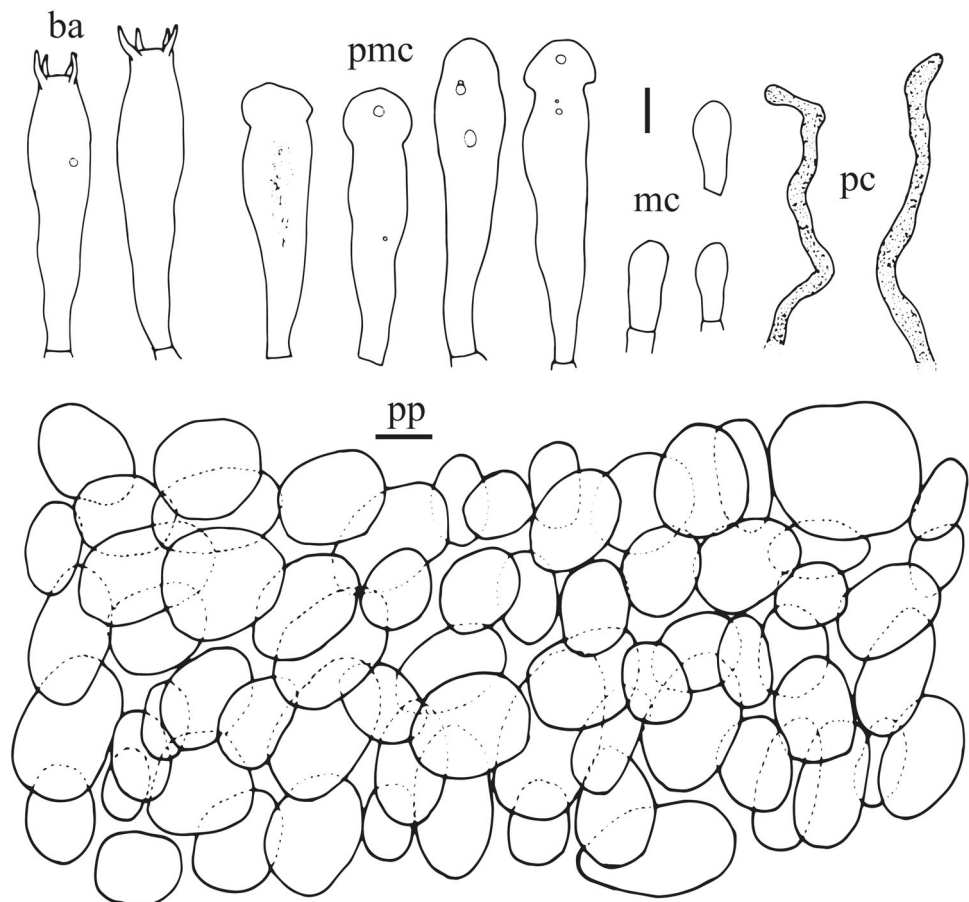
Lactarius mitratus H. Lee, Wisitr. & Y.W. Lim, **sp. nov.**

Mycobank: MB 827903

Etymology: ‘mitratus’ means hood or felt pileus, referring to the capitate or knob-like head on the apex of pleuromacrocytidia.

Holotypus: SOUTH KOREA, Gyeongsangbuk-do, Yeongju-si, Mt. Sobaek, alt. 669 m, N36 $^{\circ}55'50''$ E128 $^{\circ}29'28''$, 24 Aug 2011 (HCCN21924; **isotype**, SFC) *Pileus* 20–50 mm diam., convex then applanate to wide infundibuliform; margin first slight depression with inrolled, in age decurved, even, sometimes crenulate; surface orange yellow (4A6) to light orange (5A5), rough, dry, finely rugulose. *Lamellae* slightly decurrent to decurrent, rather distant, rarely forked, with abundant lamellulae, up to 6 mm broad, yellowish orange, staining orange to reddish brown when bruised. *Stipe* 30 – 65 \times 5 – 15 mm, cylindrical, fistulose in age; surface concolourous with lamellae or darker, surface slightly

Fig. 9 Microscopic features of *Lactarius mitratus*



longitudinally striated. *Latex* rather scarce, white, unchanging on exposure.

Basidiospores (n = 40), 7.1 – 8.1 – 8.4 – 9.5 (– 9.6) × 6.2 – 7.2 – 7.3 – 8.4 μm,

Q = 1.02 – 1.14 – 1.16 – 1.32, subglobose to ellipsoid, few globose; ornamentation amyloid, composed of up to 1.3 μm high, irregular and branched long ridges and isolated warts, forming an incomplete reticulum; plage amyloid in the distal part. *Basidia* 45.5 – 61 × 10 – 12.5 μm, 4-spored, narrowly clavate. *Pleuromacrocystidia* numerous, 47 – 61 × 10 – 12.5 μm, narrowly clavate, irregular to straight, slightly emergent beyond the hymenium; apex obtuse, mostly capitate. *Lamellar edges* consisting of marginal cells and basidia; marginal cells narrowly clavate to clavate; cheilomacrocystidia absent. *Pseudocystidia* numerous, 2–5 μm broad, aseptate, embedded to slightly emerging, irregular, sometimes branched near apex, apex rounded, often slightly broader. *Pileipellis* 90–150 μm thick, an epithelium, comprised of globose to isodiametric cells, up to 30 μm broad.

Habitat: Scattered on soil in mixed forests dominated by *Abies*.

Additional studied material: SOUTH KOREA: Jeollabuk-do, Muju-gun, Baekryeonsa temple, alt. 909 m, N35°51'38" E127°46'03", 17 Aug 2002, HCCN10589 (HCCN).

Comments: *Lactarius mitratus* is characterized by the knob-like head on the apex of pleuromacrocystidia. This species is phylogenetically closely related to *L. hirtipes* Ying (Fig. 1), However, *L. hirtipes* has lanceolate macrocystidia while *L. miratus* has capitate macrocystidia (Wang and Liu 2002).

Lactarius pectinatus H. Lee, Wisitr. & Y.W. Lim, **sp. nov.**

Mycobank: MB 827904

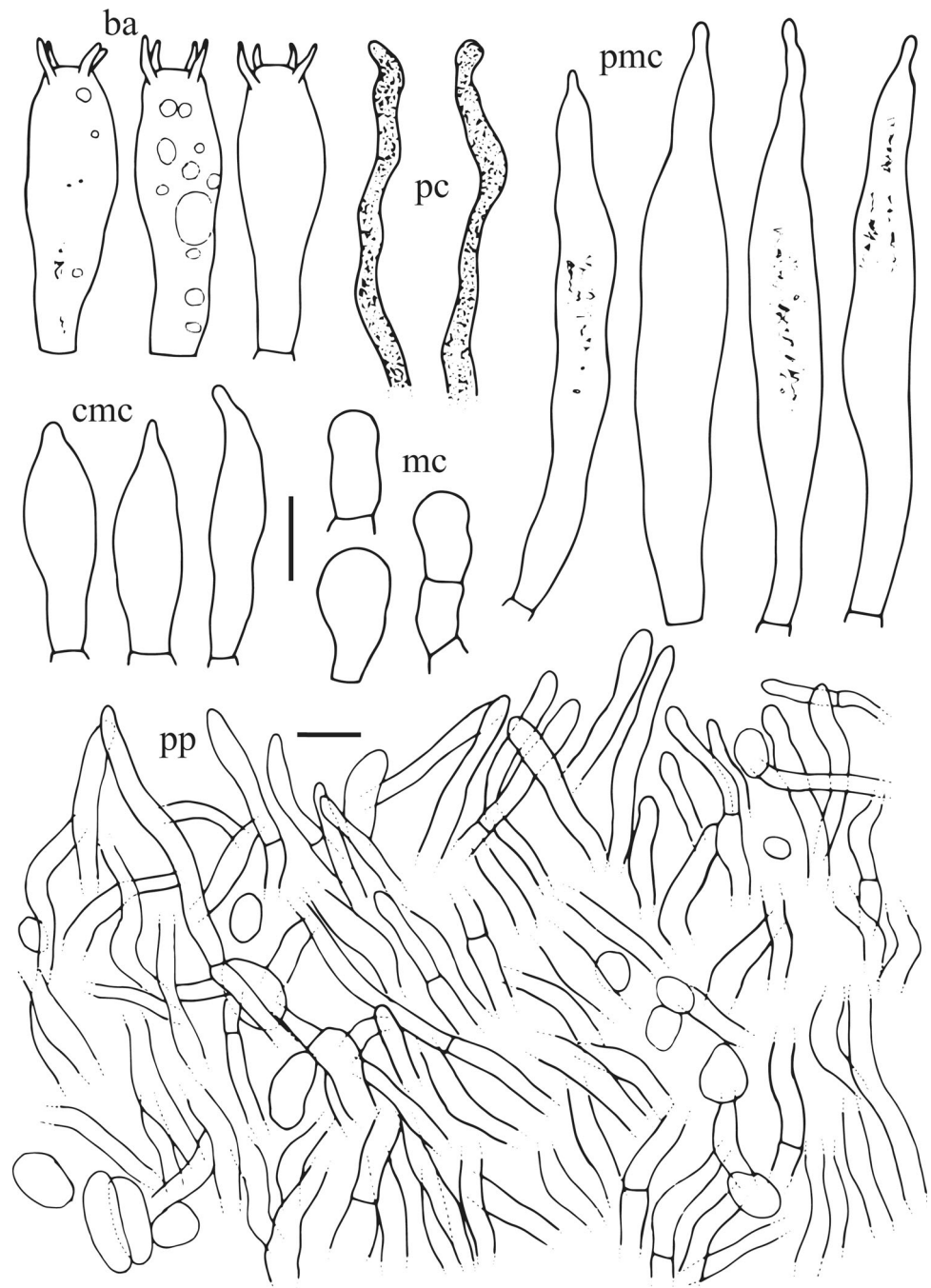
Etymology: ‘pectinatus’ means the form of a comb and refers to the radially striated and rugulose pileus margin.

Holotypus: SOUTH KOREA, Jeju-do, Jeju-si, Dongbaek-dongsan, alt. 144 m, N33°30'57" E126°43'15", 1 Jul 2015 (SFC20150701-64)

Pileus 25–45 mm diam., convex to appanate with slightly depressed centre, with obtuse umbo; margin decurved, often crenulate to radially folded; surface pale yellow (4A3) to light orange (5A4), slightly viscid in moist condition. *Lamellae* adnate to slightly decurrent, rather crowded, rarely forked near the stipe, with abundant lamellulae, up to 5 mm broad, pale yellow to pale cream, staining greyish red brown when bruised. *Stipe* 25 – 55 × 6 – 12 mm, cylindrical, fistulose; surface concolourous with pileus when young, orange brown to reddish brown with age, longitudinally striated, pruinose to slightly tomentose, with white mycelial strains at the base. *Odour* faintly fishy. *Taste* mild. *Latex* rather scarce, pale cream, unchanging on exposure, drying whitish.

Basidiospores (n = 20), 6.4 – 7.3 – 8.2 × (5.6 –) 5.7 – 6.4 – 7.1 μm, Q = 1.03 – 1.14 – 1.28, mostly subglobose to broadly ellipsoid, few globose; ornamentation amyloid, composed of up to 1.3 μm high, irregular and forked ridges and isolated warts, forming an incomplete reticulum, closed meshes present; plage inamyloid to slightly amyloid in the distal part. *Basidia* 35 – 44.5 × 8.5 – 11 μm, narrowly clavate, mostly 4-spored, 2-spored and 1-spored present. *Pleuromacrocystidia* rare, 64.5 – 86 × 5.5 – 11 μm, narrowly fusiform to lanceolate, conspicuous emergent, narrowly fusiform, irregular to straight, apex mucronate. *Lamellar edges* consisting of marginal cells, cheilomacrocystidia and basidia; marginal cells cylindrical to narrowly clavate; cheilomacrocystidia abundant, 23.5 – 43.5 × 5 – 9 μm, emergent, narrowly fusiform to lanceolate, apex mucronate. *Pseudocystidia* abundant, aseptate, mostly emergent, tortuous, 2–5 μm broad; apex rounded. *Pileipellis* a trichoderm, 75–110 μm thick, terminal cells 9.5 – 42.5 × 2 – 4 μm, cylindrical, subpellis comprise isodiametric oval cells, up to 28 μm broad.

Fig. 10 Microscopic features of *Lactarius pectinatus*



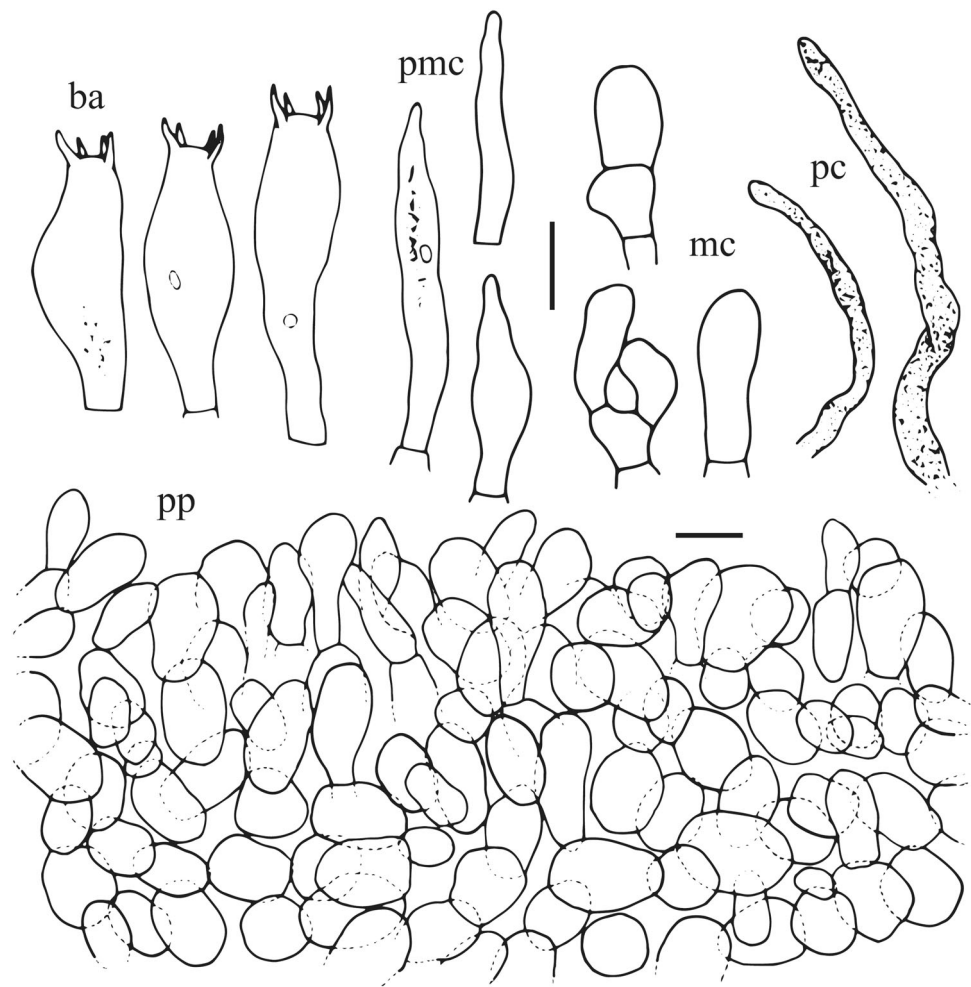
Habitat: Scattered on humid soil in mixed forests dominated by *Pinus* and evergreen *Quercus*.

Comments: *Lactarius pectinatus* is distinguished from the other species of *L.* subg. *Russularia* by its brightly yellow pileus, conspicuously pectinate pileus margin, pale cream latex, flesh staining greyish red brown on places with dried latex, and pileipellis an epithelium. This species is phylogenetically closely related to *L. imperceptus* Beardslee & Burl. (North America), *L. eucalypti* O.K. Mill. & R.N. Hilton (Australia), and *L. conglutinatus* from China

(Fig. 1). However, *L. eucalypti* can be distinguished from this species by the more reddish brown pileus (Miller & Hilton 1986). *Lactarius imperceptus* has a glabrous and zonate pileus, latex turning yellowish, and gelatinous pileipellis (Hesler and Smith 1979). *Lactarius conglutinatus* can be distinguished from *L. pectinatus* by its pale yellowish brown pileus, white, unchanging latex, and gelatinous pileipellis (Wang 2018).

Lactarius subomphaliformis H. Lee, Wisitr. & Y.W. Lim, **sp. nov.**

Fig. 11 Microscopic features of *Lactarius subomphaliformis*



Mycobank: MB 827905

Etymology: ‘sub’ means almost and ‘omphaliformis’ means *L. omphaliformis*. This name refers the similar features of *L. omphaliformis*.

Holotypus: SOUTH KOREA, Gyeonggi-do, Guri-si, Donggu-reung Royal Tombs, alt. 46 m, N37°37′07″ E127°07′50″, 11 Aug 2015 (SFC20150811-30)

Pileus 8–25 mm diam., convex then appanate to infundibuliform with obtuse umbo; margin first decurved, in age expanded, often uneven to crenulate; surface orange (6A6) to brownish orange (7C6), dry, smooth, radially rugulose to striated, cracked pattern in age, pruinose when young. **Lamellae** decurrent, rather crowded, rarely forked near the stipe, with abundant lamellulae, up to 2 mm broad, pale cream to pale orange brown, staining greyish brown when bruised. **Stipe** 10–40 × 2–4 mm, cylindrical, fistulose in age; surface concolourous with pileus or darker, pruinose to slightly tomentose, with pale cream to orange brown hairs at the base, sometimes fasciculate with stipes

of 2–3 basidiomata. **Odour** unremarkable. **Taste** mild. **Latex** rather scarce, white, unchanging on exposure.

Basidiospores (n = 20), 5.7–6.6–7.5(–8.1) × 5.0–5.4–5.9(–6.1) μm, Q = 1.11–1.21–1.33, mostly subglobose to broadly ellipsoid, rarely ellipsoid; ornamentation amyloid, composed of up to 1.1 μm high, irregular and branched ridges and isolated warts, forming an incomplete reticulum, ridge round to slightly acute; plage inamyloid to slightly amyloid in the distal part. **Basidia** 23–32 × 8–10 μm, narrowly clavate, mostly 4-spored, 2-spored and 1-spored present, contents small granules and guttulate. **Pleuromacrocytidia** rare, 19.5–44 × 2.5–6.5 μm, if present, rather small, not emergent to inconspicuous emergent, narrowly fusiform, irregular to straight, slightly acute to mucronate apex. **Lamellar edges** consisting of marginal cells and basidia; marginal cells cylindrical to narrowly clavate in general, obovoid to clavate uncommon; cheilocystidia absent. **Pseudocystidia** abundant, aseptate, 2.5–5 μm broad, tortuous, round apex. **Pileipellis** an epithelium, 60–90 μm thick; suprapellis with terminal cells 7.5–19 × 5.5–10 μm,

narrowly clavate, sometimes broadly clavate and obovoid cells, subpellis contains isodiametric cells mixed with inflated or broadly cylindrical hyphae, 7–16 μm broad, lactiferous hyphae present.

Habitat: Scattered on the ground in mixed forests dominated by *Quercus*.

Comments: *Lactarius subomphaliformis* is characterized by its slender and small basidiomata, orange pileus, cracks on the pileus center of mature specimens, the presence of

cystidia, and pileipellis an epithelium. This species is similar to *L. obscuratus* (Lasch) Fr., *L. cyathuliformis* Bon, and *L. omphaliformis* reported from Europe. These European species are all exclusively ectomycorrhizal with *Alnus* trees (Heilmann-Clausen et al. 1998), while the Korean species is found in *Quercus* forests. In addition, European species have bigger basidiospores and pleurocystidia (Heilmann-Clausen et al. 1998).



Fig. 12 Fruiting bodies of Korean species of *Lactarius* subg. *Lactarius*. **a** *L. akahatsu*, **b** *L. albidoarmeniacus*, **c** *L. aurantiozonatus*, **d** *L. austrotorminosus*, **e** *L. betulinus*, **f** *L. ciliatus*, **g** *L. cinereoreus*, **h** *L. cremicolor*, **i** *L. cyaneocinereus*, **j** *L. floridus*, **k** *L.*

hatsudake, **l** *L. inquinatus*, **m** *L. laeticolor*, **n** *L. orientitorminosus*, **o** *L. parallelus*, **p** *L. pohangensis*, **q** *L. puniceus*, **r** *L. reticulisporus*, **s** *L. spadiceus*, **t** *L. vietus*. Scale bar = 1 cm. **d** and **t** are reproduced from Lee et al. (2018)

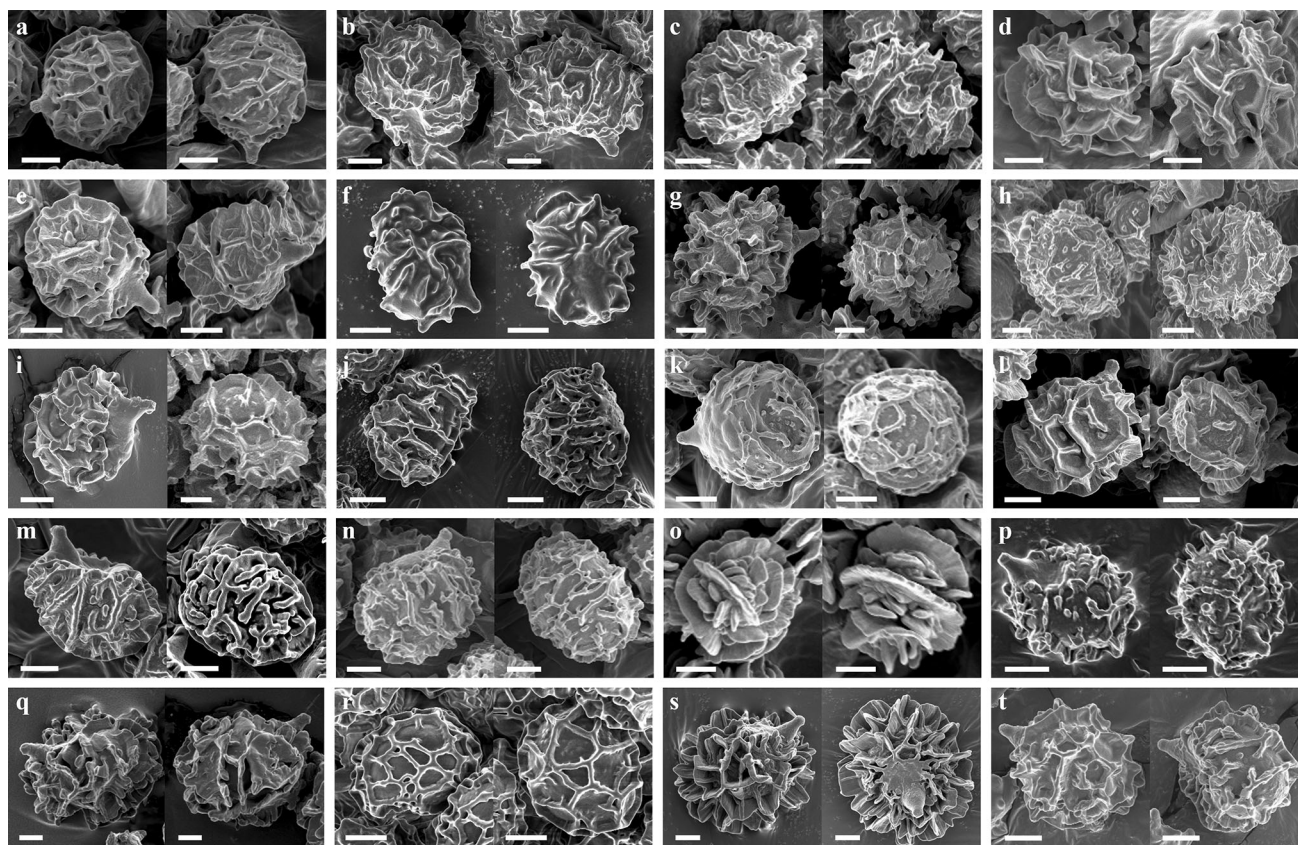


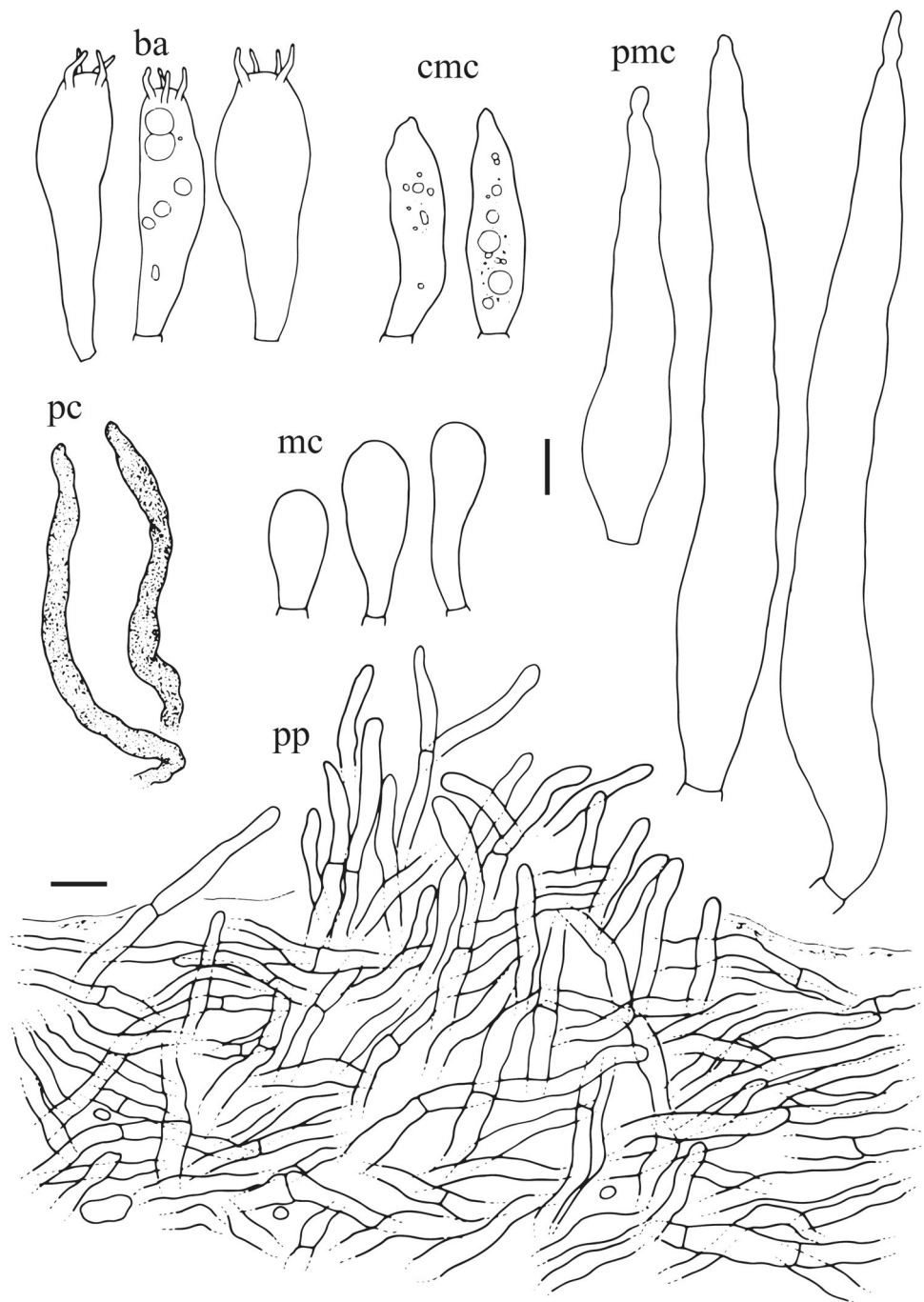
Fig. 13 Basidiospores (SEM) of Korean species of *Lactarius* subg. *Lactarius*. **a** *L. akahatsu*, **b** *L. albidoarmeniacus*, **c** *L. aurantiozonatus*, **d** *L. austrotorminosus*, **e** *L. betulinus*, **f** *L. ciliatus*, **g** *L. cinereoroseus*, **h** *L. cremicolor*, **i** *L. cyaneocinereus*, **j** *L. floridus*, **k** *L.*

hatsudake, **l** *L. inquinatus*, **m** *L. laeticolor*, **n** *L. orientitorminosus*, **o** *L. parallelus*, **p** *L. pohangensis*, **q** *L. puniceus*, **r** *L. reticulisporus*, **s** *L. spadiceus*, **t** *L. vietus*. Scale bar = 2 μ m. **d** and **t** are adapted from Lee et al. (2018)

Key to the species of *Lactarius* subgenus *Lactarius* in South Korea

1. Latex orange, reddish orange, vinaceous red 2
1. Latex transparent, white, watery white, watery cream ...
.....5
2. Latex reddish orange and unchanging; pileus tomentose;
stipe scrobiculate *L. laeticolor*
2. Latex orange or vinaceous red 3
3. Pileus scaly and tomentose; associated with *Quercus*
.....*L. aurantiozonatus*
3. Pileus glabrous; associated with *Pinus* 4
4. Latex orange; flesh staining vinaceous red when bruised
.....*L. akahatsu*
4. Latex vinaceous red; flesh staining greenish blue when
bruised*L. hatsudake*
5. Latex transparent or watery cream..... 6
5. Latex white or watery white..... 8
6. Latex transparent, changing to greyish lilac on expo-
sure..... *L. cyaneocinereus*
6. Latex watery cream..... 7
7. Pileus greyish yellow to greyish red; lamellae attach-
ment sinuate to adnate; pleuromacrocytidia pre-
sent..... *L. cinereoroseus*
7. Pileus light yellow to orange, scrobiculate; lamellae
attachment decurrent with long tooth; pleuromacro-
cytidia absent*L. floridus*
8. Latex changes to different colours on exposure
..... 9
8. Latex unchanging 13
9. Pileus glabrous; latex changing to orange brown; spore
ornamentation completely reticulate.....
.....*L. reticulisporus*
9. Pileus with tomentose to hairy margin; spore ornamen-
tation incompletely reticulate..... 10
10. Latex changing to greenish grey on exposure; associ-
ated with *Betula**L. vietus*
10. Latex changing to yellowish or reddish violet on
exposure; associated with *Quercus* 11
11. Latex changing to reddish violet; pleuromacrocy-
tidia > 80 μ m long..... *L. puniceus*

Fig. 14 Microscopic features of *Lactarius albidoarmeniacus*



- | | |
|--|---|
| <p>11. Latex changing to yellowish; pleuromacrocytidia < 60 μm long.....12</p> <p>12. Pileus azonate pileus; spore ornamentation incompletely reticulate to zebroid <i>L. ciliatus</i></p> <p>12. Pileus zonate and hygrophanous; latex changing to lemon yellow on exposure; spore ornamentation incompletely reticulate<i>L. cremicolor</i></p> <p>13. Pileipellis cutis to trichoderm, without glutinous layer..... 14</p> | <p>13. Pileipellis ixocutis to ixotrichoderm, with glutinous layer..... 16</p> <p>14. Pileus margin hairy; stipe scrobiculate; cheilomacrocytidia absent <i>L. austrotorminosus</i></p> <p>14. Pileus margin not hairy; stipe without scrobicules; cheilomacrocytidia present15</p> <p>15. Pileus brownish orange to light brown and zonate; spore ornamentation incompletely reticulate<i>L. spadiceus</i></p> |
|--|---|

15. Pileus pinkish white to reddish grey and azonate; spore ornamentation almost completely reticulate *L. albidoarmeniacus*
16. Spore ornamentation zebroid; macrocystidia cylindrical *L. parallelus*
16. Spore ornamentation incomplete to almost complete reticulum; macrocystidia fusiform to lanceolate 17
17. Pileus hygrophanous; spore ornamentation almost completely reticulate; associated with *Betula* *L. betulinus*
17. Pileus non-hygrophanous; spore ornamentation incompletely reticulate; associated with *Pinus* or *Quercus* 18
18. Pileus azonate; association with *Pinus* *L. pohangensis*
18. Pileus zonate; association with *Quercus* 19
19. Pileus orange white to brownish orange, with hairy margin; pileipellis, 150–230 μm thick *L. orientitorminosus*
19. Pileus white to yellowish white, without hairs at the margin; pileipellis, 100–220 μm thick *L. inquinatus*

Lactarius subgenus Lactarius

Lactarius albidoarmeniacus H. Lee, Wisitr. & Y.W. Lim, sp. nov.

Mycobank: MB 827931

Etymology: ‘albido’ means whitish and ‘armeniacus’ means reddish grey to apricot coloured which refers to the pale reddish grey pileus of the species.

Holotypus: SOUTH KOREA, Gangwon-do, Hongcheon-gun, Mt. Odae, alt. 751 m, N37°50'00" E128°31'52", 10 Sep 2013 (TPML130910-089; **isotypus**, SFC)

Pileus 30–75 mm diam., convex to applanate with depressed centre; margin slightly incurved, sometimes uneven; surface pinkish white (7A2) to reddish grey (8B2), darker in center (8D5, reddish brown), viscid, sometimes sticky, slightly tomentose. *Lamellae* crowded, adnate to slightly decurrent, sometimes forked near the stipe, with

abundant lamellulae, up to 3 mm broad, pale cream to cream-coloured, staining slowly yellow ochre when bruised. *Stipe* 30 – 85 \times 8 – 15 mm, cylindrical, tapering downwards, fistulose with age; surface white to pinkish white, sometimes yellow ochre spots. *Latex* rather abundant, white, unchanging on exposure.

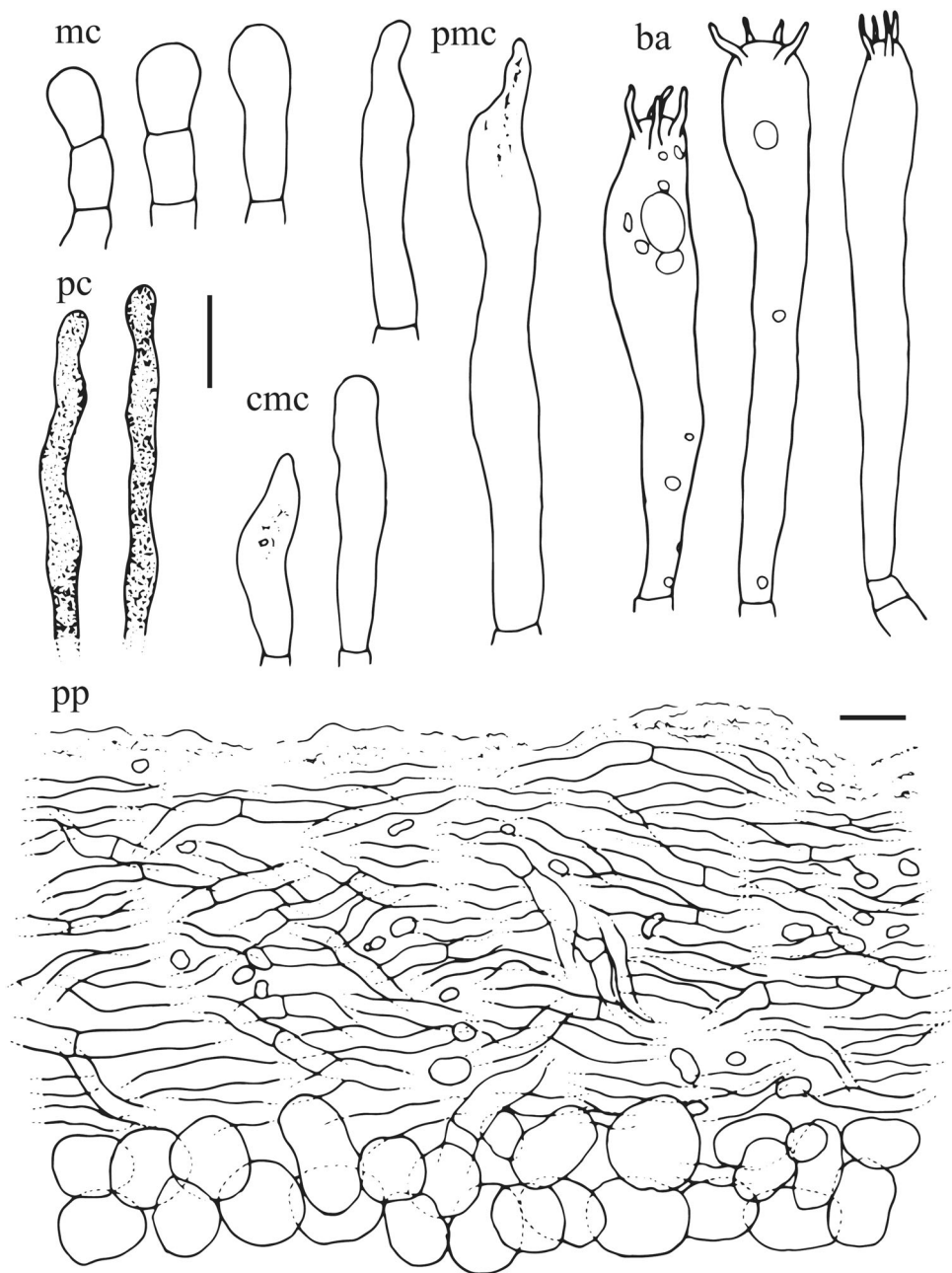
Basidiospores (n = 60), 7.9 – 8.7 – 8.8 – 9.8(– 9.9) \times 6.0 – 6.5 – 6.7 – 7.3 μm , Q = 1.18 – 1.32 – 1.36 – 1.45, broadly ellipsoid to ellipsoid; ornamentation amyloid, composed of up to 1 μm high, continuous and branched ridges and isolated warts, forming an incomplete to almost complete reticulum; plage inamyloid to slightly amyloid in distal part. *Basidia* 41 – 53 \times 8.5 – 12.5 μm , 4-spored, narrowly clavate. *Pleuromacrocystidia* abundant, 35.5 – 148.5 \times 5.5 – 16 μm , not emergent to emergent beyond the hymenium, narrowly fusiform; apex slightly acute to mucronate. *Lamellar edges* consisting of marginal cells, cheilomacrocystidia and basidia; marginal cells narrowly clavate to clavate, sometimes cylindrical; cheilomacrocystidia rare, 30.5 – 37.5 \times 5 – 9.5 μm , mostly not emergent, narrowly fusiform, irregular to straight, apex mucronate. *Pseudocystidia* numerous, aseptate, irregular, 3–5.5 μm broad, sometimes branched near apex; apex rounded, often slightly broader. *Pileipellis* (\pm) ixocutis, partially a trichoderm, 110–160 μm thick, parallel hyphae, piles of erect hyphae locally, terminal cells 15 – 45 \times 1 – 4.5 μm .

Habitat: Solitary or scattered on soil in mixed forests with *Abies* and *Quercus*.

Additional studied material: SOUTH KOREA, Gangwon-do, Wonju-si, Sangwonsa temple, alt. 1009, N37°18'23" E128°03'21", 30 Jul 2009 (HCCN18981); *ibid.*, Pyeongchang-gun, Mt. Odae, alt. 1235 m, N37°46'52" E128°33'07", 24 Sep 2009 (HCCN19087).

Comments: *Lactarius albidoarmeniacus* is phylogenetically closely related to European species (*Lactarius aquizonatus* Kytöv., *L. auriolla* Kytöv., *L. citriolens* Pouzar, *L. intermedius* Krombh. ex Berk. & Broome, *L. leonius* Kytöv., *L. resimus* (Fr.) Fr., *L. scrobiculatus* (Scop.) Fr., and *L. tuomikoskii* Kytöv.) and North American species (*L. alnicola* A.H. Sm.) (Figure 1). The new species has a

Fig. 15 Microscopic features of *Lactarius aurantiozonatus*



pinkish white to reddish grey pileus, while the others have cream to yellowish brown pigments in the pileus (Hesler and Smith 1979; Heilmann-Clausen et al. 1998).

Lactarius aurantiozonatus H. Lee, Wisitr. & Y.W. Lim, sp. nov.

Mycobank: MB 827932

Etymology: ‘aurantio’ means orange coloured and ‘zonatus’ means zonation. This name refers to the orange coloured and zonate pileus of the species.

Holotypus: SOUTH KOREA, Jeollabuk-do, Jinan-gun, Unjangan Natural Recreation Forest, alt. 414 m, N35°53'35" E127°25'34", 23 July 2014 (SFC20140723-72) *Pileus* 50–95 mm diam., convex then plano-convex to deeply funnel-shaped; margin first depressed, in age inrolled, often uneven to crenulate; surface pale yellow (3A2–3) to orange yellow (4A6), slightly darker when old, with darker to brownish orange scales, with distinct zonations, tomentose when young, viscid, shiny in moist condition. *Lamellae* rather distant, decurrent with long tooth, rarely forked, with abundant lamellulae, rather thick, up to 8 mm broad, cream-coloured when young, darker to orange

yellow in age, staining greyish orange on places with dried latex. *Stipe* 20 – 45 × 10 – 30 mm, cylindrical, tapering downwards, fistulose; surface concolourous with lamellae or paler, locally with brownish orange spots. *Odour* pleasant, fruity. *Taste* mild. *Latex* scarce, white, unchanging on exposure.

Basidiospores (n = 40), 6.9 – 7.8 – 8.3 – 9.0 × 5.5 – 6.0 – 6.1 – 6.5 μm, Q = 1.23 – 1.29 – 1.31 – 1.45, broadly ellipsoid to ellipsoid; ornamentation amyloid, composed of up to 1 μm high, parallel branched long ridges and isolated warts, forming an incomplete to almost complete reticulum, some ridges connected by thinner lines, closed meshes rare; plage amyloid in the distal part. *Basidia* 41 – 61.5 × 7.5 – 11.5 μm, 4-spored, slender, cylindrical. *Pleuromacrocystidia* not abundant, 35.5 – 68 × 5.5 – 8 μm, not emergent to slightly emergent beyond the hymenium, narrowly fusiform to cylindrical, sometimes indented at the middle, irregular to straight; apex round to mucronate. *Lamellar edges* consisting of marginal cells, cheilomacrocystidia and few basidia; marginal cells cylindrical to narrowly clavate; cheilomacrocystidia infrequent, 21.5 – 40.5 × 5 – 8 μm, narrowly fusiform, slightly emergent, apex mucronate to moniliform. *Pseudocystidia* numerous, 3–6 μm broad, aseptate, embedded to inconspicuous emergent, irregular; apex rounded and slightly broader. *Pileipellis* 70–130 μm, ixocutis, comprised of parallel and cylindrical hyphae; terminal cells 20 – 45 × 3 – 8 μm; subpellis comprised

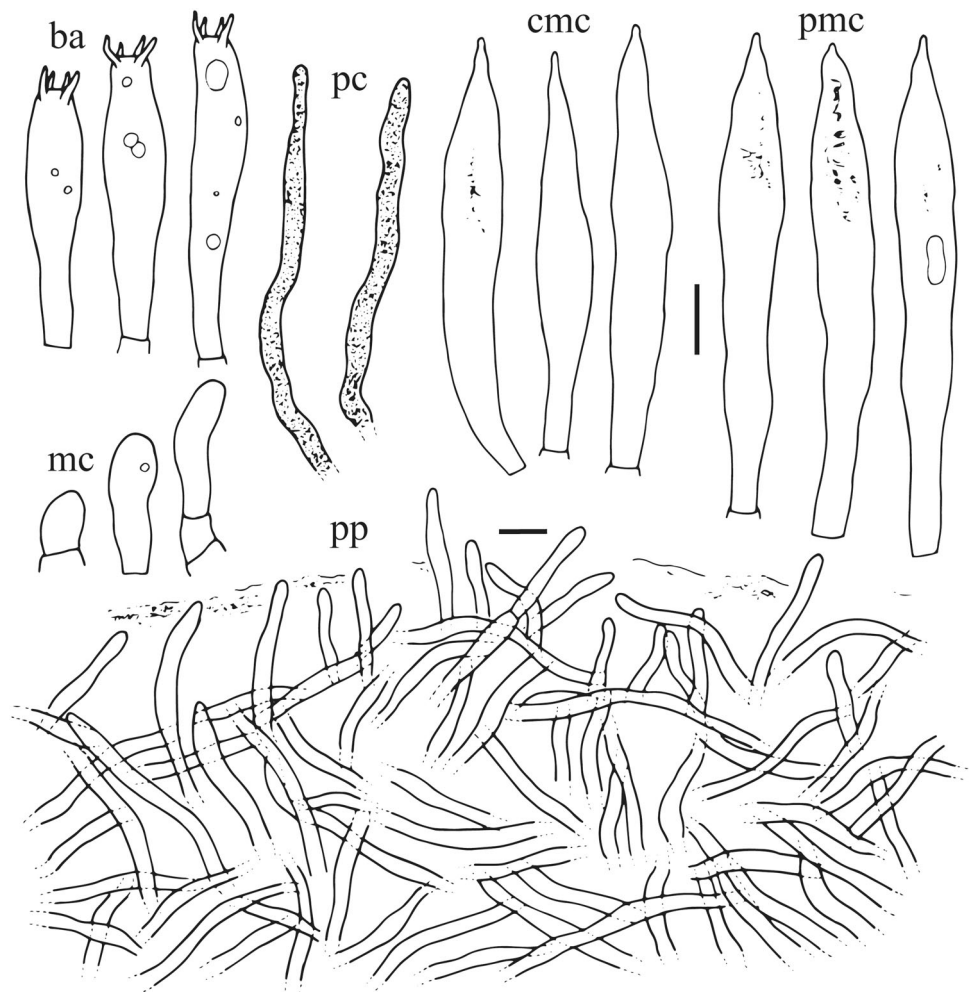
of inflated to isodiametric cells, 7 – 25 × 5 – 17 μm; lactiferous hyphae present in subpellis layer.

Habitat: Solitary or scattered mixed forests with *Pinus* and *Quercus*.

Additional studied material: SOUTH KOREA, Gangwon-do, Pyeongchang-gun, Mt. Odae, alt. 1426 m, N37°47'47" E128°32'25", 20 Aug 2005 (HCCN12999); Gyeonggi-do, Yangpyeong-gun, Saneum Natural Recreation Forest, alt. 352 m, N37°35'45" E127°34'16", 3 Sep 2012 (HCCN23407); Chungcheongnam-do, Gongju-si, Mt. Museong, alt. 162 m, N36°31'04" E127°04'59", 19 Sep 2012 (SFC20120919-79).

Comments: *Lactarius aurantiozonatus* is characterized by the pileus with orange yellow, zonate and viscid, the white unchanging latex, and decurrent lamellae with long teeth. This species is a member of section *Deliciosi* and has similar colour and morphology with European *L. salmonicolor* R. Heim & Leclair and Chinese *L. abieticola* X. H. Wang and *L. vividus* X. H. Wang et al. *Lactarius aurantiozonatus* is easily distinguished from the three species by unchanging white latex. Additionally, *L. salmonicolor* is associated with *Abies* and has larger basidiospores (Heilmann-Clausen et al. 1998). *Lactarius abieticola* can be easily distinguished from *L. aurantiozonatus* because of smaller basidiomata (25–50 mm in diam.) and broader basidia (9–15 μm in width) than *L.*

Fig. 16 Microscopic features of *Lactarius betulinus*



aurantiozonatus (Wang 2016). *Lactarius vividus* differs from *L. aurantiozonatus* by greenish tinges and shortly decurrent lamellae (Wang et al. 2015).

Lactarius betulinus H. Lee, Wisitr. & Y.W. Lim, **sp. nov.**

MycoBank: MB 827933

Etymology: ‘betulinus’ means birch tree. The name refers to the presence of the species in *Betula* forests and the putative ectomycorrhizal association with *Betula*.

Holotypus: SOUTH KOREA, Gangwon-do, Inje-gun, Wondae-ri *Betula* forest, alt. 630 m, N37°59′46″ E128°12′04″, 2 Sep 2015 (SFC20150902-79)

Pileus 35–80 mm diam., convex to applanate then becoming infundibuliform; margin first slightly inrolled, in age decurved, uneven to crenulate; surface, pinkish white (7A2) to reddish brown (9D7), with azonate or inconspicuous zonations viscid, hygrophanous. **Lamellae** crowded, adnate to slightly decurrent, often forked near the stipe, sometimes multifurcate, with abundant lamellulae, up to 8 mm broad, whitish to pale cream, turning pale ocher

when bruised. **Stipe** 30 – 60 × 10 – 25 mm, cylindrical to narrowly clavate, tapering downwards, fistulose in age; surface concoloured to pileus, paler to whitish at the base. **Odour** faintly fruity. **Taste** mild. **Latex** rather abundant, white, unchanging on exposure.

Basidiospores (n = 40), (5.8 –)5.9 – 6.5 – 7.2 × 4.9 – 5.5 – 5.6 – 6.2 μm, Q = 1.00 – 1.16 – 1.17 – 1.34, globose to broadly ellipsoid, few ellipsoid; ornamentation amyloid, composed of up to 1.1 μm high, continuous and often branched ridges and isolated warts, forming an almost complete to occasionally a complete reticulum; plage inamyloid to slightly amyloid in distal part. **Basidia** 41 – 51 × 7 – 9 μm, 4-spored, subcylindrical, sometimes cylindrical. **Pleuromacrocystidia** numerous, 72.5 – 83 × 7 – 10.5 μm, conspicuous projecting beyond the hymenium, narrowly fusiform to lanceolate; apex mucronate, sometimes moniliform. **Lamellar edges** consisting of marginal cells, cheilomacrocystidia and basidia; marginal cells cylindrical to clavate; cheilomacrocystidia numerous, 54.5 – 68 × 4 – 9.5 μm, emergent, narrowly fusiform to lanceolate, irregular to

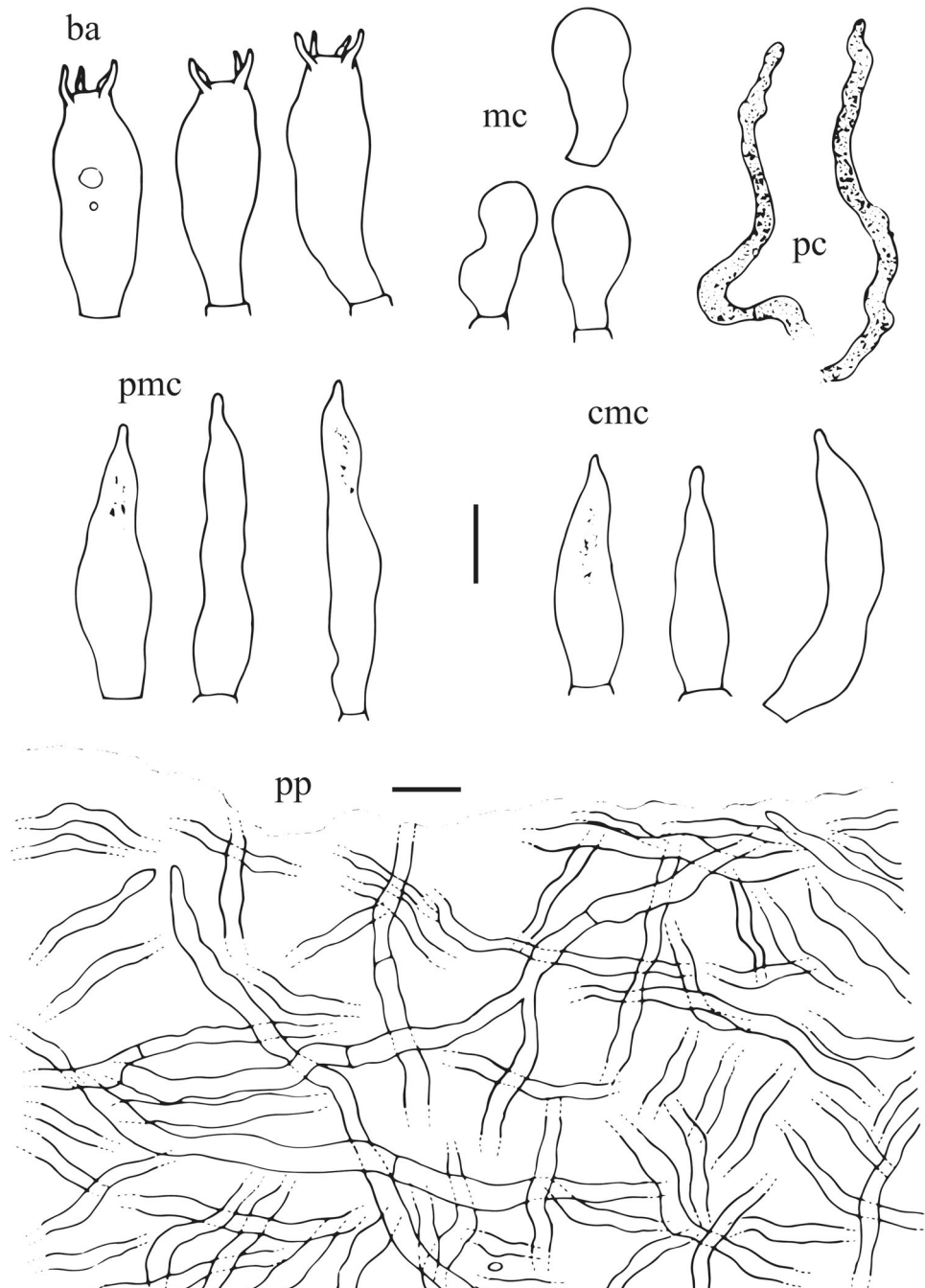
straight, apex mucronate to moniliform. *Pseudocystidia* not abundant, aseptate, irregular, 2.5–5 µm broad; apex rounded, often slightly broader. *Pileipellis* 170–290 µm thick, an ixotrichoderm, comprise of intricate and erect cylindrical hyphae, terminal cells 25 – 80 × 2.5 – 4.5 µm.

Habitat: Solitary or scattered on soil in forests dominated by *Betula*.

Additional studied material: SOUTH KOREA: Gangwon-do, Pyeongchang-gun, Mt. Odae, alt. 990 m, N37°46'51" E128°34'19", 10 Sep 2013, TPML130910-017 (TPML).

Comments: *Lactarius betulinus* is morphologically similar to *L. hysginus* (Fr.) Fr. and *L. ilicis* Sanari. *Lactarius hysginus* has a reddish, brick-coloured pileus often with a yellowish shade and is associated with *Pinus* in Europe

Fig. 17 Microscopic features of *Lactarius ciliatus*



(Heilmann-Clausen et al. 1998). *Lactarius ilicis* has a darker pileus colour than *L. betulinus* and is associated with *Quercus ilex* (Heilmann-Clausen et al. 1998).

Lactarius ciliatus H. Lee, Wisitr. & Y.W. Lim, **sp. nov.**

Mycobank: MB 827934

Etymology: ‘ciliatus’ means hairy, referring to the hairy pileus of the species.

Holotypus: SOUTH KOREA, Gangwon-do, Wonju-si, Mt. Chiak, alt. 584 m, N37°23′43″ E128°02′34″, 14 Jul 2003 (HCCN11325; **isotypus**, SFC)

Pileus 8–25 mm diam., convex to applanate with slightly depressed centre, sometimes with a small papilla; margin even, sometimes slightly uneven; surface reddish white (7A2) to dull red (8B3), sometimes with greyish red spots (8C5), tomentose to hairy, slightly viscid when young; marginal hairs dry. *Lamellae* rather distant, decurrent with long tooth, not forked, with lamellulae, up to 1 mm broad, white to pale cream, sometimes with curry colored spots. *Stipe* 10 – 20 × 2 – 5 mm, cylindrical to clavate, tapering downwards, fistulose; surface concolourous with pileus, tomentose. *Latex* rather abundant, white, changing to yellow buff on exposure.

Basidiospores (n = 40), 6.3 – 6.9 – 7.0 – 7.6 × 5.1 – 5.6 – 5.7 – 6.0 μm, Q = 1.15 – 1.22 – 1.25 – 1.36, broadly ellipsoid to ellipsoid; ornamentation amyloid, composed of up to 1 μm high, short or long ridges and isolated warts, rarely connected but never forming a

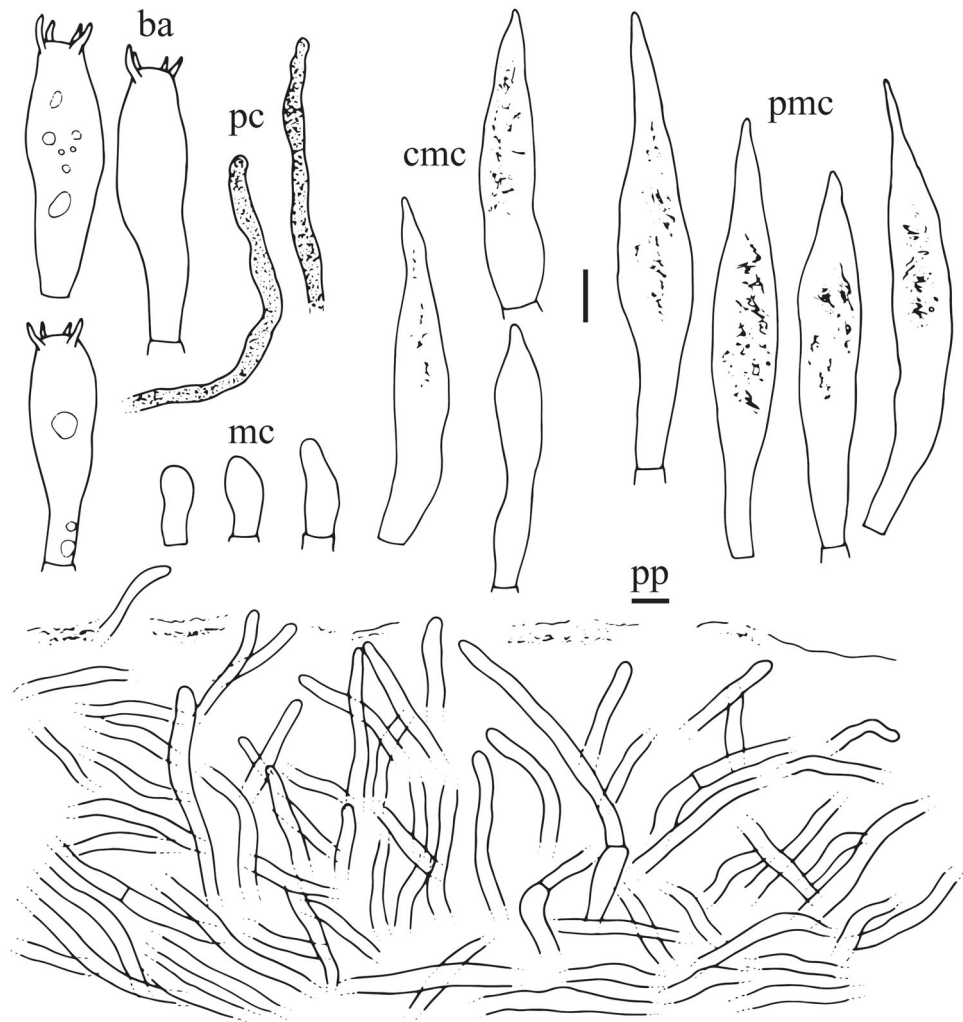
reticulum, sometimes arranged in zebra-like pattern; plage inamyloid. *Basidia* 25.5 – 32 × 7.5 – 9.5 μm, 4-spored, 1-spored present, narrowly clavate. *Pleuromacrocystidia* abundant, 24 – 41.5 × 5 – 9 μm, slightly emergent beyond the hymenium, up to 25 μm, narrowly clavate, often irregular in shape, contents fine granules locally, apex mucronate to slightly acute. *Lamellar edges* consisting of marginal cells, cheilomacrocystidia and basidia; marginal cells narrowly clavate to clavate, sometimes irregular; cheilomacrocystidia abundant, 19.5 – 30 × 5 – 9 μm, narrowly fusiform, fine granules near apex, apex slightly acute. *Pseudocystidia* numerous, aseptate, slightly emergent beyond the hymenium, cylindrical, straight to tortuous, 2.5–4.5 μm broad; apex rounded. *Pileipellis* 160–240 μm thick, an ixocutis, with a thin gelatinized layer locally, difficult to observe, parallel to ascending cylindrical hyphae, terminal cells 25 – 80 × 2.5 – 5.0 μm, apex rounded.

Habitat: Scattered to gregarious on soil in forests dominated by *Quercus*.

Additional studied material: SOUTH KOREA: Gangwon-do, Wonju-si, Mt. Chiak, alt. 428 m, N37°23′47″ E128°03′14″, 28 Aug 2002, HCCN10715.

Comments: *Lactarius ciliatus* is characterized by the small-sized basidiomata, reddish white to dull red colours, tomentose pileus, and white latex changing to yellowish buff. This species is similar to small-sized species in *L.*

Fig. 18 Microscopic features of *Lactarius cinereoroseus*



subg. *Russularia*. The former can be distinguished from all small-sized species in *L. subg. Russularia* by its yellowing latex and hairy pileus.

***Lactarius cinereoroseus* H. Lee, Wisitr. & Y.W. Lim, sp. nov.**

Mycobank: MB 827935

Etymology: ‘cinereo’ means grey and ‘roseus’ means light red. The name refers to the colour of the basidiomata.

Holotypus: SOUTH KOREA, Gyeonggi-do, Gwangju-si, Seoul National University Forest, alt. 193 m, N37°18′36″ E127°18′40″, 19 Aug 2015 (SFC20150819-46)

Pileus 20–60 mm diam., convex to applanate with slightly depressed centre; margin first slightly inrolled, in age expanded, entire, sometimes slightly crenate; surface greyish rose (11C3) to greyish ruby (12E6), sometimes dull red (10B4) to greyish red (11C4) center with yellowish grey (4B2) surroundings and margin at times paler, azonate, viscid to glutinous, sometimes slimy, rugulose.

Lamellae sinuate to adnate, sometimes slightly decurrent, rather crowded, sometimes forked near the stipe, up to 3 mm broad, whitish to pale cream, yellowish ocher in age, sometimes with pale greyish brown spots. **Stipe** 30–80 × 5–25 mm, tapering upwards, sometimes slightly ventricose, fistulose; surface whitish when young, concolourous or paler to pileus in age, often with yellowish ocher to pale reddish brown tinge. **Odour** slightly spermiatic. **Taste** mild, sometimes a little bit bitter. **Latex** rather abundant, translucent cream to watery white, unchanging on exposure.

Basidiospores (n = 40), 8.2 – 9.0 – 9.1 – 10.0 × 6.8 – 8.0 – 8.2 – 9.1 μm, Q = 1.02 – 1.15 – 1.17 – 1.33, mostly globose to broadly ellipsoid, few ellipsoid; ornamentation amyloid, composed of up to 1.3 μm high, irregular and forked long ridges and isolated warts, forming an incomplete reticulum; plage amyloid in the distal part. **Basidia** 47.5 – 64.5 × 12 – 15.5 μm, 4-spored, cylindrical to narrowly clavate. **Pleuromacrocystidia** numerous, 63 – 82.5 × 9.5 – 12 μm, mostly projecting beyond the

hymenium, narrowly fusiform to lanceolate; apex mucronate to moniliform; contents needle-like. *Lamellar edges* consisting of marginal cells, cheilomacrocytidia and basidia; marginal cells cylindrical to narrowly clavate; cheilomacrocytidia numerous, $45 - 58.5 \times 7 - 11.5$ μm , fusiform, apex mucronate. *Pseudocystidia* rare, aseptate, embedded in the hymenium, irregular, sometimes branched near apex, 2–5 μm broad; apex rounded, sometimes slightly broader. *Pileipellis* 175–275 μm thick, ixotrichoderm, comprised of intricate to erect cylindrical hyphae; terminal cells $45 - 120 \times 3 - 6$ μm .

Habitat: Scattered to gregarious on humid soil in lowlands of mixed forests dominated by *Pinus* and *Quercus*.

Additional studied material: SOUTH KOREA, Chungcheongbuk-do, Yeongdong-gun, Mt. Minjuji, alt. 694 m, N36°03'18" E127°52'38", 26 Jul 2012 (KA12-0680); Gyeonggi-do, Yangpyeong-gun Saneum Natural Recreation Forest, alt. 386 m, N37°35'57" E127°34'03", 19 Sep 2012 (KA12-1495).

Comments: *Lactarius cinereoroseus* is similar to the European species, *L. trivialis* (Fr.) Fr. The latter differs,

Fig. 19 Microscopic features of *Lactarius cremicolour*

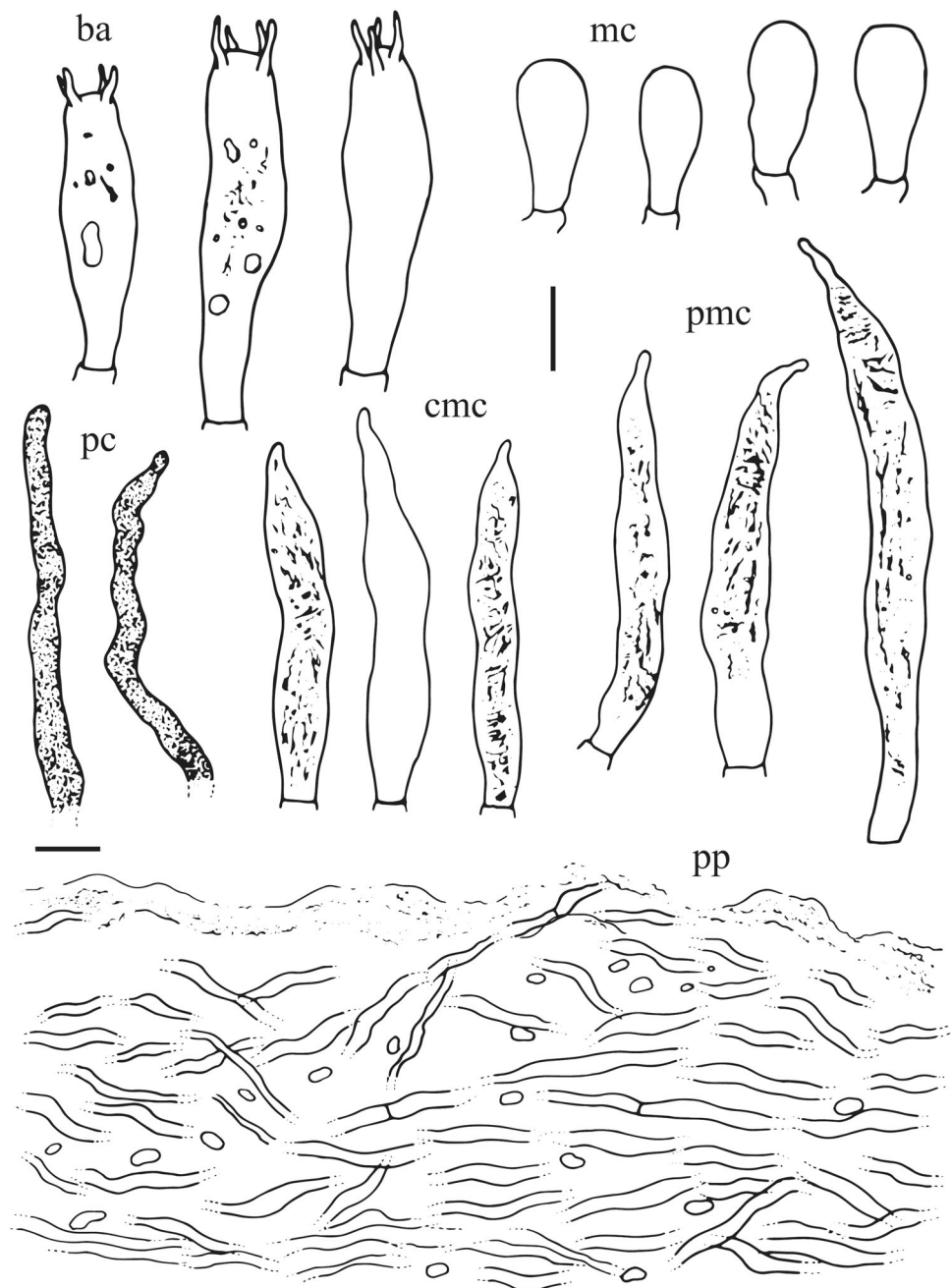
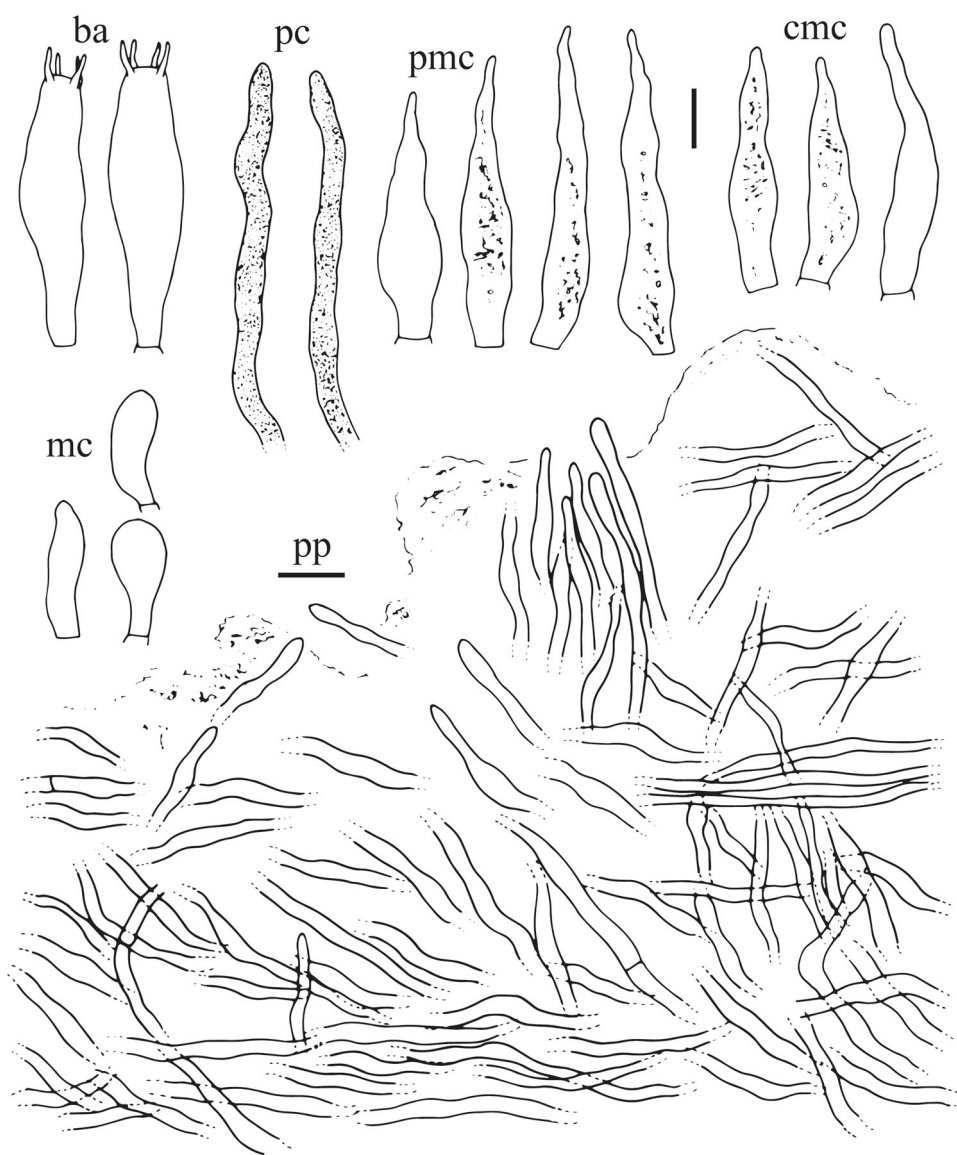


Fig. 20 Microscopic features of *Lactarius cyaneocinereus*



however, from the former by the cream latex changing to olivaceous grey and smaller pleurocystidia (Heilmann-Clausen et al. 1998).

Lactarius cremicolor H. Lee, Wisitr. & Y.W. Lim, **sp. nov.**

Mycobank: MB 827936

Etymology: ‘cremicolor’ means cream-coloured. This name refers the cream-coloured fruiting body of the species.

Holotypus: SOUTH KOREA, Jeollanam-do, Gurye-gun, Mt. Jiri, alt. 346 m, N35°15'32" E127°30'10", 3 Sep 2015 (SFC20150903-51)

Pileus 30–85 mm diam., convex to applanate then becoming infundibuliform with a deeper centre; margin slightly depressed and inrolled, in age expanded; surface,

white (–A1) to yellowish white (4A2), orange white (6A2) when old, sometimes with ocher-buff spots, viscid to slightly slimy, slightly fibrillose, hygrophanous, with concentric zonation. **Lamellae** crowded, slightly decurrent to decurrent, rarely forked near the stipe, with abundant lamellulae, up to 5 mm broad, white when young, darker to pale cream in age. **Stipe** 30 – 100 × 10 – 25 mm, central to eccentric, cylindrical to tapering downwards, fistulose; surface white to cream, pale orange brown at the base, scrobiculate, with orange brown spots, turning dark brown when old. **Odour** unremarkable, sometimes fruity. **Taste** mild. **Latex** rather abundant, white, changing lemon yellow after a while, drying pale ocher on lamellae.

Basidiospores (n = 40), 7.8 – 8.7 – 9.0 – 9.7 × 6.3 – 6.9 – 7.1 – 7.7 μm, Q = 1.16 – 1.23 – 1.30 – 1.41 μm, mostly broadly ellipsoid to ellipsoid; ornamentation

amyloid, composed of up to 1.1 μm high, short ridges and isolated warts, forming an incomplete partially, often connected by thinner lines; plage inamyloid to weakly amyloid in the distal part. *Basidia* 32 – 43.5 \times 9 – 13.5 μm , 4-spored, narrowly clavate, contents small granule and guttulate. *Pleuromacrocystidia* numerous, 20 – 59.5 \times 4 – 7.5 μm , projecting up to 29 μm , cylindrical to narrowly fusiform, irregular to straight, apex mostly mucronate, occasionally moniliform. *Lamellar edges* consisting of marginal cells, cheilomacrocystidia and basidia; marginal cells cylindrical; cheilomacrocystidia numerous, 35 – 51 \times 5.5 – 7.5 μm , slightly emergent beyond the marginal cells, narrowly fusiform, apex mucronate to round, some contents small guttulate. *Pseudocystidia* numerous, aseptate, embedded to inconspicuous emergent, irregular, 2.5–5.5 μm broad; apex rounded, often slightly broader. *Pileipellis* 90–210 μm thick, an ixocutis to locally ixotrichoderm, with mounds of erect hyphae; suprapellis 4–7 μm broad of intricate, parallel and erect thin hyphae.

Habitat: Scattered to gregarious on soil in mixed forests dominated by *Abies* and *Quercus*.

Additional studied material: SOUTH KOREA, Jeollabuk-do, Muju-gun, Mt. Jeoksang, alt. 751 m, N35°57'27" E127°41'59", 4 Sep 2010 (HCCN20394); Gyeonggi-do, Euijeongbu-si, Mt. Wondobong, alt. 135 m, N37°42'24" E127°02'07", 20 Jul 2011 (HCCN21514); Seoul, Gwanak-gu, Mt. Gwanak, alt. 134 m, N37°27'48" E126°56'42", 31 Aug 2012 (SFC20120831-09).

Comments: *Lactarius cremicolor* is morphologically similar to *L. yazoensis* Hesler & A.H. Sm. originated from North America. However, this species differs from *L. yazoensis* by its hygrophanous pileus and abundant cheilomacrocystidia (Hesler and Smith 1979). Moreover, *L. yazoensis* has nearly zebroid spore ornamentation while *L. cremicolor* has incomplete reticulum (Hesler and Smith 1979).

***Lactarius cyaneocinereus* H. Lee, Wisitr. & Y.W. Lim, sp. nov.**

MycoBank: MB 827937

Etymology: ‘cyaneo’ means blue and ‘cinereus’ means grey. The name refers to colour change of the latex.

Holotypus: SOUTH KOREA, Jeollabuk-do, Jinan-gun, Mt. Cheonban, alt. 505 m, N35°48'59" E127°31'57", 11 Sep 2014 (SFC20140911-26)

Pileus 30–90 mm diam., convex to applanate with slightly depressed centre; margin first inrolled, in age expanded, entire, hispid with 3 mm long hairs; surface light orange (5A4) to brownish yellow (5C7), darker towards the center,

paler in age, in most cases inconspicuously zonate, occasionally distinctively zonate, tomentose, viscid to glutinous. *Lamellae* adnate to slightly deccurrent, rather crowded, sometimes forked near the stipe, up to 4 mm broad, whitish to pale cream, greyish brown in age, turning lilac to ultramarine blue after bruising. *Stipe* 30 – 80 \times 10 – 25 mm, cylindrical, sometimes tapering upward, fistulose; surface pale cream when young, concolourous to pileus in age, often with reddish brown. *Odour* faintly fruity. *Taste* mild to slightly bitter. *Latex* rather abundant, transparent turning white quickly when isolated, then becoming greyish lilac to bluish grey.

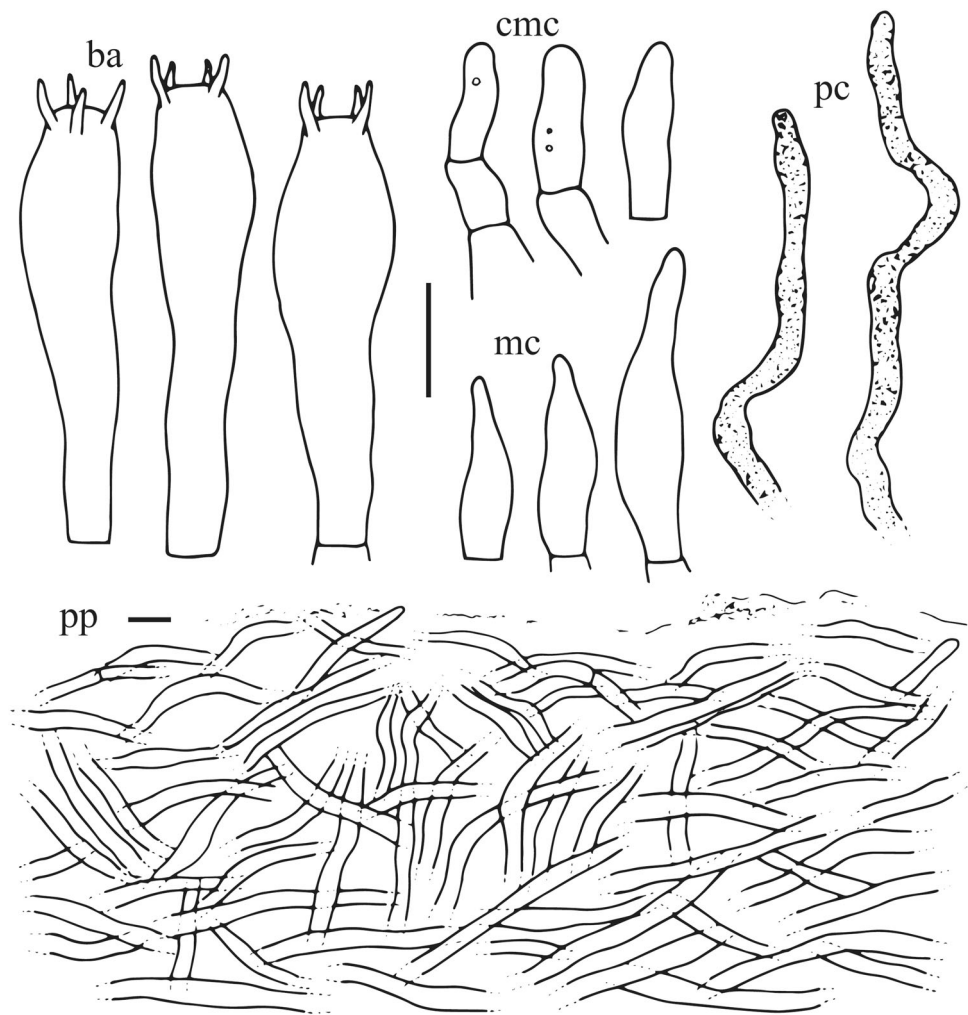
Basidiospores (n = 40), 7.9 – 8.7 – 8.8 – 9.5 \times (6.1 –)6.2 – 7.0 – 7.4 – 8.0 μm , Q = 1.12 – 1.19 – 1.25 – 1.37, subglobose to broadly ellipsoid; ornamentation amyloid, composed of up to 1.1 μm high, ridges forming an incomplete reticulum and isolated warts; plage inamyloid. *Basidia* 44.5 – 56 \times 8.5 – 13.5 μm , 4-spored, narrowly clavate, contents small granule and guttulate. *Pleuromacrocystidia* numerous, 26 – 67.5 \times 5.5 – 12 μm , often projecting beyond the hymenium, up to 35 μm , narrowly fusiform to cylindrical and broader in the middle or near the base, irregular to straight, apex mucronate to moniliform, contents needle-like. *Lamellar edges* comprised of marginal cells, cheilomacrocystidia and basidia; marginal cells mostly cylindrical to narrowly clavate with broader rounded apex; cheilomacrocystidia numerous, 25.5 – 45.5 \times 5.5 – 8.5 μm , often projecting beyond the marginal cells, up to 30 μm , narrowly fusiform with mucronate apex. *Pseudocystidia* numerous, aseptate, embedded to inconspicuous emergent, irregular, sometimes branched near apex, 3–7 μm broad; apex rounded, often slightly broader. *Pileipellis* an ixocutis to ixotrichoderm, 130–280 μm thick, intricate to parallel hyphae, locally with mounds of erect hyphae; terminal cells 40 – 75 \times 4 – 10 μm .

Habitat: Solitary or scattered on soil or rotten wood in *Quercus* forests.

Additional studied material: SOUTH KOREA, Gangwon-do, Inje-gun, Baekdamsa temple, alt. 533 m, N38°09'25" E128°23'05", 16 Aug 2002 (HCCN10496); Gyeongsangbuk-do, Sangju-si, Seongjubong Natural Recreation Forest, alt. 301 m, N36°32'02" E128°01'20", 19 Jul 2013 (SFC20130719-71).

Comments: *Lactarius cyaneocinereus* is morphologically similar to Thai species (*L. formosus* H.T. Le & Verbeke) and European species (*L. repraesentaneus* Britzelm and *L. speciosus* Burl.). Thai species differ from *L. cyaneocinereus* by the dark purple discolouration of latex upon exposure to air (Le et al. 2007a). *L. repraesentaneus* has a brighter yellow pileus and longer hairs on the pileus (up to

Fig. 21 Microscopic features of *Lactarius floridus*



5 mm) than *L. cyaneocinereus* (Heilmann-Clausen et al. 1998). *Lactarius speciosus* differs from *L. cyaneocinereus* by the absence of pleurocystidia and the capitate apex of cheilocystidia (Heilmann-Clausen et al. 1998).

Lactarius floridus H. Lee, Wisitr. & Y.W. Lim, **sp. nov.**

Mycobank: MB 827938

Etymology: ‘floridus’ means bright and fancy, referring to the vivid yellow fruiting body.

Holotypus: SOUTH KOREA, Chungcheongbuk-do, Chungju-si, Mt. Boryeon, alt. 301 m, N37°04′38″ E127°47′02″, 6 Sep 2012 (TPML120906-027; **isotypus**, SFC)

Pileus 35–80 mm diam., convex then applanate to infundibuliform with slightly depressed centre; margin first inrolled, in age decurved, even; surface light yellow (3A5) to orange (5A7), slightly viscid, tomentose when young, scaly, azonate when young, becoming more zonate when mature. **Lamellae** decurrent with long tooth, rather distant, rarely forked near the stipe, with abundant lamellulae, up to

10 mm broad, cream to pale yellow, turning greyish brown when bruised. **Stipe** 40 – 95 × 10 – 25 mm, cylindrical to slightly ventricose, tapering downwards, fistulose; surface concolourous with pileus, often scrobiculate with darker colour, smooth. **Odour** unremarkable. **Taste** mild. **Latex** rather abundant, white to watery pale cream, unchanging on exposure.

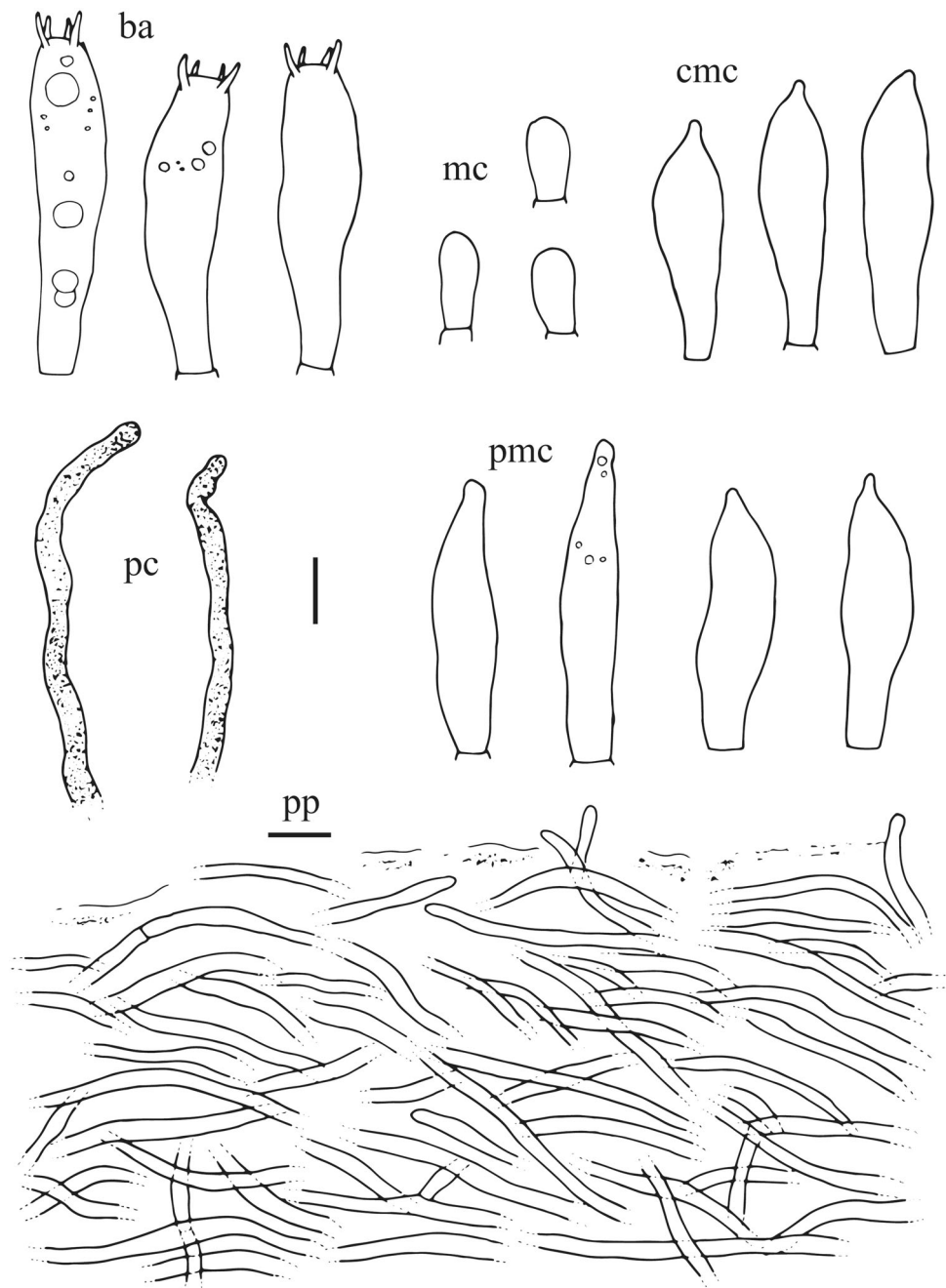
Basidiospores (n = 20), (6.2 –)6.5 – 7.6 – 8.7 × 5.7 – 6.6 – 7.5(– 7.6) μm, Q = 1.03 – 1.16 – 1.30, subglobose to broadly ellipsoid; ornamentation amyloid, composed of up to 0.5 μm high, branched long ridges and isolated warts, forming an incomplete to sometimes an almost complete reticulum, forming closed meshes, isolated warts not abundant; plage inamyloid to weakly amyloid in distal part. **Basidia** 42 – 55 × 9.5 – 12.5 μm, 4-spored, cylindrical to narrowly clavate. **Pleuromacro-cystidia** absent. **Lamellar edges** consisting of marginal cells and cheilomacrocystidia; marginal cells cylindrical to narrowly clavate; cheilomacrocystidia numerous, 13 – 29.4 × 5.5 – 7 μm, emergent, fusiform to lanceolate; apex mucronate. **Pseudocystidia** not abundant, mostly

embedded, aseptate, irregular, sometimes branched near the apex, 2–4 μm broad; apex rounded, often slightly broader. *Pileipellis* 125–170 μm thick, an ixocutis, comprise of parallel to intricate cylindrical hyphae, locally with erect hyphae, terminal cells 25 – 65 \times 3 – 7 μm .

Habitat: Solitary or scattered on soil in *Quercus* forests.

Comments: *Lactarius floridus* is well characterized by its vivid yellow to orange pileus, scrobiculate stipe, and white to watery cream latex with unchanging reaction. The closest relative of this species is *L. austrozonarius* H.T. Le & Verbeken from Thailand (Fig. 1). The Thai species is distinguished from *L. floridus* by a pale yellow to orange

Fig. 22 Microscopic features of *Lactarius inquinatus*



brown pileus, larger basidiospores (7.2–8.9–10.5–12.2 × 7–8.4–9.2–10.2 μm), and higher basidiospore ornamentation (up to 2.5 μm) (Le et al. 2007a).

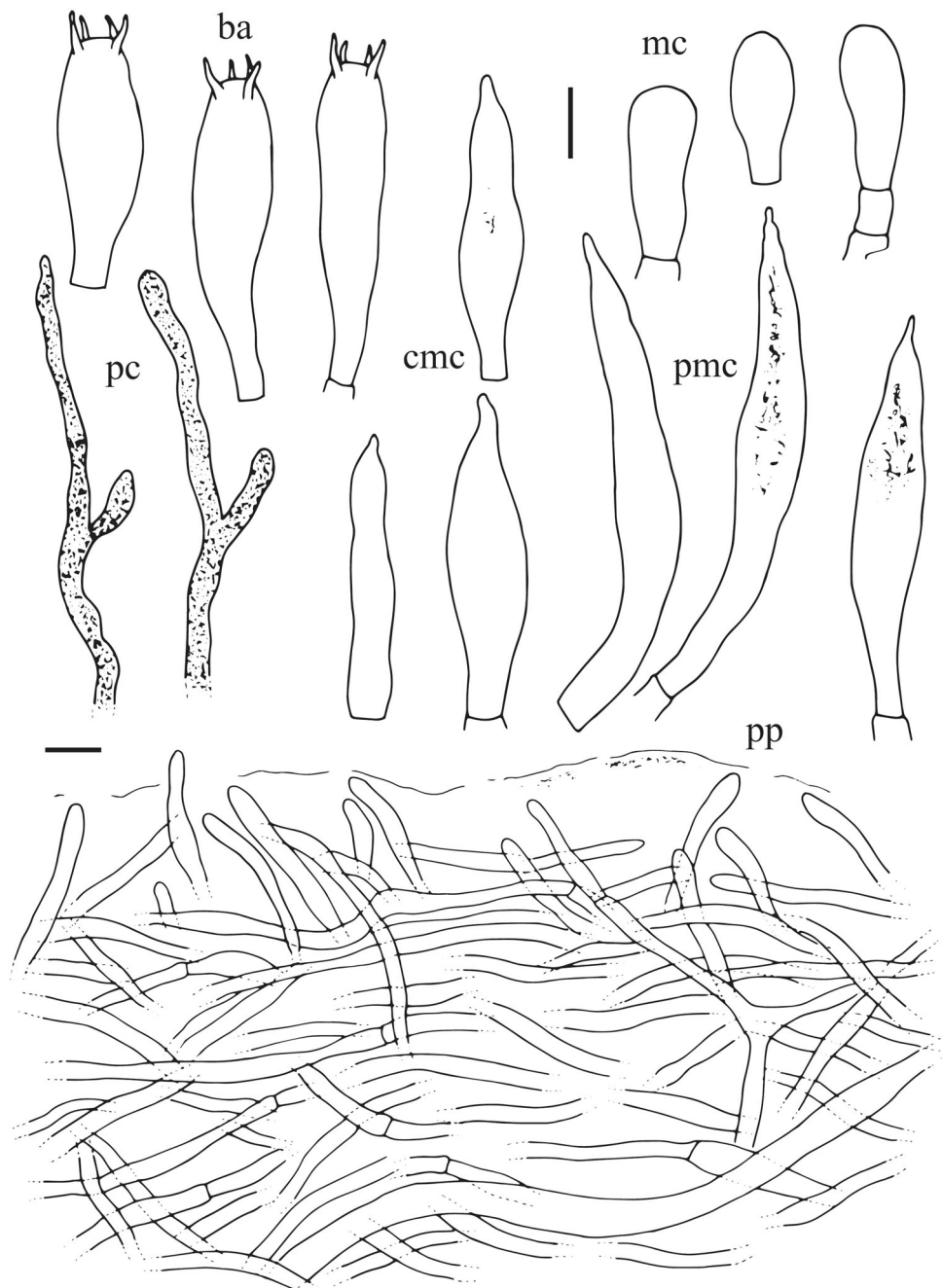
Lactarius inquinatus H. Lee, Wisitr. & Y.W. Lim, **sp. nov.**

Mycobank: MB 827939

Etymology: ‘inquinatus’ means stained. It refers to the reddish brown tinges on the pileus and stipe.

Holotypus: SOUTH KOREA, Gangwon-do, Inje-gun, Yongdae Natural Recreation Forest, alt. 489 m, N38°14′01″ E128°21′01″, 1 Sep 2015 (SFC20150901-06) *Pileus* 55–80 mm diam., convex to funnel-shaped depression; margin slightly decurved, in age expanded, even, sometimes slightly uneven; surface white (–A1) to yellowish white (4A2), with greyish brown (7D2) to reddish brown (8D5) patches or spots near the center, sometimes densely zonate with greyish orange (5B5) when dry, slightly viscid. *Lamellae* rather crowded, adnate to subdecurrent, rarely forked near stipe, with abundant lamellulae,

Fig. 23 Microscopic features of *Lactarius orientitormentosus*



up to 6 mm broad, white to white chrome, turning pale reddish brown when bruised. *Stipe* 20–35 × 10–25 mm, cylindrical to narrowly clavate, tapering downwards, solid; surface white to white chrome, with greyish orange to reddish brown spots. *Odour* fruity. *Taste* mild. *Latex* rather abundant, watery white, unchanging on exposure.

Basidiospores (n = 40), 6.0–7.0–7.2–8.4 × 5.2–5.7–5.8–6.4 μm, Q = 1.03–1.19–1.24–1.43, mostly subglobose to ellipsoid, few globose; ornamentation amyloid, composed of up to 1.1 μm high, parallel with branches long ridges and isolated warts, sometimes connected by thin lines, forming an incomplete to almost complete reticulum; plage distally to totally amyloid. *Basidia* 34.5–50.5 × 7–9.5 μm, 2 or 4-spored, cylindrical to narrowly clavate. *Pleuromacrocystidia* not abundant, 35–46.5 × 7.5–10 μm, mostly embedded deep in the hymenium, fusiform, apex mucronate, contents needle-like. *Lamellar edges* consisting of marginal cells, cheilomacrocystidia; marginal cells cylindrical to clavate; cheilomacrocystidia rare, 28.5–41.5 × 8–10 μm, fusiform to narrowly clavate, apex mostly mucronate. *Pseudocystidia* numerous, aseptate, mostly embedded, sometimes emergent, irregular, 2–6 μm broad, sometimes branched near apex; apex rounded, sometimes slightly broader. *Pileipellis* 100–220 μm thick, ixocutis, comprised of parallel to intricate cylindrical hyphae; terminal cells 55–130 × 3–5 μm.

Habitat: Solitary or scattered on soil or litter layer in forests dominated by *Quercus*.

Additional studied material: SOUTH KOREA, Gangwon-do, Inje-gun, Baekdamsa temple, alt. 510 m, N38°09'28" E128°22'34", 10 Sep 2006 (HCCN14668); *ibid.*, Pyeongchang-gun Mt. odae, alt. 829 m, N37°46'16" E128°34'42", 22 Jul 2012 (HCCN22638).

Comments: *Lactarius inquinatus* is characterized by a white to yellowish white pileus, lamellae staining pale reddish brown when bruised, and watery white latex. This species is similar to *L. evosmus* Kühner & Romagn., but *L. evosmus* differs by having lower basidiospore ornamentation with less connected ridges and a distinct sweetish apple-like smell (Heilmann-Clausen et al. 1998). *Lactarius zonarius* (Bull.) Fr. also is similar morphologically to *L. inquinatus*, but the former differs from the latter by its paler colour and subreticulate basidiospores (Heilmann-Clausen et al. 1998).

Lactarius orientitorminosus H. Lee, Wisitr. & Y.W. Lim, sp. nov.

Mycobank: MB 827940

Etymology: ‘orienti’ means eastern and ‘torminosus’ refers to the European *Lactarius torminosus*. This name refers to the similar morphology with *L. torminosus* and its origin in East Asia (South Korea).

Holotypus: SOUTH KOREA, Gangwon-do, Taebaek-si, Mt. Hambaek, alt. 1365 m, N37°09'24" E128°54'59", 28 Sep 2011 (TPML110928-063; **isotypus**, SFC)

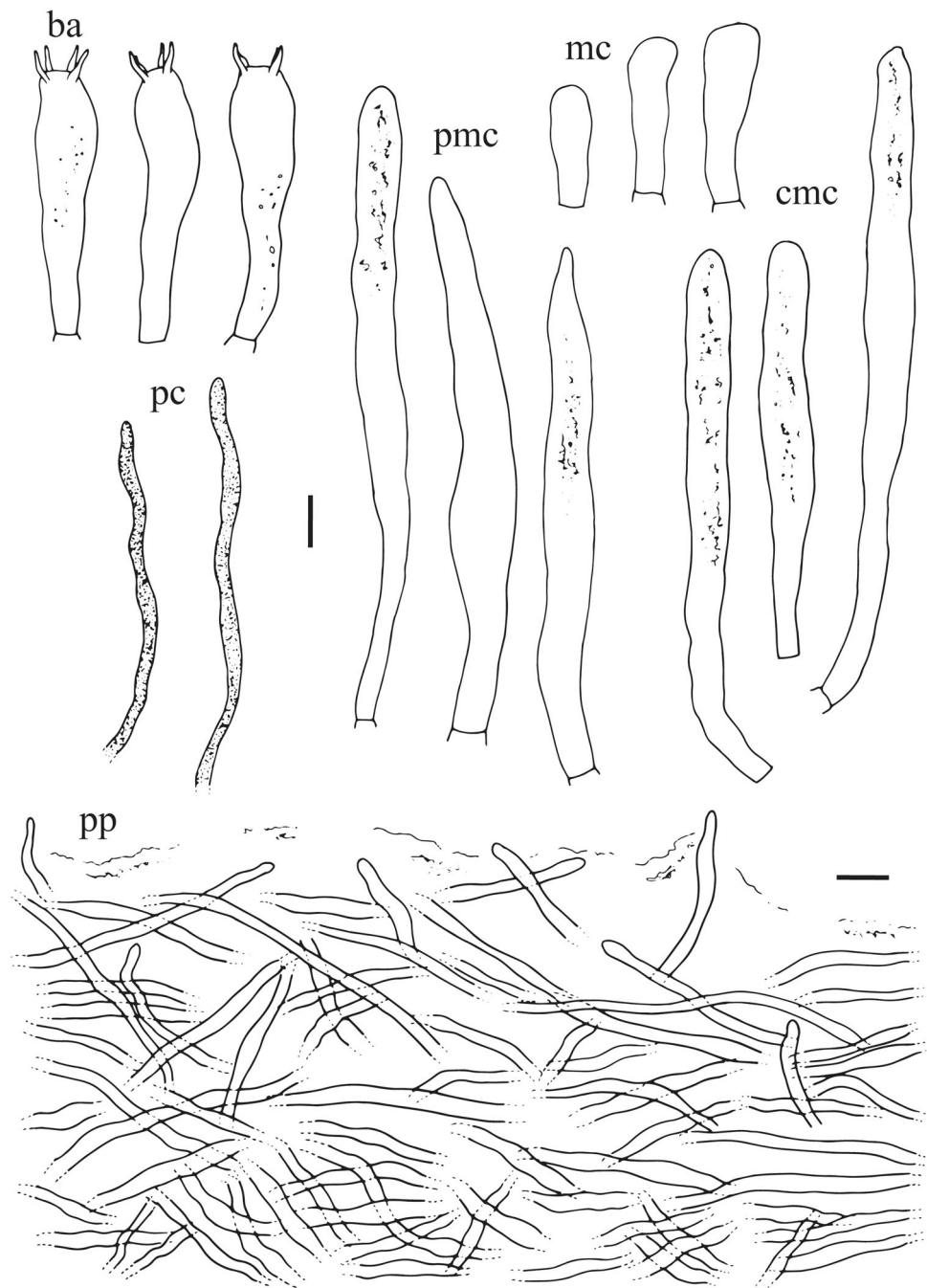
Pileus 30–65 mm diam., broadly convex to deep funnel-shaped depression; margin inrolled; surface orange white (6A2) to brownish orange (6C6), slightly darker when old, with distinct brownish zonations, rather smooth in the center, with adpressed, up to 8 mm long hairs near the margin. *Lamellae* crowded, slightly decurrent to decurrent, rarely forked near the stipe, with abundant lamellulae, up to 3 mm broad, pinkish white when young, darker to pale ocher in age. *Stipe* 25–70 × 10–20 mm, cylindrical, tapering downwards, fistulose; surface pale brown to brownish orange, whitish at the base, sometimes with reddish brown spots. *Latex* rather scarce, white, unchanging on exposure. *Basidiospores* (n = 40), (7.6–)7.8–9.0–9.4–11.0 × (6.4–)6.5–7.1–7.3–8.2 μm, Q = 1.05–1.26–1.32–1.59, subglobose to ellipsoid; ornamentation amyloid, composed of up to 0.5 μm high, parallel with branched ridges and isolated warts, forming an incomplete to sometimes an almost complete reticulum, some ridges connected by lower lines; plage mostly inamyloid. *Basidia* 38.5–48 × 9–11.5 μm, 4-spored, narrowly clavate. *Pleuromacrocystidia* numerous, 52.5–71 × 6–10 μm, mostly projecting beyond the hymenium, fusiform to lanceolate, sometimes moniliform, apex mucronate to slightly acute, contents needle-like. *Lamellar edges* consisting of marginal cells, cheilomacrocystidia and some basidia; marginal cells cylindrical to narrowly clavate; cheilomacrocystidia numerous, 34–52 × 6–12.5 μm, fusiform to lanceolate, slightly emergent, apex mucronate. *Pseudocystidia* numerous, aseptate, mostly embedded, rarely inconspicuous emergent, irregular to bent, 4–7 μm broad; apex rounded, sometimes slightly broader. *Pileipellis* 150–230 μm thick, an ixocutis, comprised of parallel and cylindrical hyphae; terminal cells 20–75 × 3–8 μm.

Habitat: Solitary or scattered on soil in mixed forests dominated by *Quercus*.

Additional studied material: SOUTH KOREA: Gangwon-do, Pyeongchang-gun, Sangwonsa temple, alt. 903 m, N37°47'20" E128°34'02", 15 Sep 2009, HCCN18837 (HCCN).

Comments: *Lactarius orientitorminosus* is similar to two European species, *L. torminosus* (Schaeff.) Gray and *L. torminosulus* Knudsen & T. Borgen. However, the Korean

Fig. 24 Microscopic features of *Lactarius parallelus*



species differs in the length of pileus hairs, colour of basidiomata and spore size. The length of pileus hairs of this species is intermediate between *L. torminosus* (up to 10 mm) and *L. torminosulus* (up to 5 mm) (Heilmann-Clausen et al. 1998). *Lactarius torminosus* has orange white to brownish orange pileus while the pilei of other two species are more ochraceous.

Lactarius parallelus H. Lee, Wisitr. & Y.W. Lim, **sp. nov.**

Mycobank: MB 827941

Etymology: ‘parallelus’ means parallel. The name defines the zebroid like ornamentation which consists of parallel ridges.

Holotypus: SOUTH KOREA, Jeju-do, Seogwipo-si, Mt. Geomunoreum, alt. 360 m, N33°27′20″ E126°42′53″, 2 Jul 2004 (HCCN12093; **isotypus**, SFC)

Pileus 45–70 mm diam., convex then applanate, sometimes slightly depressed centre; margin inrolled, even, sometimes slightly uneven; surface violet white (16A2) to violet grey (17B2), with distinct zonation, dull red (9B4) to dark

magenta (13F7), rugose near the center, slightly pruinose when young, sometimes slightly viscid. *Lamellae* rather distant, adnate to slightly decurrent, sometimes forked, with lamellulae, up to 8 mm broad, pale cream to cream, sometimes pinkish buff. *Stipe* 40 – 60 × 10 – 20 mm, cylindrical, tapering downwards, firm; surface white to pale grey, with pale violet grey spots. *Latex* rather scarce, translucent white, unchanging on exposure.

Basidiospores (n = 60), 6.0 – 6.6 – 6.8 – 7.6 × (4.6 –)4.8 – 5.5 – 5.7 – 6.4 μm, Q = 1.13 – 1.19 – 1.23 – 1.41, subglobose to broadly ellipsoid to ellipsoid; ornamentation amyloid, composed of up to 1.4 μm high, short parallel to long ridges and isolated warts, irregularly arranged in zebra-like pattern, forming a discontinuous line; plage amyloid in a distal part. *Basidia* 36 – 48.5 × 9 – 10.5 μm, 4-spored, narrowly clavate to clavate.

Pleuromacrocyttidia abundant, 63 – 111 × 6.5 – 7.5 μm, projecting beyond the hymenium, up to 55 μm, cylindrical, contents granules, apex mostly rounded to slightly acute, occasionally capitate. *Lamellar edges* consisting of marginal cells, cheilomacrocyttidia and basidia; marginal cells cylindrical; cheilomacrocyttidia abundant, 61 – 97.5 × 6.5 – 9.5 μm, cylindrical, contents granules, apex rounded. *Pseudocystidia* numerous, aseptate, embedded to inconspicuous

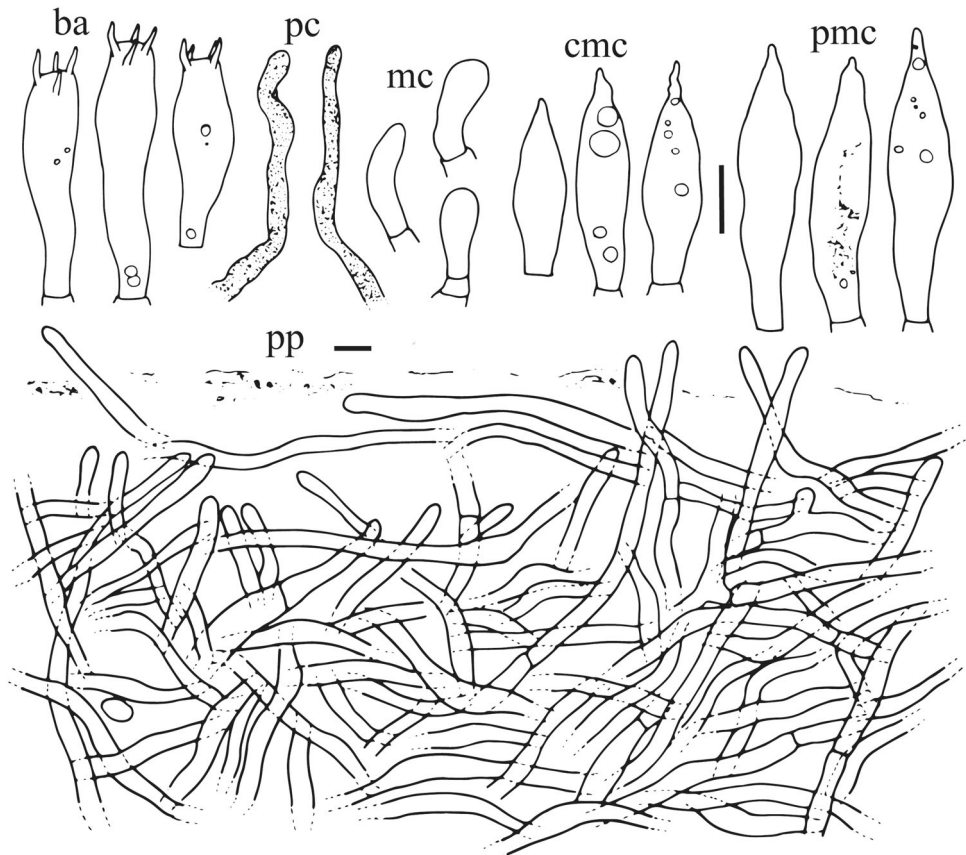
emergent, irregular, 2–4 μm broad; apex rounded. *Pileipellis* 160–210 μm thick, an ixocutis to an intricate ixotrichoderm, with a thin gelatinized layer locally, difficult to observe; composed of ascending and sinuous hyphae, rarely erect and cylindrical, terminal cells 60 – 130 × 2.5 – 5 μm.

Habitat: Solitary or scattered on ground in forests dominated by *Pinus*.

Additional studied material: SOUTH KOREA, Gyeongsangnam-do, Yangsan-si, Tongdosa temple, alt. 179 m, N35°29'18" E129°03'48", 29 May 1994 (HCCN1025G); Jeju-do, Jeju-si, Mt. hala, alt. 656 m, N33°25'09" E126°36'47", 1 Jul 1992 (HCCN4404); *ibid.*, alt. 745 m, N33°22'57" E126°37'13", 31 Jul 2003 (HCCN11459); Gangwon-do, Wonju-si, Mt. Chiak, alt. 358 m, N37°24'08" E128°03'01", 27 May 2004 (HCCN11979).

Comments: *Lactarius parallelus* is easily recognized in the field by the violet grey pileus with magenta zonation, rather distant lamellae and white latex with unchanging reaction. The pale-colouration of this species is similar to the European *L. circellatus* Fr. but the latex color change and association with *Carpinus* trees differentiates the European species from *L. parallelus* (Heilmann-Clausen et al. 1998).

Fig. 25 Microscopic features of *Lactarius pohangensis*



Microscopically, *L. circellatus* has smaller cystidia (pleuromacrocystidia: $45 - 70 \times 7.5 - 8.5 \mu\text{m}$, cheilomacrocystidia: $35 - 60 \times 5.5 - 7 \mu\text{m}$) and a thinner pileipellis ($70-100 \mu\text{m}$ thick) than *L. parallelus* (Heilmann-Clausen et al. 1998).

Lactarius pohangensis H. Lee, Wisitr. & Y.W. Lim, **sp. nov.**

Mycobank: MB 827942

Etymology: ‘pohangensis’ refers to the Pohang city, the locality of the type specimen.

Holotypus: SOUTH KOREA Gyeongsangbuk-do, Pohangsi, Mt. Sangdae, alt. 197 m, N36°10′58″ E129°18′22″, 30 Sep 2016 (SFC20160930-04)

Pileus 35–65 mm diam., convex to applanate with slightly depressed centre; margin decurved, margin uneven to crenulate; surface pale yellow (4A3) to orange white (5A2), light brown (7D8) to reddish brown (8E7) at the center, viscid, often rugulose, azonate to faintly zonate near the margin. *Lamellae* crowded, adnate to slightly decurrent, sometimes forked near the stipe, with abundant lamellulae, up to 5 mm broad, pale cream to cream, becoming pinkish buff when bruised. *Stipe* 30 – 70 × 10 – 18 mm, firm, cylindrical, slightly tapering downwards, solid; surface concolourous to pileus, longitudinally striated in age. *Odour* faintly fruity. *Taste* mild. *Latex* rather abundant, watery white, unchanging on exposure.

Basidiospores (n = 20), $5.6 - 6.8 - 7.9 \times 5.0 - 5.6 - 6.2 \mu\text{m}$, Q = 1.03 – 1.22 – 1.52, subglobose to ellipsoid; ornamentation amyloid, composed of up to 0.5 μm high, rarely branched short ridges and isolated warts, forming an incomplete reticulum; plage amyloid in distal part. *Basidia* $35.5 - 46 \times 8.5 - 11.5 \mu\text{m}$, 4-spored, cylindrical to narrowly clavate. *Pleuromacrocystidia* rather abundant, $35.5 - 59 \times 7.5 - 10.5 \mu\text{m}$, conspicuously projecting beyond the hymenium, narrowly fusiform to lanceolate; apex mucronate, sometimes moniliform, rarely obtuse. *Lamellar edges* consisting of marginal cells, cheilomacrocystidia and basidia; marginal cells cylindrical to narrowly clavate; cheilomacrocystidia numerous, $34.5 - 41.5 \times 9.5 - 11 \mu\text{m}$, emergent, narrowly fusiform to lanceolate, apex mucronate to moniliform. *Pseudocystidia* not abundant, aseptate, irregular, sometimes branched near the apex, 3–7 μm broad; apex round, often slightly broader. *Pileipellis* 150–210 μm thick, an ixocutis, comprised of parallel to intricate cylindrical hyphae, locally with erect hyphae; terminal cells $20 - 70 \times 4 - 9 \mu\text{m}$.

Habitat: Scattered to gregarious on soil in *Pinus densifolia* forests with numerous *Tricholoma matsudake*.

Comments: *Lactarius pohangensis* is characterized by the pale yellow to orange white pileus with darker center, watery white latex, and the association with *Pinus* trees.

This species is similar to *L. alpinus* Peck. However, the latter differs by having thin macrocystidia (4–7 μm in width), the presence of a papilla on the pileus, and its association with *Alnus* (Hesler and Smith 1979).

Lactarius puniceus H. Lee, Wisitr. & Y.W. Lim, **sp. nov.**

Mycobank: MB 827943

Etymology: ‘puniceus’ means reddish violet which refers to the reddish violet discolouration of latex.

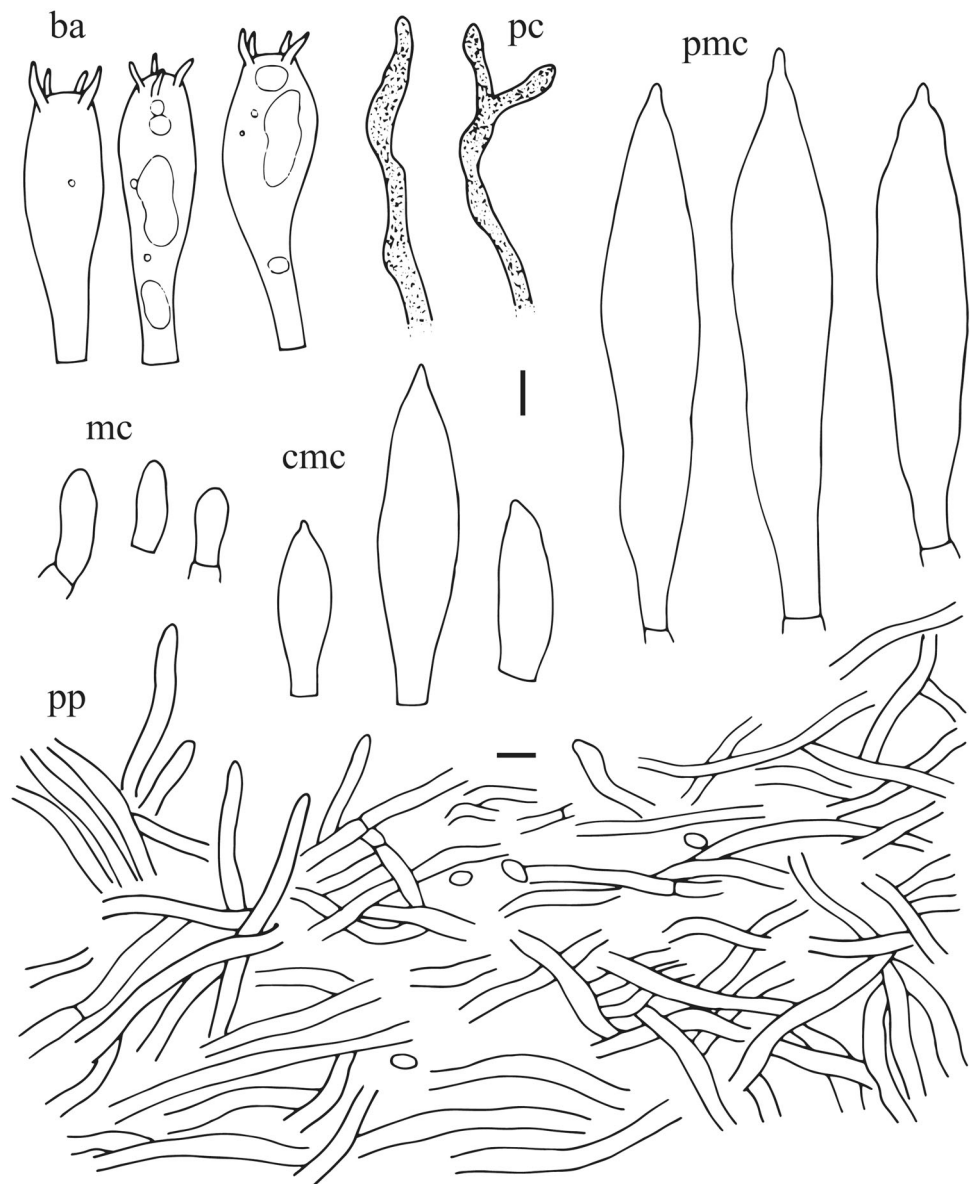
Holotypus: SOUTH KOREA, Jeollabuk-do, Muju-gun, Mt. Deogyu, alt. 744 m, N35°53′36″ E127°45′03″, 28 Aug 2015 (SFC20150828-51)

Pileus 70–130 mm diam., convex then applanate with more deep depression; margin slightly inrolled, in age expanded, even to slightly uneven; surface yellowish white (4A2) to greyish orange (5B3), sometimes reddish lilac (14C5) tinges, viscid. *Lamellae* fairly crowded, decurrent with rather long tooth, without forking, with abundant lamellulae, up to 10 mm broad, pale cream to cream, dark reddish violet when bruised. *Stipe* 50 – 85 × 20 – 40 mm, cylindrical, sometimes clavate, tapering downwards, solid; surface white to whitish chrome, scrobiculate, with conspicuous, olivaceous-buff, lilac to dark reddish violet spots. *Odour* unremarkable. *Taste* slightly acrid. *Latex* rather abundant, translucent to watery white turning reddish violet on exposure, drying dark reddish violet on lamellae.

Basidiospores (n = 40), $(9.4 -)9.6 - 10.7 - 11.2 - 12.8 \times (8.0 -)8.2 - 9.3 - 9.7 - 11.1 \mu\text{m}$, Q = 1.02 – 1.14 – 1.16 – 1.33, mostly globose to broadly ellipsoid, few ellipsoid; ornamentation amyloid, composed of up to 1.2 μm high, irregular and branched long ridges and isolated warts, forming an incomplete reticulum; plage inamyloid. *Basidia* $54 - 67.5 \times 13 - 17 \mu\text{m}$, 4-spored, narrowly clavate, sometimes contents small granules and guttate. *Pleuromacrocystidia* numerous, $85 - 113.5 \times 14 - 18.5 \mu\text{m}$, mostly projecting beyond the hymenium, narrowly fusiform to lanceolate; apex mucronate to moniliform; contents needle-like. *Lamellar edges* consisting of marginal cells, cheilomacrocystidia and few basidia; marginal cells cylindrical to clavate; cheilomacrocystidia numerous, $31.5 - 55.5 \times 8.5 - 12 \mu\text{m}$, fusiform to narrowly clavate, apex mostly obtuse. *Pseudocystidia* numerous, aseptate, embedded to slightly emerging, irregular, 3–7 μm broad, sometimes branched near apex; apex rounded, sometimes slightly broader. *Pileipellis* 190–310 μm thick, an ixotrichoderm, comprised of parallel to intricate cylindrical hyphae, locally with erect hyphae; terminal cells $35 - 90 \times 2 - 8 \mu\text{m}$.

Habitat: Solitary or scattered on soil or litter layer in forests dominated by *Quercus*.

Fig. 26 Microscopic features of *Lactarius puniceus*



Additional studied material: SOUTH KOREA, Seoul, Gangdong-gu, Gildong ecological Park, alt. 54 m, N37°32'29" E127°09'23", 7 Sep 2012 (HCCN23527).

Comments: *Lactarius puniceus* is similar to members in the European 'uvidus' group such as *Lactarius aspideus* (Fr.) Fr., *L. uvidus* (Fr.) Fr., and *L. violascens* (J. Otto) Fr. *Lactarius aspideus* has smaller basidiospores ($6.7 - 9.5 \times 5.6 - 7.8 \mu\text{m}$) with lower ornamentation ($0.5 \mu\text{m}$ high) and is associated with *Salix* trees (Heilmann-Clausen et al. 1998). *Lactarius uvidus* has a greyish pink pileus and is associated with *Betula* and *Picea* trees. Microscopically, this species has smaller pleurocystidia ($50 - 65 \times 8 - 10 \mu\text{m}$) and slender terminal hyphae ($1-4 \mu\text{m}$ broad) in pileipellis than those of *L. puniceus* (Heilmann-Clausen et al. 1998). Morphological characters

that distinguish *L. violascens* from the new species are dark purple latex discolouration and smaller pleurocystidia ($40 - 80 \times 8 - 13 \mu\text{m}$) (Heilmann-Clausen et al. 1998).

Lactarius reticulisporus H. Lee, Wisitr. & Y.W. Lim, **sp. nov.**

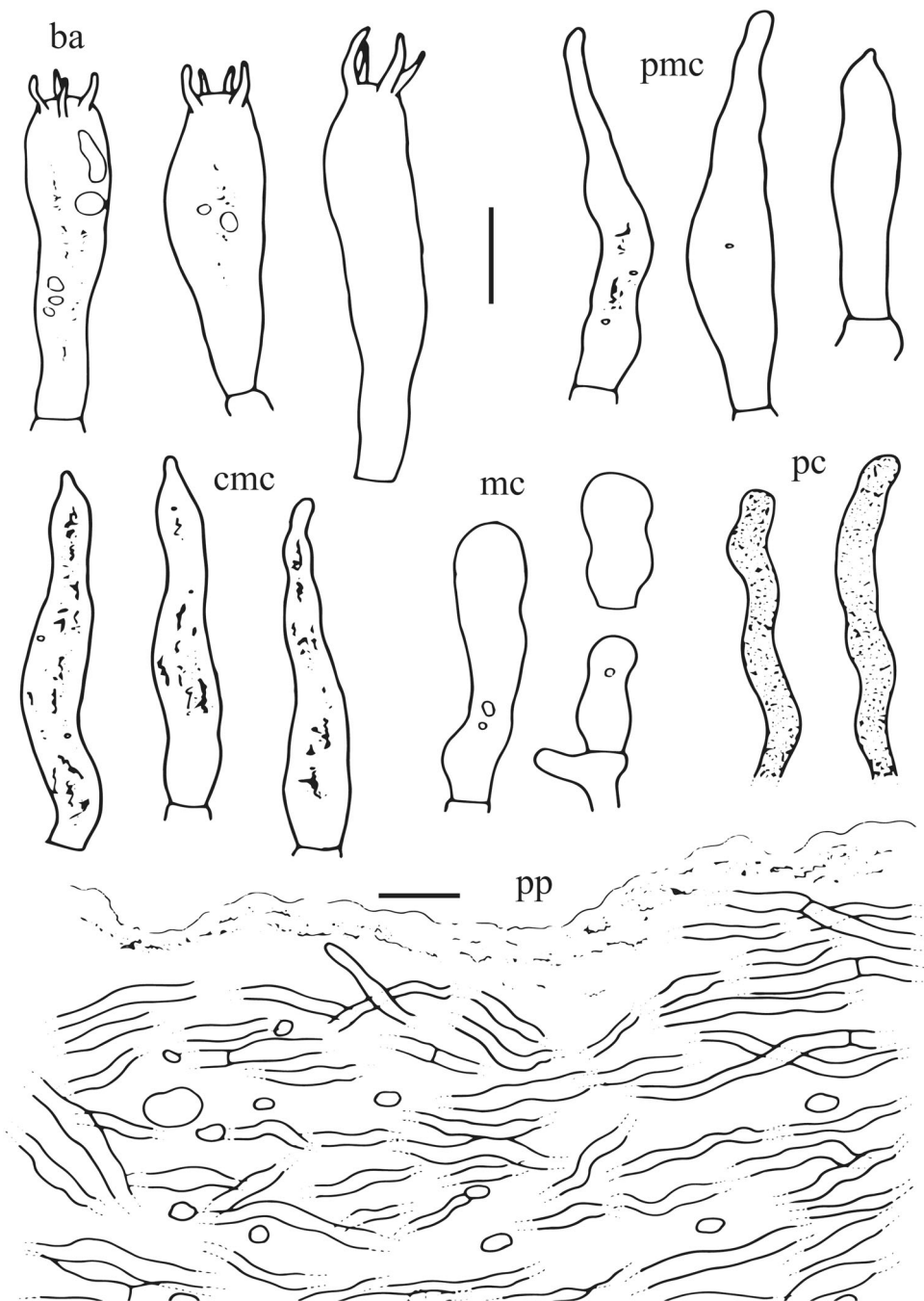
MycoBank: MB 827944

Etymology: 'reticulisporus' refers to the complete reticulum on basidiospores of this species.

Holotypus: SOUTH KOREA, Gangwon-do, Yangyang-gun, Mt. Jeombong, alt. 868 m, N38°02'49" E128°27'58", 7 Sep 2016 (SFC20160907-41)

Pileus 40–150 mm diam., convex then funnel-shaped depression; margin slightly inrolled, in age decurved, even

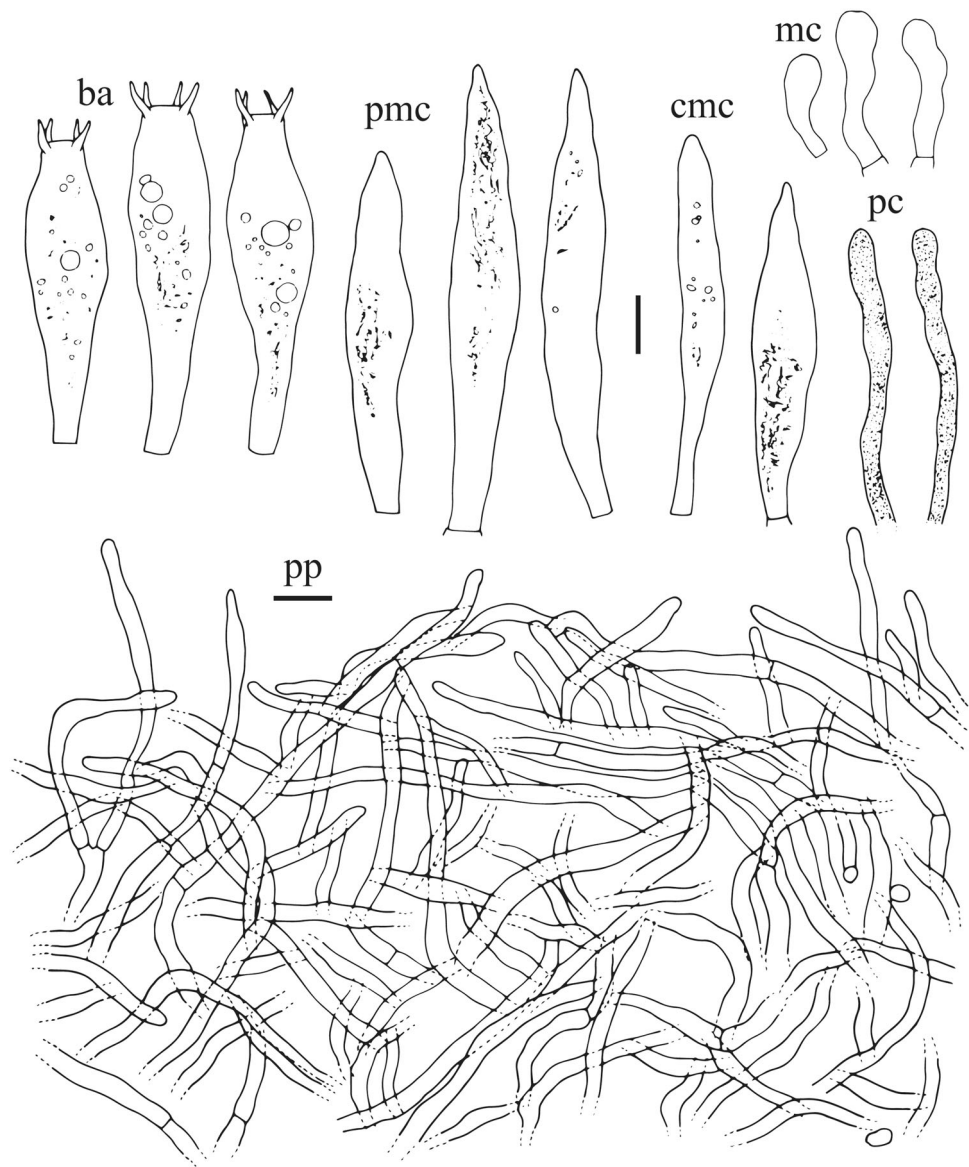
Fig. 27 Microscopic features of *Lactarius reticulisporus*



to uneven; surface white (–A1) to orange white (5A2), sometimes with pale orange to pink and when old ocher-buff spots, dry, smooth, sometimes rugose. *Lamellae* rather distant, slightly decurrent to decurrent, rather thick, fimbriate, with abundant lamellulae, up to 10 mm broad, pale cream when young, small brown spots on lamellar edge in age, turning pale ocher when bruised. *Stipe* 15 – 70 × 15 – 35 mm, cylindrical, sometimes ventricose, rarely clavate, tapering downwards, solid; surface white to pale grey, with orange white to orange brown spots. *Latex* white drying orange brown on lamellae.

Basidiospores (n = 60), 5.9 – 6.5 – 7.4 – 8.0 × 4.6 – 5.1 – 5.6 – 6.1 (– 6.2) μm, Q = 1.19 – 1.27 – 1.31 – 1.41, broadly ellipsoid to ellipsoid; ornamentation amyloid, composed of up to 0.8 μm high, ridges, forming a complete reticulum, densely reticulate locally; plage inamyloid. *Basidia* 37.3 – 48.6 × 6 – 11.1 μm, 4-spored, narrowly clavate. *Pleuromacrocytidia* abundant, 35 – 59 × 2.5 – 6.5 μm, slightly emergent beyond the hymenium, cylindrical to narrowly clavate, irregular, contents granules and needle-like, apex mucronate to moniliiform. *Lamellar edges* consisting of marginal cells,

Fig. 28 Microscopic features of *Lactarius spadiceus*



cheilomacrocytidia and basidia; marginal cells cylindrical to narrowly clavate; cheilomacrocytidia abundant, $26.5 - 53 \times 4 - 6.5 \mu\text{m}$, cylindrical to narrowly clavate, contents granules, apex mucronate to moniliform. *Pseudocystidia* numerous, aseptate, embedded to slightly emergent, cylindrical, tortuous, $2.5-5 \mu\text{m}$ broad; apex rounded. *Pileipellis* $170-260 \mu\text{m}$ thick, an ixocutis, a dense layer of parallel and cylindrical hyphae underneath a thin gelatinized layer; terminal cells $20 - 85 \times 2 - 6.5 \mu\text{m}$.

Habitat: Solitary or scattered on soil in forests dominated by *Quercus*.

Additional studied material: SOUTH KOREA, Jeollanam-do, Gurye-gun, Mt. Jiri, alt. 504 m, N35°14'04" E127°36'23", 8 Sep 2005 (HCCN13149); Gangwon-do,

Wonju-si, Mt. Chiak, alt. 440 m, N37°23'46" E128°03'16", 12 Sep 2006 (HCCN14705).

Comments: *Lactarius reticulisporus* is phylogenetically closely related to *L. alboscrobiculatus* H.T. Le & Verbeken and *L. alboscrobiculatus* var. *roseopurpureus* H.T. Le & Verbeken (Fig. 1). While the new species has white latex drying to orange brown, *L. alboscrobiculatus* has white to cream latex with an unchanging reaction (Le et al. 2007a) and *L. alboscrobiculatus* var. *roseopurpureus* has lamellae staining greyish on places with dried latex (Le et al. 2007a).

Lactarius spadiceus H. Lee, Wisitr. & Y.W. Lim, **sp. nov.**

MycoBank: MB 827945

Etymology: ‘spadiceus’ means bright brown which refers to the light brown coloured pileus.

Holotypus: SOUTH KOREA, Jeollabuk-do, Muju-gun, Mt. Bakseok, alt. 549 m, N36°00′24″ E127°50′30″, 7 Aug 2012 (TPML120807-021; **isotypus**, SFC)

Pileus 30–95 mm diam., convex then infundibuliform with a depressed centre; margin inrolled, in age decurved, even; surface brownish orange (6C3) to light brown (7D5), distinctively zonate, slightly fibrillose, viscid. **Lamellae** adnate to slightly decurrent, crowded, rarely forked near the stipe, up to 3 mm broad, whitish to pale cream, often with yellowish ocher tinges. **Stipe** 60 – 90 × 10 – 20 mm, cylindrical, sometimes slightly ventricose, fistulose in age; surface whitish, with yellowish ocher to pale orange brown scrobicules. **Latex** rather scarce, white and unchanging on exposure.

Basidiospores (n = 20), 9.4 – 10.7 – 11.7 × 7.8 – 8.7 – 9.7(– 10.0) μm, Q = 1.11 – 1.19 – 1.22 – 1.28, subglobose to broadly ellipsoid; ornamentation amyloid, composed of up to 2.2 μm high, irregular ridges and isolated warts, forming almost complete reticulate, closed meshes present locally, crests slightly acute; plage amyloid in the distal part. **Basidia** 41.5 – 63.5 × 13.5 – 16.5 μm, 4-spored, narrowly clavate. **Pleuromacrocystidia** numerous, 44 – 97.5 × 9 – 15.5 μm, mostly projecting beyond the hymenium, up to 55 μm, narrowly fusiform to fusiform; apex mucronate to slightly acute; contents needle-like. **Lamellar edges** sterile, comprised of marginal cells and cheilomacrocystidia; marginal cells mostly cylindrical with capitate apex, some flexuous cylindrical to narrowly clavate; cheilomacrocystidia numerous, 21.5 – 71 × 4 – 10.5 μm, slightly projecting beyond the marginal cells, narrowly fusiform, apex mucronate to slightly acute, contents partially needle-like, small granules present. **Pseudocystidia** numerous, aseptate, embedded to inconspicuous emergent, irregular to bent, 3–6 μm broad; apex rounded. **Pileipellis** a loose and poorly differentiated cutis to trichoderm, 250–350 μm thick, composed of intricate to erect hyphae; terminal cells 25 – 70 × 2 – 4 μm.

Habitat: Scattered to gregarious on soil in mixed forests dominated by *Pinus* and *Quercus*.

Additional studied material: SOUTH KOREA, Chunchongbuk-do, Yeongdong-gun, Mt. Minjuji, alt. 674 m, N36°03′08″ E127°49′50″, 19 Jun 2012 (KA12-0268).

Comments: *Lactarius spadiceus* forms a clade with members of section *Deliciosi*. Before this study, only two species (*L. porninsis* Rolland and *L. splendens* Hesler & A.H. Sm.) in this section have been known to have white unchanging latex (Nuytinck et al. 2017). From this study, two species (*L. aurantiozonatus*, see above, and *L. spadiceus*) with unchanging white latex are added. Among four species with white latex, *L. porninsis* can be distinguished from *L. spadiceus* by its smaller basidiospores (6.3 – 9.6 × 5.2 – 7.3 μm) and the absence of scrobicules on the stipe (Heilmann-Clausen et al. 1998). The pileus of *L. splendens* is more vivid and azonate (Hesler and Smith 1979). Microscopically, this species lacks cheilocystidia on lamellar edges. *Lactarius aurantiozonatus* can be easily distinguished from *L. spadiceus* by its orange yellow and vivid pileus colour. The other closely related species in the phylogeny, *L. rubrilacteus* Hesler & A.H. Sm., has an orange brown pileus with concentric zonation and reddish latex (Hesler and Smith 1979).

Key to the species of *Lactarius* subgenus *Plinthogalus* in South Korea

1. No latex color change2
1. Latex color change5
2. Pileus with concentric light brown zones
.....*L. fulvescens*
2. Pileus without zonation..... 3
3. Dark coloured basidiomata, commonly dark brown and more blackish brown in the centre*L. ustulatus*
3. Pale coloured basidiomata, orange to pale brown..... 4
4. Pileipellis thicker than 100 μm*L. alutaceus*
4. Pileipellis thinner than 100 μm*L. cucurbitoides*
5. Latex color change to lilac on exposure.....
.....*L. atromarginatus*
5. Latex color change to pinkish and lamellae medium crowded6
6. Spore ornamentation lower than 1.5 μm.....
.....*L. albidocinereus*
6. Spore ornamentation higher than 1.5 μm 7
7. Latex changing immediately pinkish.....
.....*L. alboroseus*
7. Latex changing to pinkish in few minutes 8
8. Pileipellis 150–190 μm thick; basidia smaller than 40 μm; 2-spored basidia present*L. incarnatus*
8. Pileipellis 90–150 μm thick; basidia larger than 45 μm..... *L. aurantiacopallens*



Fig. 29 Fruiting bodies of Korean species of *Lactarius* subgenus *Plinthogalus*. **a** *L. albidocinereus*, **b** *L. alboroseus*, **c** *L. alutaceus*, **d** *L. atromarginatus*, **e** *L. aurantiacopallens*, **f** *L. cucurbitoides*, **g** *L.*

fulvescens, **h** *L. incarnatus*, **i** *L. ustulatus*. Scale bar = 1 cm. **d** and **f** are reproduced from Lee et al. (2018) and (2015a), respectively

Lactarius subgenus *Plinthogalus*

Lactarius alboroseus H. Lee, Wisitr. & Y.W. Lim, **sp. nov.**

Mycobank: MB 827946

Etymology: ‘alboroseus’ means pink or pale rose, referring to the pink discolouration of latex.

Holotypus: SOUTH KOREA, Jeollabuk-do, Muju-gun, Mt. Deogyu, alt. 914 m, N35°53′08″ E127°43′39″, 28 Aug 2015 (SFC20150828-39)

Pileus 40–90 mm diam., convex then appanate with slightly depressed centre; margin first decurved, in age expanded, even to crenate, sometimes radially folded; surface greyish orange (5B3) to light brown (6D6), often with cream (4A3) tinges, dry, pruinose, slightly tomentose slightly tomentose, sometimes rugose in age. **Lamellae** slightly deccurent to deccurent, rather crowded, sometimes forked near the stipe, up to 5 mm broad, whitish to pale

cream when young, yellowish ocher to buff in age. **Stipe** 40 – 100 × 8 – 20 mm, cylindrical, sometimes tapering upwards, often irregularly compressed, fistulose with age; surface whitish, often with yellowish ocher to pinkish ocher tinges. **Odour** unremarkable. **Taste** extremely acrid. **Latex** abundant, white changing to pink in a few seconds, finally drying whitish.

Basidiospores (n = 60), 6.9 – 7.7 – 8.0 – 8.7 × 6.0 – 6.8 – 7.0 – 7.6 μm, Q = 1.06 – 1.12 – 1.13 – 1.28, subglobose to broadly ellipsoid; ornamentation amyloid, composed of up to 1.6 μm high, often branched long ridges intermixed with lower short ridges and warts; plage distally amyloid to almost totally amyloid. **Basidia** 36 – 52 × 10.5 – 16.5 μm, 4-spored, narrowly clavate. **Pleuromacrocytidia** absent. **Lamellar edges** consisting of marginal cells, cheiloleptocystidia and basidia; marginal cells narrowly clavate to clavate; cheiloleptocystidia abundant, 37 – 46 × 5.5 – 9 μm, narrowly fusiform to fusiform, apex rounded to mucronate. **Pseudocystidia**

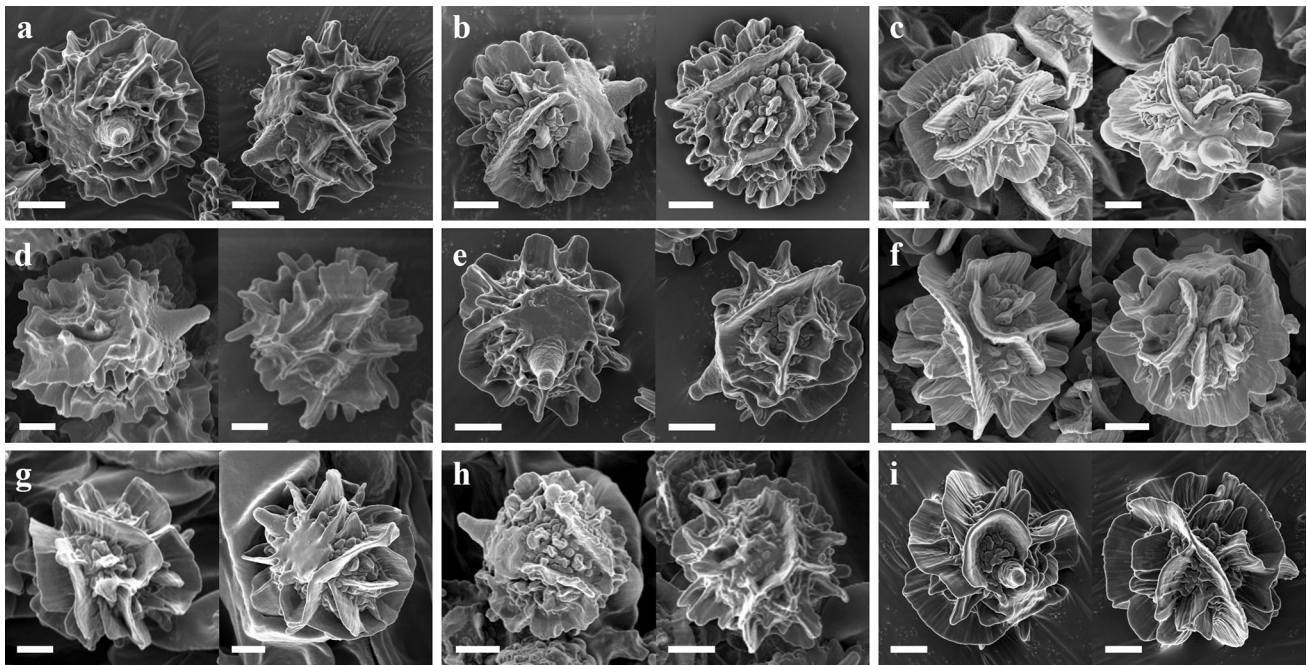


Fig. 30 Basidiospores (SEM) of Korean species of *Lactarius* subg. *Plinthogalus*. **a** *L. albidocinereus*, **b** *L. alboroseus*, **c** *L. alutaceus*, **d** *L. atromarginatus*, **e** *L. aurantiacopallens*, **f** *L. cucurbitoides*, **g** *L.*

fulvescens, **h** *L. incarnatus*, **i** *L. ustulatus*. Scale bar = 2 μ m. **d** and **f** are adapted from Lee et al. (2018) and (2015a), respectively

numerous, aseptate, emergent beyond the hymenium, cylindrical, 3–6 μ m broad, often branched, with refringent contents; apex rounded, *Pileipellis* 150–180 μ m thick, a trichopalisade; terminal hyphae parallel to ascending to erect, cylindrical, apex rounded, terminal cells 20 – 38.5 \times 3 – 4.5 μ m; subpellis composed of globose to ovoid to lanceolate elements 11.5 – 25 \times 10 – 19.5 μ m.

Habitat: Scattered to gregarious on humid soil in mixed forests dominated by *Fraxinus* and *Pinus*.

Additional studied material: SOUTH KOREA, Gangwon-do, Inje-gun, Baekdamsa temple, alt. 533 m, N38°09'12" E128°23'28", 1 Sep 2007 (HCCN15640); Chungcheongnam-do, Geumsan-gun, Mt. Jinak, alt. 383 m, N36°04'51" E127°26'51", 25 Sep 2012 (KA12-1557).

Comments: *Lactarius alboroseus* can be distinguished from a morphologically similar species, *L. incarnatus* (see below) by immediate pinkish discoloration of latex after exposure to air, while the latter species showed slow latex colour change. The host tree of the two species is different: *Lactarius alboroseus* is associated with *Fraxinus* and *Pinus* while *L. incarnatus* with *Quercus*.

Fig. 31 Microscopic features of *Lactarius alboroseus*

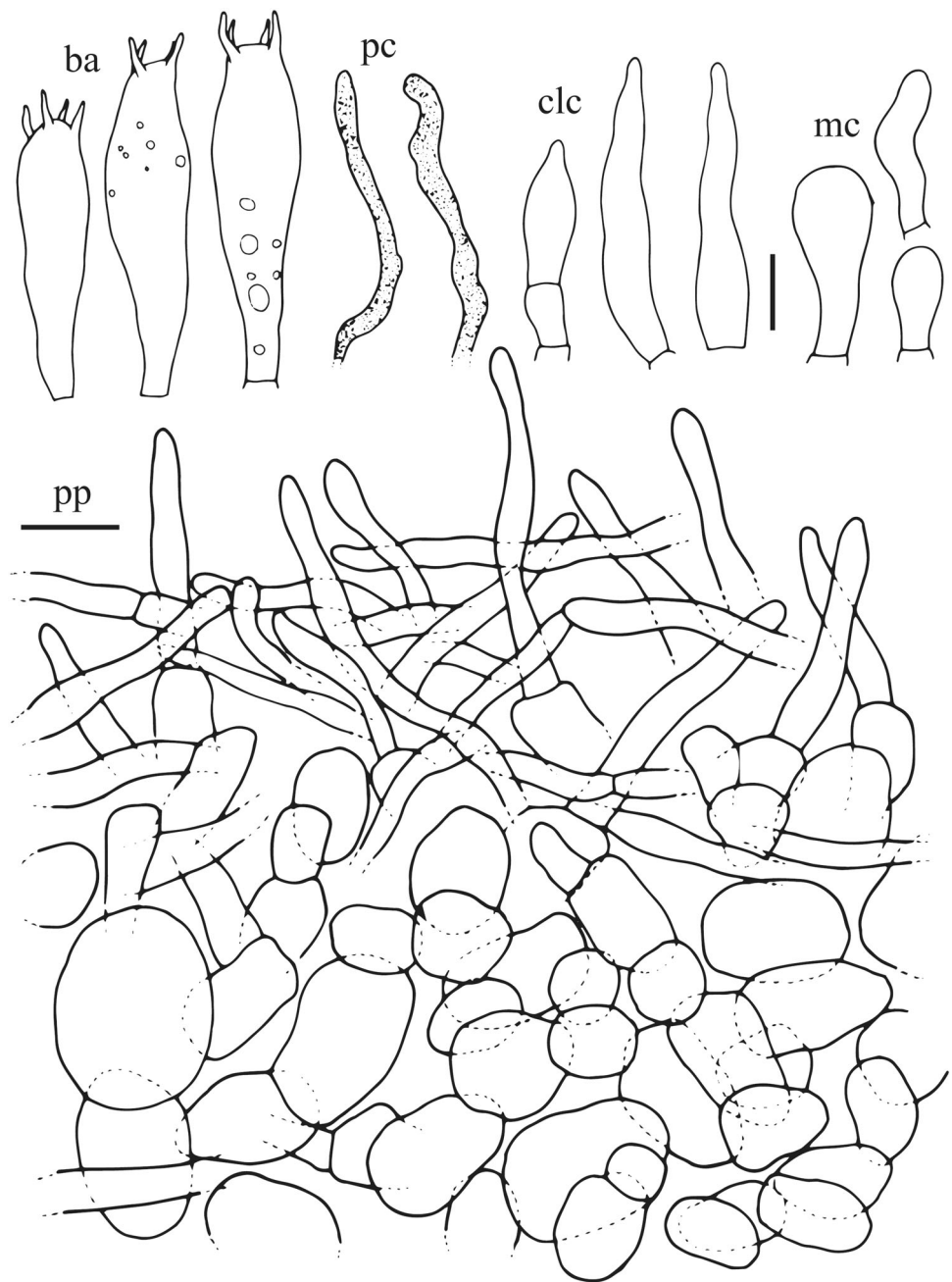
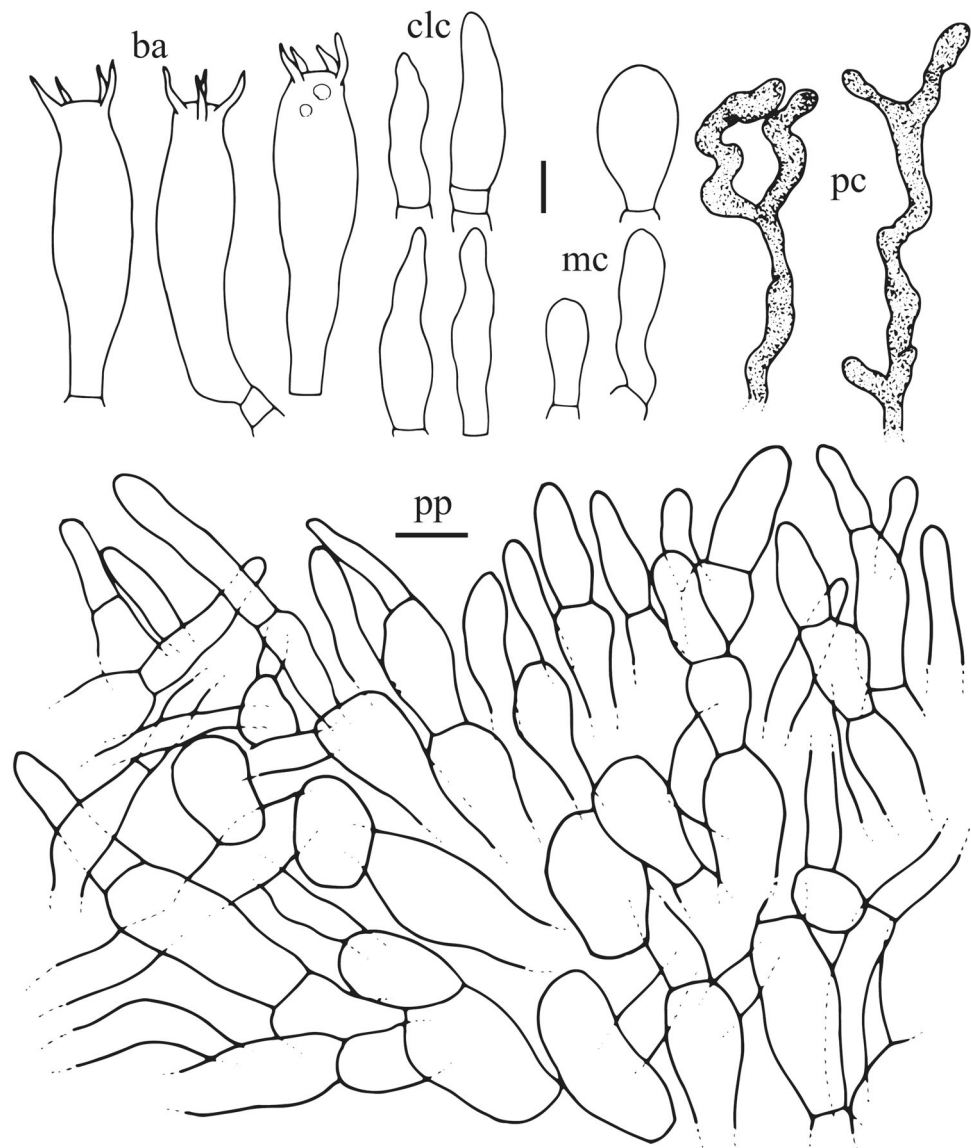


Fig. 32 Microscopic features of *Lactarius alutaceus*



***Lactarius alutaceus* H. Lee, Wisitr. & Y.W. Lim, sp. nov.**

Mycobank: MB 827947

Etymology: ‘alutaceus’ means leather-yellow, referring to the pale and dull yellow colour of the pileus.

Holotypus: SOUTH KOREA, Chungcheongnam-do, Boryeong-si, Seongjusan Natural Recreation Forest, alt. 238 m, N36°20′08″ E126°39′56″, 25 Jul 2012 (SFC20120725-22)

Pileus 20–45 mm diam., convex to applanate with slightly depressed centre; margin decurved, shortly grooved to rugulose, sometimes crenate; surface yellowish white (3A2) to cream (4A3), greyish brown (5D3) at the center, often with greyish brown tinges, dry, slightly tomentose, radially rugose to rugulose in age. **Lamellae** adnate to

slightly deccurrent, distant, never forked, up to 6 mm broad, with only one lamellulae between 2 lamellae, cream to greyish yellow, slowly staining pinkish when bruised. **Stipe** 20–40 × 5–15 mm, cylindrical to tapering downwards, fistulose; surface whitish or concolourous to pileus, often with pale greyish brown tinges, slightly pubescent when young. **Odour** agreeable. **Taste** mild. **Latex** rather scarce, white, unchanging on exposure.

Basidiospores (n = 60), 7.1–7.8–8.0–8.7(–8.9) × 6.6–7.2–7.5–8.1 μm,

Q = 1.01–1.06–1.09–1.14, globose to subglobose; ornamentation amyloid, composed of up to 2.1 μm high, thick ridges and clusters of warts, short ridges between thick ridges, winged; plage distally to almost totally amyloid. **Basidia** 41–50 × 12–14 μm, 4-spored, narrowly clavate. **Pleuromacrocytidia** absent. **Lamellar edges**

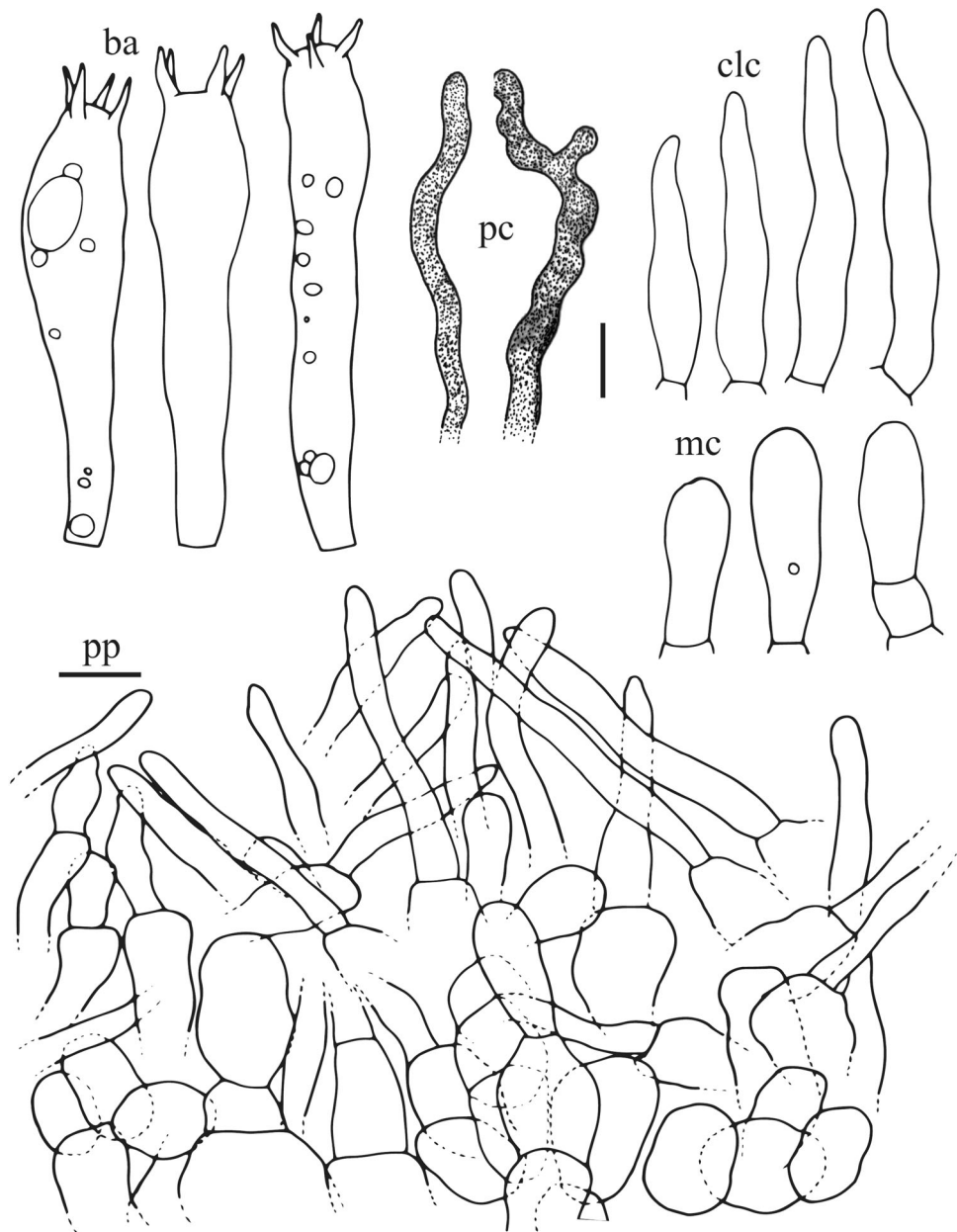
consisting of marginal cells, cheileptocystidia and few basidia; marginal cells narrowly clavate to clavate, sometimes cylindrical; cheileptocystidia abundant, $24.5 - 39.5 \times 5.5 - 8.5 \mu\text{m}$, cylindrical to narrowly fusiform, apex rounded. *Pseudocystidia* numerous, aseptate, emergent from the hymenium, cylindrical, $3 - 4.5 \mu\text{m}$ broad, often branched, filled with granules; apex rounded. *Pileipellis* 100–190 μm thick, a trichopalisade; terminal hyphae erect, cylindrical, terminal cells $10.5 - 23 \times 6.5 - 10 \mu\text{m}$, apex rounded; subpellis composed of inflated to narrowly clavate or ovoid cells, $11.5 - 21 \times 6.5 - 10 \mu\text{m}$.

Habitat: Solitary or scattered on loam or sandy loam soil in forests dominated by *Quercus*.

Additional studied material: SOUTH KOREA, Gangwon-do, Pyeongchang-gun, Mt. Odae, alt. 989 m, N37°46'50" E129°34'20", 23 Aug 1993 (HCCN849G).

Comments: *Lactarius alutaceus* is easily confused with *L. cucurbitoides*. Both species are found in *Quercus* forest in South Korea. However, the new species has greyish brown tinges and less numerous lamellulae while *L. cucurbitoides* is rather pale orange to pale yellow. Microscopically, *L. alutaceus* differs from *L. cucurbitoides* by having pileipellis layer (Lee et al. 2015b) and less helically arranged spore ornamentation.

Fig. 33 Microscopic features of *Lactarius aurantiacopallens*



Lactarius aurantiacopallens H. Lee, Wisitr. & Y.W. Lim, **sp. nov.**

Mycobank: MB 827948

Etymology: ‘aurantiaco’ means orange and ‘pallens’ means pale. The name refers to the unicoloured pale orange basidiomata.

Holotypus: SOUTH KOREA, Jeollabuk-do, Muju-gun, Mt. Deogyu, alt. 614 m, N35°54′03″ E127°46′29″, 28 Aug 2015 (SFC20150828-26)

Pileus 40–90 mm diam., convex to applanate with slightly depressed centre, sometimes with tiny umbo; margin first decurved, in age expanded, even to uneven, sometimes crenate; surface orange white (5A2) to pale brownish orange (6C3), dry, slightly pruinose, slightly tomentose. **Lamellae** adnate to slightly deccurrent, rather crowded, rarely forked near the stipe, up to 4 mm broad, whitish to pale cream when young, yellowish ocher to pinkish buff in age. **Stipe** 50 – 110 × 10 – 15 mm, cylindrical, often tapering downwards, sometimes irregularly compressed, fistulose in age; surface whitish, often with yellowish ocher to pinkish tinges. **Odour** unremarkable. **Taste** acrid. **Latex** abundant, white changing to pink in a few minutes, pale cream when dry.

Basidiospores (n = 60), 6.2 – 6.8 – 7.4 – 8.0 × 5.4 – 6.0 – 6.5 – 7.2 μm, Q = 1.05 – 1.13 – 1.16 – 1.28, mostly subglobose to broadly ellipsoid; ornamentation amyloid, composed of up to 1.8 μm high, often branched long and high ridges and small warts, sometimes forming an incomplete reticulum; plage distally amyloid. **Basidia** 47 – 66 × 10 – 12 μm, 4-spored, narrowly clavate. **Pleuromacrocystidia** absent. **Lamellar edges** consisting of marginal cells, cheiloleptocystidia and basidia; marginal cells cylindrical; cheiloleptocystidia abundant, 22 – 45 × 3.5 – 7 μm, narrowly fusiform, occasionally tortuous, apex rounded. **Pseudocystidia** numerous, aseptate, emergent beyond the hymenium, cylindrical, 3–5 μm broad, branched, contents refringent and crystalline; apex rounded. **Pileipellis** 90–150 μm thick, a trichopalisade to palisade; terminal hyphae erect, cylindrical, terminal cells 16 – 36 × 3 – 4 μm, apex rounded; subpellis composed of globose to inflated cells, 8 – 16.5 × 6 – 10 μm.

Habitat: Solitary or scattered on soil in lowland of mixed forests dominated by *Acer*, *Fraxinus*, and *Quercus*.

Additional studied material: SOUTH KOREA, Gangwon-do, Wonju-si, Mt. Chiak, alt. 403 m, N37°25′02″ E128°56′24″, 5 Sep 2006 (HCCN14564); Gangwon-do, Taebaek-si, Mt. Taebaek, alt. 1119 m, N37°06′42″ E128°56′24″, 24 Jul 2012 (HCCN22693).

Comments: *Lactarius aurantiacopallens* is morphologically similar to two new species, *L. alboroseus* (see above)

and *L. incarnatus* (see below). This species has a thinner pileipellis (90–150 μm thick) than those of *L. alboroseus* (150–180 μm thick) and *L. incarnatus* (150–190 μm thick).

Lactarius fulvescens H. Lee, Wisitr. & Y.W. Lim, **sp. nov.**

Mycobank: MB 827949

Etymology: ‘fulvescens’ means becoming tawny, referring to the orange brown tinges on full-grown specimens.

Holotypus: SOUTH KOREA, Chungcheongbuk-do, Goe-san-gun, Mt. Songni, alt. 360 m, N36°32′33″ E127°50′01″, 4 Sep 2012 (TPML120904-023; **isotypus**, SFC)

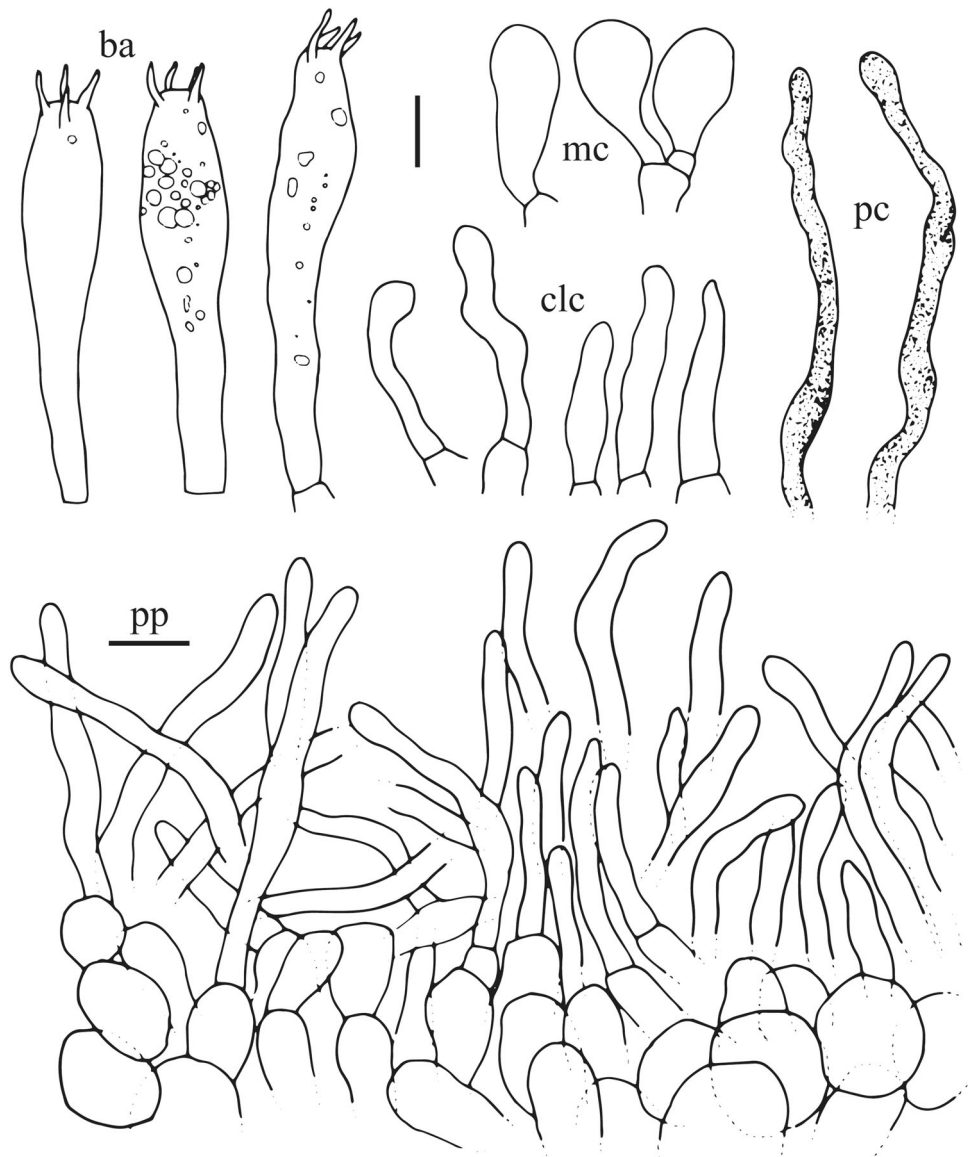
Pileus 30–120 mm diam., convex then applanate to infundibuliform with deeply depressed centre; margin first decurved, in age expanded, often uneven, sometimes crenate; surface dull, cream (4A3) to orange white (5A2), greyish brown (5D3) at the center, dry, tomentose, rugulose in age, azonate when young, later getting faint brownish (5D8) zones near the margin, with light brown tinges. **Lamellae** adnate to slightly deccurrent, rather distant, rarely forked near the stipe, up to 6 mm broad, whitish to pale cream, turning pinkish or unchanging when bruised. **Stipe** 30 – 70 × 8 – 30 mm, cylindrical, sometimes tapering upwards; surface white, pubescent when young, sometimes longitudely striated. **Latex** rather abundant, white, unchanging on exposure.

Basidiospores (n = 60), 7.2 – 8.1 – 9.4 – 10.4 × 6.4 – 7.3 – 8.1 – 9.3 (– 9.7) μm, Q = 1.07 – 1.12 – 1.16 – 1.29, subglobose to broadly ellipsoid; ornamentation amyloid, composed of up to 2.3 μm high, thick and coarse ridges often branched to arranged in zebra-like pattern, short ridges or isolated warts present; plage totally amyloid. **Basidia** 53.5 – 66.5 × 9.5 – 15 μm, 4-spored, narrowly clavate to clavate. **Pleuromacrocystidia** absent. **Lamellar edges** consisting of marginal cells, cheiloleptocystidia and basidia; marginal cells cylindrical to narrowly clavate, occasionally capitate; cheiloleptocystidia abundant, 13 – 37.5 × 3.5 – 6.5 μm, mostly cylindrical, straight to tortuous, apex rounded. **Pseudocystidia** numerous, aseptate, embedded to slightly emergent beyond the hymenium, irregularly cylindrical, straight to tortuous, 2–6 μm broad; apex rounded. **Pileipellis** 60–100 μm thick, a trichopalisade; terminal hyphae mostly erect, cylindrical, terminal cells 16.5 – 36.5 × 3 – 5.5 μm; subpellis composed of globose to narrowly clavate cells, 10.5 – 27.5 × 6 – 15.5 μm.

Habitat: Solitary or scattered on soil in mixed forests dominated by *Pinus* and *Quercus*.

Additional studied material: SOUTH KOREA, Gangwon-do, Donghae-si, alt. 206 m, N37°30′49″ E129°02′54″, 4 Oct 2007 (HCCN15868); *ibid.*, Yeongweol-gun,

Fig. 34 Microscopic features of *Lactarius fulvescens*



Beopheungsa temple, alt. 484 m, N37°22'21" E128°15'26", 8 Sep 2012 (HCCN23574).

Comments: This species is reminiscent of *L. oomsisiensis* Verbeken & Halling reported from Paupa New Guinea, Thailand, and Laos. The latter differs from *L. fulvescens* by

having latex changing to yellow and smaller basidiospores ornamented with an incomplete reticulum (Le et al. 2007b). Another similar species is *L. friabilis* H.T. Le & D. Stubbe from Thailand, which has a similar coloured pileus surface but white latex turning pinkish (Le et al. 2007b).

Lactarius incarnatus H. Lee, Wisitr. & Y.W. Lim, **sp. nov.**

Mycobank: MB 827950

Etymology: ‘incarnatus’ means flesh-coloured or pink, referring to the pink discolouration of latex.

Holotypus: SOUTH KOREA, Chungcheongbuk-do, Boeun-gun, Mt. Songni, alt. 397 m, N36°32'60" E127°50'20", 20 Sep 2011 (TPML110920-069; **isotypus**, SFC)

Pileus 30 – 50 mm diam., convex to applanate with slightly depressed centre, sometimes with tiny umbo; margin first decurved, in age expanded, even to crenate; surface greyish orange (5B3) to brownish orange (6D3), often with greyish brown tinges, dry, pruinose, sometimes rugose in age. *Lamellae* adnate to slightly deccurent, rather crowded, very rarely forked, up to 4 mm broad, whitish to pale cream when young, cream to buff in age. *Stipe* 35 – 60 × 8 – 15 mm, cylindrical, sometimes tapering upwards, fistulose with age; surface whitish to pale ocher, often with yellowish ocher tinges. *Odour* unremarkable, sometimes faintly fruity. *Taste* very acrid. *Latex* rather abundant, white changing to pink in a few minutes, finally drying whitish.

Basidiospores (n = 80), (6.1 –)6.2 – 6.9 – 7.5 – 8.5 × (5.2 –)5.4 – 6.0 – 6.6 – 7.5(– 8.0) μm, Q = 1.05 – 1.11 – 1.15 – 1.28, mostly subglobose to broadly ellipsoid; ornamentation amyloid, composed of up to 1.9 μm high, often forked irregular ridges intermixed with smaller warts; plage distally amyloid. *Basidia* 34.5 – 39 × 11 – 12 μm, 2 or 4-spored, narrowly

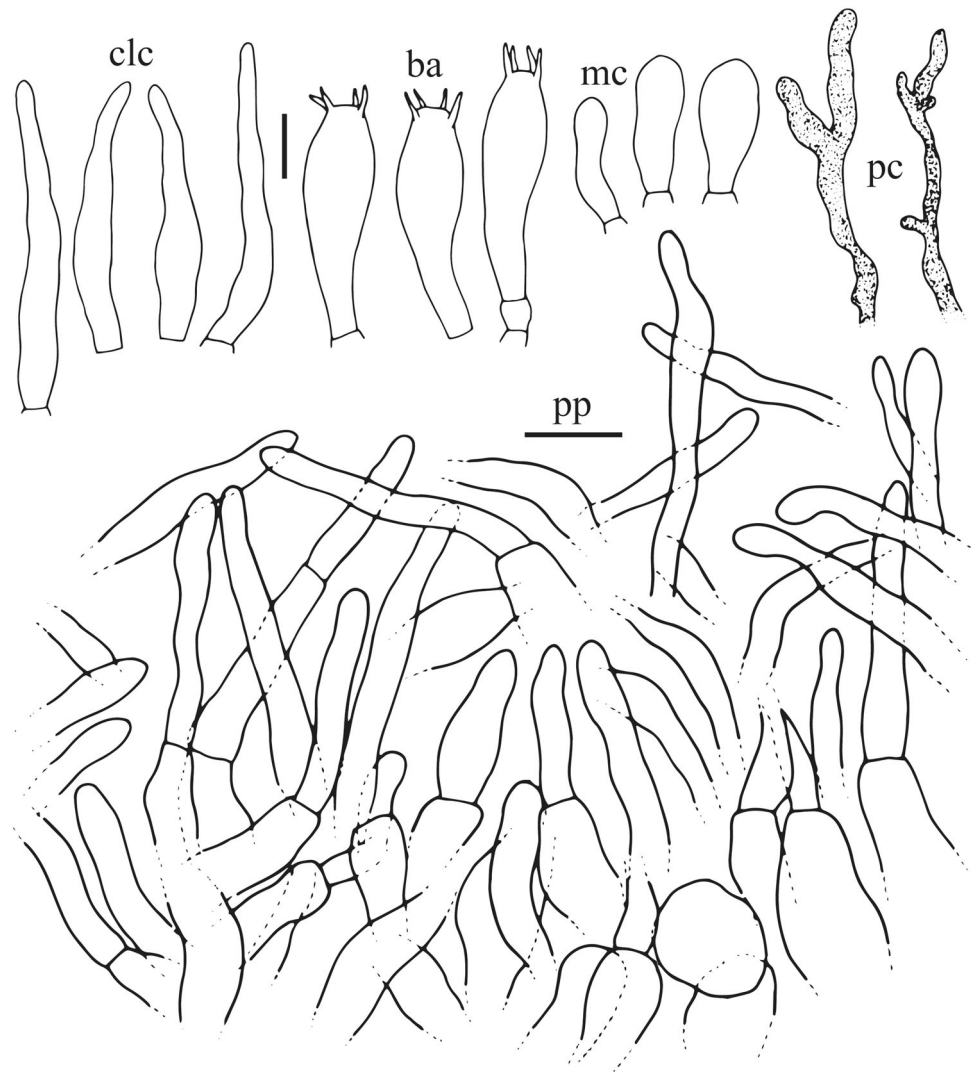
clavate. *Pleuromacrocytidia* absent. *Lamellar edges* consisting of marginal cells, cheiloleptocystidia and basidia; marginal cells cylindrical to narrowly clavate; cheiloleptocystidia abundant, 22 – 45 × 4 – 6 μm, narrowly fusiform, apex rounded. *Pseudocystidia* numerous, aseptate, often emergent beyond the hymenium, cylindrical, 3–4.5 μm broad, branched to tortuous, contents with refringent particles; apex rounded. *Pileipellis* 150–190 μm thick, a trichopalisade; terminal hyphae intricate to erect, cylindrical, terminal cells 20.5 – 50.5 × 3 – 4 μm, apex rounded; subpellis composed of inflated to ovoid cells, 10.5 – 18.5 × 6.5 – 10 μm.

Habitat: Solitary or scattered on humid soil near brooks in forests dominated by *Quercus*.

Additional studied material: SOUTH KOREA, Jeollabuk-do, Muju-gun, Mt. Deogyu, alt. 731 m, N35°53'09" E127°46'26", 7 Jul 2006 (HCCN13840); Gyeonggi-do, Gapyeong-gun, Mt. Yumyeong, alt. 378 m, N37°35'13" E127°29'33", 23 Jul 2010 (HCCN19933).

Comments: *Lactarius incarnatus* is one of the Korean species with pinkish discoloring latex and can be confused with three Asian species (*L. albidocinereus*, *L. alboroseus*, see above, and *L. aurantiacopallens*, see above). The basidiospores of *L. albidocinereus* have modest ornamentation and more interconnections between ridges compared to *L. incarnatus* (Shi et al. 2018). Immediate latex discoloration of *L. alboroseus* and a thin pileipellis of *L. aurantiacopallens* are characters that distinguish these species from *L. incarnatus* (See the descriptions of the species in the present paper).

Fig. 35 Microscopic features of *Lactarius incarnatus*



Lactarius ustulatus H. Lee, Wisitr. & Y.W. Lim, **sp. nov.**

Mycobank: MB 827952

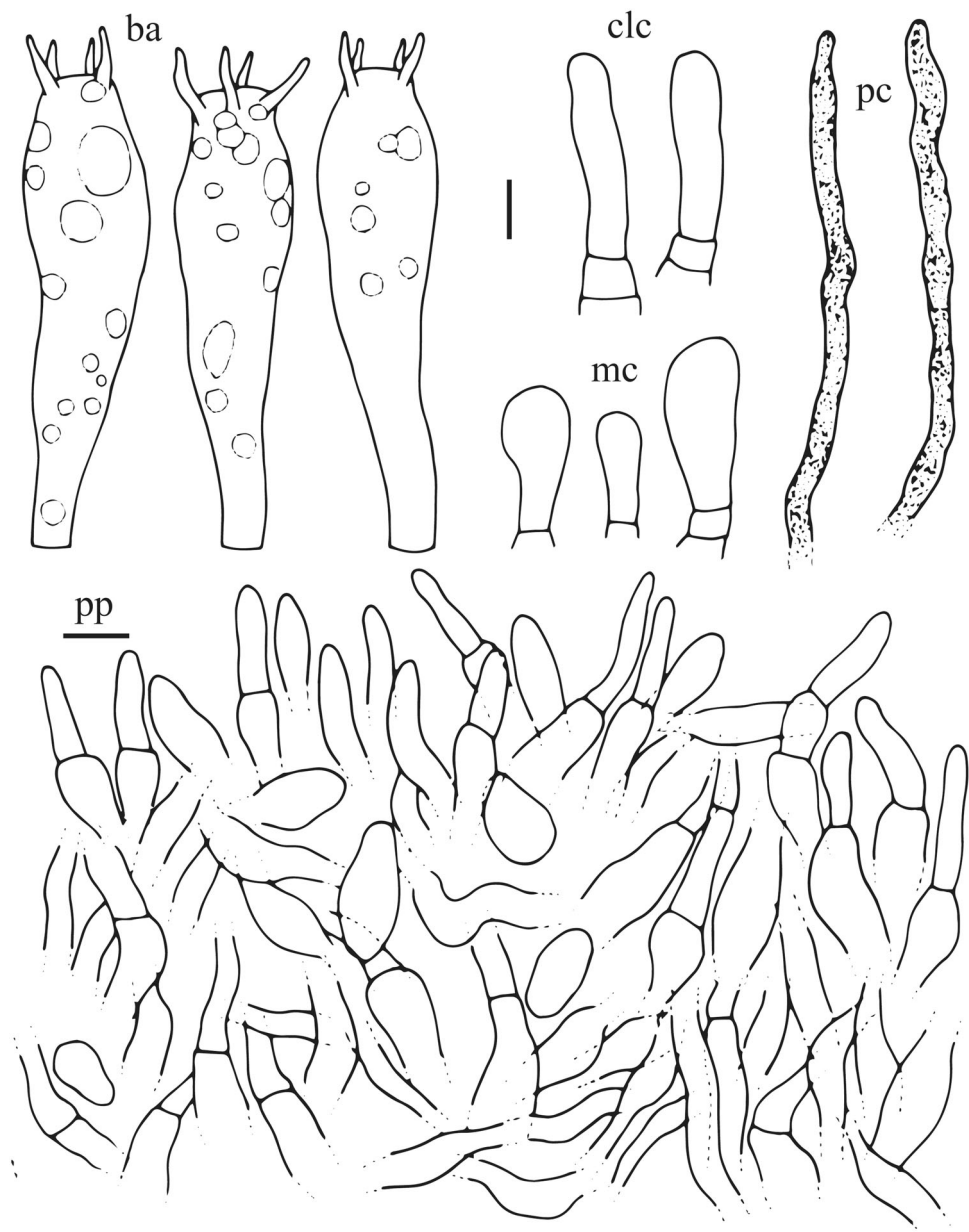
Etymology: ‘ustulatus’ means scorched wood, referring to the blackish brown colour of pileus.

Holotypus: SOUTH KOREA, Gyeonggi-do, Goyang-si, Seo-o-reung Royal Tombs, alt. 60 m, N37°37′47″ E126°53′50″, 26 Jul 2016 (SFC20160726-79)

Pileus 20–70 mm diam., convex to applanate with slightly depressed centre; margin first decurved, in age slightly uplifted, shortly grooved to rugulose, sometimes crenate; surface greyish orange (6B3) to light brown (7D6), dark brown (7F4–6) to almost black at the center, darker toward center, dry, pruinose to velutinous, uneven. *Lamellae* adnate to slightly decurrent, rather distant, very rarely forked near the stipe, up to 10 mm broad, pale cream to greyish orange, turning pinkish slowly when bruised. *Stipe*

20 – 40 × 5 – 18 mm, cylindrical, sometimes tapering downwards, fistulose with age; surface concolourous to pileus, pubescent, sometimes fasciculate with stipes of 2–4 basidiomata. *Odour* unremarkable. *Taste* mild to slightly acrid. *Latex* rather scarce, white, unchanging on exposure. *Basidiospores* (n = 60), 7.6 – 8.4 – 8.8 – 9.6 (– 9.8) × 7.1 – 7.6 – 8.0 – 8.7 (– 8.8) μm, Q = 1.00 – 1.08 – 1.12 – 1.23, globose to broadly ellipsoid; ornamentation amyloid, composed of up to 2.1 μm high, thick ridges and clusters of lower warts, short ridges between the thick ridges; plage distally to almost totally amyloid. *Basidia* 45 – 63 × 11.5 – 16 μm, 4-spored, narrowly clavate to clavate. *Pleuromacrocystidia* absent. *Lamellar edges* consisting of marginal cells, cheiloleptocystidia and few basidia; marginal cells narrowly clavate to clavate, sometimes cylindrical; cheiloleptocystidia numerous, 20.5 – 34.5 × 5.5 – 9 μm, cylindrical to narrowly fusiform, apex rounded.

Fig. 36 Microscopic features of *Lactarius ustulatus*



Pseudocystidia numerous, aseptate, emergent from the hymenium, sometimes projecting between basidia and basidioles, cylindrical, 3–6 μm broad, often branched near the apex; apex rounded. *Pileipellis* 60–125 μm thick, a trichopalisade; terminal hyphae erect, cylindrical, terminal cells 8 – 26 \times 5.5 – 9 μm , apex rounded; subpellis composed of inflated to isodiametric cells, 6 – 19.5 \times 5 – 10 μm .

Habitat: Solitary or scattered on soil with moss or short grass under very old *Acer* and *Quercus* trees in mixed forests.

Additional studied material: SOUTH KOREA, Gyeonggi-do, Guri-si, Dong-gu-reung Royal Tombs, alt. 38 m,

N37°37'07" E127°07'57", 11 Aug 2015 (SFC20150811-51); *ibid.*, Goyang-si, Seo-o-reung Royal Tombs, alt. 54 m, N37°37'58" E126°53'32", 13 Aug 2015 (SFC20150813-63).

Comments: *Lactarius ustulatus* is easily recognized by its dry surface, dark reddish brown with darker center, wrinkled pileus, contrasting lamellae colour, and unchanging white latex. This species can be confused with *L. cucurbitoides*. However, the latter often has a darker lamellae and smaller basidiospores (7.0 – 8.4 \times 6.8 – 8.0 μm) than those of *L. ustulatus* (Lee et al. 2015b).

Discussion

Diversity of *Lactarius* in South Korea

Through a comprehensive analysis of 729 *Lactarius* specimens collected over 57 years, a total of 49 species were identified in a multilocus phylogenetic analysis. Surprisingly, only 17 species were previously described *Lactarius* species, while at least 28 others were confirmed as new species. These results indicate that identification of *Lactarius* species based on morphology alone is insufficient, and that a multilocus phylogenetic approach is necessary. This study also highlights the problems associated with using European and North American nomenclature with Asian *Lactarius* species. Among the 17 previously described species, 15 were described from Asia while only two (*L. tabidus* and *L. vietus*) were conspecific with European species. Our results strongly suggest that Asian *Lactarius* species are rarely conspecific to those of other continents (Le et al. 2007a; Nuytinck et al. 2007; Wisitrassameewong et al. 2016).

Recent studies suggest that the majority of *Lactarius* species do not have intercontinental distributions, but are endemic to specific geographical regions or a single continent (Miller and Hilton 1986; Verbeken and Horak 2000; Verbeken 2001). The low intercontinental conspecificity of *Lactarius* between Asia and Europe or North America is probably due to the geographical barriers such as high mountain ranges and the oceans. On the other hand, Korean species that are also found in Europe, such as *L. tabidus* and *L. vietus*, are associated with a wide range of host trees with a broad distribution such as *Betula* spp. (Heilmann-Clausen et al. 1998; Lee et al. 2018). Many *Lactarius* species are distributed throughout Korean Peninsula due to similar vegetation and host range. Four species (*L. akahatsu*, *L. hatsudake*, *L. laeticolor*, and *L. subzonarius*) that were originally reported from Japan (Tanaka 1890; Hongo 1957b, 1960) are common in East Asia. *L. akahatsu* and *L. hatsudake* have been recorded in pine forests in China (Nuytinck et al. 2006), Japan (Hongo 1977), and Thailand (Le et al. 2007a). *L. subzonarius* was collected in *Abies* forests in this study, which is consistent with previous studies (Hongo 1957b; Nuytinck et al. 2006). *L. atromarginatus* and *L. austrotorminosus* are associated with the Fagaceae in the tropical rain forests of New Guinea and Thailand (Verbeken and Horak 2000; Le et al. 2007a, b). Similarly, Korean samples were found in Fagaceae forests. *Lactarius cinnamomeus* is associated with 2–3-needle pines, *Pinus yunnanensis* in China (Wang 2007) and *P. kesiya* in both Thailand and Vietnam (Wisitrassameewong et al. 2015). It was also collected in 2-needle pine (*P. densiflora*) forest in Korea (this study).

Previously, 49 species belonging to *Lactarius* s.str. were reported in Korea (Lee et al. 2015b), yet only 10 were detected in this study. Of the 39 remaining recorded species, five, 27 and seven species were originally reported from Asia, Europe and North America, respectively. Considering the very low intercontinental conspecificity of *Lactarius*, few European and North American species are likely to be distributed in Korea, and most nomenclature currently on record for Asian species at large is likely incorrect. For example, *L. subatlanticus*, *L. subhirtipes*, and *L. subomphaliformis* were misidentified as the European species *L. camphoratus* (Bull.) Fr. When *L. camphoratus* was reported in Korea, detailed morphological descriptions were not provided (Park et al. 1986). The sequence data from European specimens of *L. camphoratus* (KT165318, Belgium) did not match those of our specimens, and thus *L. camphoratus* does not seem to exist in Korea (*L.* subgenus *Russularia* 1 in Fig. 1). In the case of Asian species, *L. gracilis* Hongo was first described in Japan (Hongo 1957a) and later reported in Korea (Bok and Shin 1985). The Korean specimens labeled as *L. gracilis* were identified as *L. qinlingensis*. However, *L. gracilis* may indeed be present in Korea because it was originally described in Japan and has a wide distribution in Asia (Wang 2007; Wisitrassameewong et al. 2014b). Further study is needed to determine whether the other four Asian species (*L. castanopsidis* Hongo, *L. cyathula* f. *japonicus* Hongo, *L. flavidulus* S. Imai, and *L. sakamotoi* S. Imai) exist in Korea.

Two subgenera (subg. *Russularia* and *Plinthogalus*) of the genus *Lactarius* are supported by the phylogenetic analysis using the ITS, nrLSU, and *rpb2* regions (Stubbe 2012; Verbeken et al. 2014; Wisitrassameewong et al. 2016). However, the basal branch of subg. *Lactarius* is not well supported, nor does it form a clade (Buyck et al. 2008). We used the *mcm7* locus in the phylogenetic analysis because it clarified phylogenetic relationships of many fungal taxonomic groups at taxonomic ranks ranging from genus to class (Schmitt et al. 2009; Tretter et al. 2013). *mcm7* as well as *rpb2* are powerful molecular markers for resolving phylogenetic clades of the genus *Lactarius*, both at low and high taxonomic ranks. However, the monophyly of *L.* subg. *Lactarius* is not supported by sequence data from these two loci.

Morphological characters of Korean *Lactarius* species

Together with genetic information, the use of a combination of characters was effective for species delimitation of the genus *Lactarius*: latex colour and latex discolouration, hispid pileus margin, basidiospore ornamentation, pileipellis structure and the presence/absence of macrocystidia (Stubbe 2012; Wisitrassameewong 2015). As some

morphological characters were previously used for infrageneric classification, similar characters such as pileipellis type, pileus zonation, macrocystidia, and spore ornamentation seem to be important for distinguishing subgenera of *Lactarius*. However, none of these characters clearly support the subgeneric classification when many species are included globally. Rather, there is a tendency to change from the basal subgenus *Plinthogalus* to the derived subgenera, *Lactarius* and *Russularia*: from azonation to zonation, macrocystidia absence to presence, trichopalisade pileipellis to typically (ixo \pm) cutis or trichoderm pileipellis or other forms, white or transparent latex to various colors (Fig. 2).

Most members of the *L.* subg. *Russularia* have a dry surface and orange brown to warm reddish brown basidiomata with unchanging latex (Wisitrassameewong 2015; Wisitrassameewong et al. 2016). Other common characters in this group are diverse pileipellis structures and either cheilo- or pleuro-macrocytidia or both macrocytidia. Nine out of 16 Korean species have unchanging white latex with three possible forms: opaque, translucent, and transparent. Yellow latex discoloration and pileus zonation are shared characters among species in the *chrysorrheus* group within subg. *Russularia* (*L. chrysorrheus*, *L. citrinus*, *L. indochrysorrheus*, *L. lutescens*, *L. vinaceorufescens*, and *L. xanthogalactus*) (Hesler and Smith 1979; Heilmann-Clausen et al. 1998; Wisitrassameewong 2015; Wisitrassameewong et al. 2016). Species in the *quietus* group (*L. aquosus* H.T. Le & K.D. Hyde, *L. quietus* (Fr.) Fr., *L. orientaliquietus*, and *L. subzonarius*) typically have white to watery white latex with zonate pileus and both of cheilo- and pleuro-macrocytidia (Heilmann-Clausen et al. 1998; Wisitrassameewong et al. 2015, 2016). Small sized species (average pileus diameter smaller than 25 mm) were detected in this subgenus. They are phylogenetically closely related and divided into two groups. One group includes four Chinese species (*L. neglectus*, *L. qinlingensis*, *L. subatlanticus*, and *L. subhirtipes*), two Thai species (*L. glabrigracilis* Wisitr. & Nuytinck and *L. perparvus* Wisitr. & F. Hampe), and a Japanese species (*L. gracilis*). Another includes a new Korean species and a European species (*L. omphaliformis*) (Fig. 1).

The sticky surface, pileus zonation, both type of macrocystidia, typically (ixo \pm) cutis or trichoderm pileipellis, presence of scrobicules in the stipe and/or pileus, hairy or woolly pileus margin, and gelatinous pileipellis are general characters in the *L.* subg. *Lactarius* (Hesler and Smith 1979; Heilmann-Clausen et al. 1998; Le et al. 2007a; Nuytinck and Verbeken 2007). Latex colour and discoloration are especially important for specific identification in *L.* subg. *Lactarius* (Hesler and Smith 1979; Heilmann-Clausen et al. 1998). Various colours of latex, zonated pileus, and presence of both types of macrocystida

seem to be autapomorphic. Many Korean species show various latex discoloration: yellow (*L. cremicolor*), buff (*L. ciliatus*), orange brown (*L. reticulisporus*), greenish grey (*L. vietus*), greyish lilac (*L. cyaneocinereus*), and reddish violet (*L. puniceus*). All species in the *uvidus* group, *L. formosus*, *L. dryadophilus* Kühner, *L. repraesentaneus* Britzelm., *L. speciosus*, *L. uvidus*, *L. puniceus*, and *L. cyaneocinereus* have pinkish to violet discoloration of latex. Some species can be easily recognized by basidiospore ornamentation. For example, *L. reticulisporus* has complete reticulate basidiospores and *L. parallelus* has zebroid basidiospores (Fig. 16). Yet, these characters do not reflect phylogenetic signals at any level greater than species.

Lactarius subg. *Plinthogalus* is characterized by a dull greyish or brownish coloured pileus with a dry, velvety, and azonate surface, pinkish context discoloration, trichopalisade pileipellis, absence of macrocystidia and presence of cheileptocystidia (Heilmann-Clausen et al. 1998; Le et al. 2007b; Stubbe et al. 2008; Lee et al. 2015a). These characters appear to be plesiomorphic because this subgenus is located in the basal clade. Korean species have these characters with the exception of *L. fulvescens*, which is easily recognized by its concentric zonation. None of the species found in Korea have macrocystidia. However, three African species (*L. miniatescens* Verbeken & Van Rooij, *L. nudus* R. Heim, and *L. pulchrispermus* Verbeken) and two Southeast Asian species (*L. javanicus* Verbeken & E. Horak and *L. crassiusculus* H.T. Le & D. Stubbe) are known to have macrocystidia (Heim 1955; Verbeken 1996; Verbeken et al. 2001; Van Rooij et al. 2003; Le et al. 2007b). Korean species in clade 8 are closely related to species from South East Asia (*L. friabilis* H.T. Le & D. Stubbe and *L. oomsisiensis* Verbeken & Halling) and North America (*L. subplinthogalus* Coker). This clade is consistent with the Asian-American clade presented by Stubbe (2012). Members in this clade have broad and distantly spaced lamellae and high spore ornamentation (up to 2–2.5 μ m) (Hesler and Smith 1979; Verbeken et al. 2002; Le et al. 2007b). The Korean species in clade 9 are intermingled with species in the European-American clade suggested by Stubbe (2012) (*Lactarius acris* (Bolton) Gray, *L. azonites* (Bull.) Fr., *L. picinus* Fr., *L. pterosporus* Romagn., *L. romagnesii* Bon, *L. ruginosus* Romagn., and *L. subruginosus* J. Blum ex Bon from Europe and *L. fumosibrunneus* A.H. Sm. & Hesler and *L. fumosus* Peck from North America). This is the first report of an Asian species in this clade. The Asian and European species in this clade have pink to red latex discoloration while the North American species have unchanging white latex (Figs. 1 and 2, Hesler and Smith 1979; Heilmann-Clausen et al. 1998). All Korean species in this subgenus also have trichopalisade pileipellis. A few tropical species such as *L.*

mirabilis D. Stubbe et al. and *L.* sect. *pseudofuliginosi*) and one subalpine species, *L. ferruginascens* K. Das et al., in the subg. *Plinthogalus* have ixotrichoderm type pileipellis (Verbeken 2000; Stubbe et al. 2007; Das et al. 2017).

In conclusion, we confirmed 49 species of *Lactarius* from Korea, including at least 28 species new to science, based on morphological and multilocus phylogenetic approaches. Our results show that identification of *Lactarius* species using morphological data alone is often unreliable due to considerable overlap of characters among species. In addition to the combination of defining characters such as pileipellis, macrocystidia, spore ornamentation, and latex colour, the application of molecular methods is necessary for infrageneric classification and species identification in Korean *Lactarius*. Since many previously collected specimens had no associated information regarding host plants, the ecological relevance of *Lactarius* species remains unclear. Therefore, further investigation of the host plants of *Lactarius* is required in order to better understand the general ecology of *Lactarius* species.

Acknowledgements We would like to thank Dr. Soon Ja Seok, Prof. Jong Kyu Lee, Dr. Sang-Kuk Han, and Dr. Changmu Kim for providing sample support. This research was supported by the project on the survey and excavation of Korean indigenous species of the National Institute of Biological Resources (NIBR 201701104 and NIBR 201801105) under the Ministry of Environment of the Republic of Korea.

Open Access This article is distributed under the terms of the Creative Commons Attribution 4.0 International License (<http://creativecommons.org/licenses/by/4.0/>), which permits unrestricted use, distribution, and reproduction in any medium, provided you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons license, and indicate if changes were made.

References

- Basso MT 1999. *Lactarius* Pers. Fungi Europaei, vol. 7. Mykoflora, Alassio
- Bok JD, Shin GC (1985) Taxonomic studies on the genus *Lactarius* of Korea (I). Korean J Mycol 13(4):249–262
- Buyck B, Hofstetter V, Eberhardt U, Verbeken A, Kauff F (2008) Walking the thin line between *Russula* and *Lactarius*: the dilemma of *Russula* subsect. *Ochricompactae*. Fungal Divers 28:15–40
- Buyck B, Hofstetter V, Verbeken A, Walley R (2010) Proposal 1919: to conserve *Lactarius* nom. Cons. (Basidiomycota) with avconserved type. Taxon 59:295–296
- Castresana J (2000) Selection of conserved blocks from multiple alignments for their use in phylogenetic analysis. Mol Biol Evol 17(4):540–552
- Cho HJ, Park MS, Lee H, Oh S-Y, Wilson AW, Mueller GM, Lim YW (2018) A systematic revision of the ectomycorrhizal genus *Laccaria* from Korea. Mycologia 110(5):948–961
- Cléménçon H (1973) Zwei verbesserte Präparierlösungen für die mikroskopische Untersuchung von Pilze. Z Pilzkd 38:49–53
- Cui YY, Cai Q, Tang LP, Liu JW, Yang ZL (2018) The family Amanitaceae: molecular phylogeny, higher-rank taxonomy and the species in China. Fungal Divers 91:5–230
- Darriba D, Taboada GL, Doallo R, Posada D (2012) jModelTest 2: more models, new heuristics and parallel computing. Nat Methods 9(8):772
- Das K, Verbeken A, Nuytinck J (2015) Morphology and phylogeny of four new *Lactarius* species from Himalayan India. Mycotaxon 130(1):105–130
- Das K, Verbeken A, Chakraborty D, Avchar R, Baghela A (2017) Morphological and phylogenetic evidence for two new *Lactarius* species (Russulales, Basidiomycota) from India. Cryptogam Mycol 38(4):453–467
- Eberhardt U, Verbeken A (2004) Sequestrate *Lactarius* species from tropical Africa: *L. angiocarpus* sp. nov. and *L. dolichocaulis* comb. nov. Mycol Res 108(9):1042–1052
- Gardes M, Bruns TD (1993) ITS primers with enhanced specificity for basidiomycetes—application to the identification of mycorrhizae and rusts. Mol Ecol 2:113–118
- Heilmann-Clausen J, Verbeken A, Vesterholt J (1998) The genus *Lactarius*: fungi of Northern Europe, vol 2. Svampetryk, Mundelstrup, DK
- Heim R (1955) Les lactaires d’Afrique intertropicale. Bull Jard Bot l’État Brux 25:1–91
- Herrera M, Montoya L, Bandala VM (2018) Two *Lactarius* species (subgenus *Plinthogalus*) in ectomycorrhizal association with tropical *Quercus* trees in eastern Mexico. Mycologia 110:1033–1046
- Hesler LR, Smith AH (1979) North American species of *Lactarius*. University of Michigan Press, Ann Arbor, p 841
- Hongo T (1957a) Notes on Japanese larger fungi 10. J Jpn Bot 32(5):141–146
- Hongo T (1957b) Notes on Japanese larger fungi 11. J Jpn Bot 32(7):208–214
- Hongo T (1960) Agaricales of Japan 1-3. Russulaceae. Acta Phytotaxon Geobot 18:129–146
- Hongo T (1971) Notulae mycologicae 10. Mem Shiga Univ 21:62–68
- Hongo T (1977) Higher fungi of the Bonin Islands I. Mem Natl Sci Mus (Tokyo) 10:31–41
- Hongo T (1979) Notes on Japanese larger fungi 22. J Jpn Bot 54(10):301–310
- Imai S (1935) Studies on the Agaricaceae of Japan. II. *Lactarius* in Hokkaido. Bot Mag (Tokyo) 49:603–610
- Katoh K, Standley DM (2013) MAFFT multiple sequence alignment software versions 7: improvement in performance and usability. Mol Biol Evol 30:772–780
- Kim CS, Jo JW, Kwag YN, Sung GH, Lee SG, Kim SY, Shin CH, Han SK (2015) Mushroom flora of Ulleung-gun and a newly recorded *Bovista* species in the Republic of Korea. Mycobiology 43(3):239–257
- Kirk PM, Cannon PF, Minter DW, Stalpers JA (2008) Dictionary of the fungi. CAB International, Wallingford, Wallingford
- Kornerup A, Wanscher JH (1978) Methuen handbook of colour, 3rd edn. Eyre Methuen Ltd., London
- Kränzlin F 2005. Fungi of Switzerland, vol 6, Russulaceae: *Lactarius*, *Russula*. Verlag Mykologia, Luzern
- Largent D, Johnson D, Watling R (1977) How to identify mushrooms to genus III: microscopic features. Mad River Press Inc., Eureka, California
- Le HT, Stubbe D, Verbeken A, Nuytinck J, Lumyong S, Desjardin DE (2007a) *Lactarius* in Northern Thailand: 1. *Lactarius* subgenus *Piperites*. Fungal Divers 24:173–224
- Le HT, Stubbe D, Verbeken A, Nuytinck J, Lumyong S, Desjardin DE (2007b) *Lactarius* in Northern Thailand: 2. *Lactarius* subgenus *Plinthogali*. Fungal Divers 27:61–94

- Lee WD, Lee H, Fong JJ, Oh SY, Park MS, Quan Y, Jung PE, Lim YW (2014) A checklist of the Basidiomycetous macrofungi and a record of five new species from Mt. Oseo in Korea. *Mycobiology* 42(2):132–139
- Lee H, Park MS, Jung PE, Fong JJ, Oh SY, Verbeken A, Lim YW (2015a) *Lactarius cucurbitoides* (Russulales, Basidiomycota), a new species from South Korea supported by molecular and morphological data. *Phytotaxa* 205(3):168–176
- Lee YS, Lim YW, Kim JJ, Yun HY, Kim C, Park JY (2015b) National list of species of Korea: Basidiomycota. National Institute of Biological Resources, Korea, p 364
- Lee H, Park MS, Jung PE, Eimes JA, Seok SJ, Lim YW (2017) Re-evaluation of the taxonomy and diversity of *Russula* section *Foetentinae* (Russulales, Basidiomycota) in Korea. *Mycoscience* 58:351–360
- Lee H, Park JY, Wisitrassameewong K, Kim MJ, Park MS, Kim NK, Lee JK, Lim YW (2018) First report of eight milkcap species belonging to *Lactarius* and *Lactifluus* in Korea. *Mycobiology* 46(1):1–12
- Liu YL, Whelen S, Hall BD (1999) Phylogenetic relationships among ascomycetes: evidence from an RNA polymerase II subunit. *Mol Biol Evol* 16:1799–1808
- Matheny PB (2005) Improving phylogenetic inference of mushrooms with RPB1 and RPB2 nucleotide sequences (*Inocybe*, Agaricales). *Mol Phylogenet Evol* 35:1–20
- Matheny PB, Wang Z, Binder M, Curtis JM, Lim YW, Nilsson RH, Hughes KW, Hofstetter V, Ammirati JF, Schoch CL, Langer E, Langer G, McLaughlin DJ, Wilson AW, Frøslev T, Ge Z-W, Kerrigan RW, Slot JC, Yang Z-L, Baroni TJ, Fischer M, Hosaka K, Matsuura K, Seidl MT, Vauras J, Hibbett DS (2007) Contributions of *rpb2* and *tef1* to the phylogeny of mushrooms and allies (Basidiomycota, Fungi). *Mol Phylogenet Evol* 43(2):430–451
- Miller OK, Hilton RN (1986) New and interesting Agarics from Western Australia. *Sydowia* 39:126–137
- Miller MA, Pfeiffer W, Schwartz T (2010) Creating the CIPRES science gateway for inference of large phylogenetic trees. SC10 Workshop on Gateway Computing Environments (GCE10)
- Montoya L, Bandala VM (1996) Additional new records on *Lactarius* from Mexico. *Mycotaxon* 57:425–450
- Montoya L, Bandala VM (2003) Studies on *Lactarius*: a new combination and two new species from Mexico. *Mycotaxon* 85:393–407
- Neuhoff W (1956) Die Milchlinge (*Lactarii*). Die Pilze Mitteleuropas, vol. 2b. Julius Klinkhardt, Bad Heilbrunn Obb
- Nuytinck J, Ammirati JF (2014) A new species of *Lactarius* sect. *Deliciosi* (Russulales, Basidiomycota) from western North America. *Botany* 92(10):767–774
- Nuytinck J, Verbeken A (2003) *Lactarius sanguifluus* versus *Lactarius vinosus*—molecular and morphological analyses. *Mycol Progress* 2(3):227–234
- Nuytinck J, Verbeken A (2007) Species delimitation and phylogenetic relationships in *Lactarius* section *Deliciosi* in Europe. *Mycol Progress* 111:1285–1297
- Nuytinck J, Wang XH, Verbeken A (2006) Descriptions and taxonomy of the Asian representatives of *Lactarius* sect. *Deliciosi*. *Fungal Divers* 22:171–203
- Nuytinck J, Verbeken A, Miller SL (2007) Worldwide phylogeny of *Lactarius* section *Deliciosi* inferred from ITS and glyceraldehyde-3-phosphate dehydrogenase gene sequences. *Mycologia* 99(6):820–832
- Nuytinck J, Verbeken A, Saar I, Lambert H, Bérubé J, Voitek A (2017) *Lactarius splendens*, a second species with white latex in *Lactarius* section *Deliciosi*. *Botany* 95(8):859–863
- Park WH, Lee JH (2011) New wild fungi of Korea. Kyo-Hak Publishing Co., Seoul
- Park SS, Cho DH, Lee JY (1986) The flora of higher fungi in Mt. Jiri Areas (I). *Korean J Mycol* 15:71–75
- Park MS, Fong JJ, Lee H, Oh SY, Jung PE, Min YJ, Lim YW (2013) Delimitation of *Russula* subgenus *Amoenula* in Korea using three molecular markers. *Mycobiology* 414:191–201
- Pegler DN, Fiard JP (1979) Taxonomy and ecology of *Lactarius* (Agaricales) in the Lesser Antilles. *Kew Bull* 33:601–628
- Persoon CH (1797) Tentamen dispositionis methodicae fungorum in classes, ordines, genera et familias, cum supplemento adjecto. Petrum Philippum Wolf, Leipzig
- Rogers SO, Bendich AJ (1994) Extraction of total cellular DNA from plants, algae and fungi. In: Gelvin SB, Schilperoort RA (eds) Plant molecular biology manual. Kluwer Academic Publishers, Boston, pp 183–190
- Romagnesi H (1985) Les Russules d' Europe et d' Afrique du Nord. Reprint with supplement. J. Cramer, Lehre
- Ronquist F, Huelsenbeck JP (2003) MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19:1572–1574
- Rozen S, Skaletsky HJ (2000) Primer3 on the WWW for general users and for biologist programmers. *Methods Mol Biol* 132:365–386
- Sanmee R, Dell B, Lumyong P, Izumori K, Lumyong S (2003) Nutritive value of popular wild edible mushrooms from northern Thailand. *Food Chem* 82(4):527–532
- Schmitt I, Crespo A, Divakar PK, Fankhauser JD, Herman-Sackett E, Kalb K, Nelsen MP, Nelson NA, Rivas-Plata E, Shimp AD, Widhelm T, Lumbsch HT (2009) New primers for promising single-copy genes in fungal phylogenetics and systematics. *Persoonia* 23:35–40
- Schoch CL, Seifert KA, Huhndorf S, Robert V, Spouge JL, Levesque CA, Chen W, Bolchacova E, Voigt K, Crous PW (2012) Nuclear ribosomal internal transcribed spacer (ITS) region as a universal DNA barcode marker for Fungi. *Proc Natl Acad Sci* 109:6241–6246
- Shi SF, Wang XH, Bau T (2018) Three new species of *Lactarius* (Russulaceae, Russulales) from Northeast China. *Mycoscience* 59(3):206–217
- Singer R (1986) The Agaricales in modern taxonomy, 4th edn. Koeltz, Koenigstein
- Singer R, Araujo I, Ivory MH (1983) The ectotrophically mycorrhizal fungi of the neotropical lowlands, especially central Amazonia. *Beih Nova Hedwig* 77:1–352
- Stamatakis A (2006) RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* 22:2688–2690
- Stubbe D (2012) Systematics and phylogeny of *Lactarius* subgenus *Plinthogalus* sensu lato. Ph.D. thesis, Ghent University, Gent, Belgium
- Stubbe D, Verbeken A, Watling R (2007) Blue-staining species of *Lactarius* subgenus *Plinthogali* in Malaysia. *Belg J Bot* 140(2):197–212
- Stubbe D, Nuytinck J, Verbeken A (2008) *Lactarius* subgenus *Plinthogalus* of Malaysia. *Fungal Divers* 32:125–156
- Stubbe D, Nuytinck J, Verbeken A (2010) Critical assessment of the *Lactarius gerardii* species complex (Russulales). *Fungal Biol* 114(2–3):271–283
- Stubbe D, Wang XH, Verbeken A (2012) New combinations in *Lactifluus*. 2. *L.* subg. *Gerardii*. *Mycotaxon* 119(1):483–485
- Suortti T, Von Wright A, Koskinen A (1983) Necatorin, a highly mutagenic compound from *Lactarius necator*. *Phytochemistry* 22(12):2873–2874
- Tamura K, Stecher G, Peterson D, Filipiński A, Kumar S (2013) MEGA6: molecular evolutionary genetics analysis version 6.0. *Mol Biol Evol* 30(12):2725–2729
- Tanaka N (1890) On Hatsudake and Akahatsu, two species of Japanese edible fungi. *Bot Mag (Tokyo)* 4:392–396

- Tretter ED, Johnson EM, Wang Y, Kandel P, White MM (2013) Examining new phylogenetic markers to uncover the evolutionary history of early-diverging fungi: comparing MCM7, TSR1 and rRNA genes for single- and multi-gene analyses of the Kickxellomycotina. *Persoonia* 30:106–125
- Unipal P, Das K, Bhatt RP (2018) Two novel species of *Lactarius* subgenus *Plinthogalus* from Uttarakhand Himalaya. *Phytotaxa* 338(3):255–264
- Uyekli H (1936) Vegetation in the Kwa-San hill and the environs of Suigen. *Bull Agric For College* 5:1–155
- Van Rooija P, De Keselb A, Verbeke A (2003) Studies in tropical African *Lactarius* species (Russulales, Basidiomycota) 11. Records from Benin. *Nova Hedwig* 77(1–2):221–251
- Verbeke A (1996) New taxa of *Lactarius* (Russulaceae) in tropical Africa. *Bull Jard Bot Natl Belgique* 65:197–213
- Verbeke A (2000) Studies in tropical African *Lactarius* species. 8. A synopsis of the subgenus *Plinthogali*. *Persoonia* 17(3):377–406
- Verbeke A (2001) Worldwide systematics of *Lactarius*: a state of art. *Micol Veg Mediterr* 16:71–88
- Verbeke A, Horak E (1999) *Lactarius* (Basidiomycota) in Papua New Guinea. 1. Species of tropical lowland habitats. *Aust Syst Bot* 12(6):767–779
- Verbeke A, Horak E (2000) *Lactarius* (Basidiomycota) in Papua New Guinea. 2. Species of tropical-montane rainforests. *Aust Syst Biol* 13(5):649–707
- Verbeke A, Nuytinck J (2013) Not every milkcap is a *Lactarius*. *Scripta Bot Belgica* 51:162–168
- Verbeke A, Walley R (2010) Fungus flora of tropical Africa vol 2: monograph of *Lactarius* in tropical Africa. National Botanic Garden of Belgium, Belgium
- Verbeke A, Horak E, Desjardin DE (2001) Agaricales of Indonesia. 3. New records of the genus *Lactarius* (Basidiomycota, Russulales) from Java. *Sydowia* 53(2):261–289
- Verbeke A, Bougher NL, Halling R (2002) *Lactarius* (Basidiomycota, Russulaceae) in Papua New Guinea. 3. Two new *Lactarius* species in subgenus *Plinthogali*. *Aust Syst Bot* 15(6):765–771
- Verbeke A, Nuytinck J, Buyck B (2011) New combinations in *Lactifluus*. 1. *L.* subgenera *Edules*, *Lactariopsis* and *Russulopsis*. *Mycotaxon* 118:447–453
- Verbeke A, Van de Putte K, De Crop E (2012) New combinations in *Lactifluus*. 3. *L.* subgenera *Lactifluus* and *Piperati*. *Mycotaxon* 120:443–450
- Verbeke A, Stubbe D, Van de Putte K, Eberhardt U, Nuytinck J (2014) Tales of the unexpected: angiocarpous representatives of the Russulaceae in tropical South East Asia. *Persoonia* 32:13–24
- Vilgalys R, Hester M (1990) Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several *Cryptococcus* species. *J Bacteriol* 172(8):4238–4246
- Vincenot L, Popa F, Laso F, Donges K, Rexer KH, Kost G, Yang ZL, Nara K, Selosse MA (2017) Out of Asia: biogeography of fungal populations reveals Asian origin of diversification of the *Laccaria amethystina* complex, and two new species of violet *Laccaria*. *Fungal Biol* 121:939–955
- Von Wright A, Knuutinen J, Lindroth S, Pellinen M, Widen KG, Seppä EL (1982) The mutagenicity of some edible mushrooms in the Ames test. *Food Chem Toxicol* 20(3):265–267
- Wang XH (2007) Type studies of *Lactarius* species published from China. *Mycologia* 99(2):253–268
- Wang XH (2016) Three new species of *Lactarius* sect. *Deliciosi* from subalpine-alpine regions of central and southwestern China. *Cryptogam Mycol* 37(4):493–508
- Wang XH (2017a) Seven new species of *Lactarius* subg. *Lactarius* (Russulaceae) from southwestern China. *Mycosystema* 36:1463–1482
- Wang XH (2017b) Two new species of *Lactarius* subg. *Russularia* from subalpine regions of southwestern China. *J Fungal Res* 15(4):222–228
- Wang XH (2018) Fungal biodiversity profiles 71–80. *Cryptogam Mycol* 39(4):419–446
- Wang XH, Liu PG (2002) *Lactarius chichuensis* and *L. hirtipes*, two easily confused species. *Mycotaxon* 84:391–400
- Wang XH, Nuytinck J, Verbeke A (2015) *Lactarius vividus* sp. nov. (Russulaceae, Russulales), a widely distributed edible mushroom in central and southern China. *Phytotaxa* 231(1):63–72
- Wang GS, Song Y, Li JW, Xia SY, Qiu LH (2018a) *Lactarius verrucosporus* sp. nov. and *L. nigricans* sp. nov., two new species of *Lactarius* (Russulaceae) from southern China. *Phytotaxa* 364(3):227–240
- Wang XH, Das K, Horman J, Antonin V, Baghela A, Chakraborty D, Hembrom ME, Nakasone K, Ortiz-Santana B, Vizzini A, Hofstetter V, Buyck B (2018b) Fungal biodiversity profiles 51–60. *Cryptogam Mycol* 39(2):211–258
- White TJ, Bruns T, Lee S, Taylor J (1990) Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis MA, Gelfand DH, Sninsky JJ, White TJ (eds) PCR protocols: a guide to methods and applications. Academic Press, San Diego, pp 315–322
- Wisitrassameewong K (2015) Diversity and phylogeny of *Lactarius* subgenus *Russularia* in Southeast Asia. Ph.D. thesis, Ghent University, Gent, Belgium
- Wisitrassameewong K, Nuytinck J, Hyde KD, Verbeke A (2014a) *Lactarius* subgenus *Russularia* (Russulaceae) in Southeast Asia: 1. Species with very distant gills. *Phytotaxa* 158(1):23–42
- Wisitrassameewong K, Nuytinck J, Hampe F, Hyde KD, Verbeke A (2014b) *Lactarius* subgenus *Russularia* (Russulaceae) in South-East Asia: 2. Species with remarkably small basidiocarps. *Phytotaxa* 188(4):181–197
- Wisitrassameewong K, Nuytinck J, Le Thanh H, De Crop E, Hampe F, Hyde K, Verbeke A (2015) *Lactarius* subgenus *Russularia* (Russulaceae) in South-East Asia, 3: new diversity in Thailand and Vietnam. *Phytotaxa* 207(3):215–241
- Wisitrassameewong K, Looney BP, Le HT, De Crop E, Das K, Van de Putte K, Eberhardt U, Jiayu G, Stubbe D, Hyde KD, Verbeke A, Nuytinck J (2016) *Lactarius* subgenus *Russularia* (Basidiomycota, Russulales): novel Asian species, worldwide phylogeny and evolutionary relationships. *Fungal Biol* 120(12):1554–1581
- Yamin-Pasternak S (2008) A means of survival, a marker of feasts: mushrooms in the Russian Far East. *Ethnology* 47(2):95–107
- Zhao Q, Feng B, Yang ZL, Dai YC, Wang Z, Tolgor B (2013) New species and distinctive geographical divergences of the genus *Sparassis* (Basidiomycota): evidence from morphological and molecular data. *Mycol Progress* 12:445–454

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.