Taxonomic study of *Collybiopsis* (Omphalotaceae, Agaricales) in the Republic of Korea with seven new species

Ji Seon Kim\(^1\), Yoonhee Cho\(^1\), Ki Hyeong Park\(^1\), Ji Hyun Park\(^2\), Minkyeong Kim\(^3\), Chang Sun Kim\(^4\), Young Woon Lim\(^1\)

\(^1\) School of Biological Sciences and Institute of Microbiology, Seoul National University, Seoul 08826, Republic of Korea
\(^2\) Water Supply and Sewerage Research Division, National Institute of Environmental Research, Incheon 22689, Republic of Korea
\(^3\) Microorganism Resources Division, National Institute of Biological Resources, Incheon, Republic of Korea
\(^4\) Forest Biodiversity Division, Korea National Arboretum, Pocheon-si 11186, Republic of Korea

Corresponding author: Young Woon Lim (ywlim@snu.ac.kr)

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**Abstract**

*Collybiopsis* is a genus of the gymnopoid/marasmioid complex of the family Omphalotaceae. The classification system of *Collybiopsis* has recently undergone large changes through molecular approaches. The new classification system has not been applied for *Collybiopsis* in the Republic of Korea, and general research on this genus was also lacking. In this study, we analyzed the *Collybiopsis* species in the Republic of Korea by assessing all gymnopoid/marasmioid specimens collected nationwide for ten years by combining morphological approaches and multilocus (ITS + nrLSU) phylogenetic analysis. We thus confirmed that 16 species of *Collybiopsis* are present in the Republic of Korea, including two previously unreported species (*Co. nulloita* and *Co. dichroa*) and seven new species (*Co. albicantipes* sp. nov., *Co. clavicystidiata* sp. nov., *Co. fulva* sp. nov., *Co. orientisubmuda* sp. nov., *Co. subumbilicata* sp. nov., *Co. undulata* sp. nov., and *Co. vellerea* sp. nov.). A thorough examination of the *Collybiopsis* suggested that it is difficult to distinguish or identify the species based on morphological characteristics only; a combined molecular approach is needed for accurate identification. The *Collybiopsis* database of the Republic of Korea is updated, and information on the new species is provided. Five new combinations from *Marasmiellus* to *Collybiopsis* are also proposed (*Co. istanbulensis* comb. nov., *Co. koreana* comb. nov., *Co. omphalodes* comb. nov., *Co. pseudomphalodes* comb. nov., and *Co. ramuliciola* comb. nov.).

**Keywords**

*Collybia*, gymnopoid, *Gymnopus*, ITS, *Marasmiellus*, marasmioid, nrLSU
Introduction

**Collybiopsis** Earle (1909) is a genus of gymnopoid/marasmioid mushrooms belonging to the family Omphalotaceae Bresinsky (Earle 1909; Petersen and Hughes 2021). Species of **Collybiopsis** are characterized by collybioid, gymnopoid, marasmielloid, omphaloid, and pleurotoid basidiomata; free to decurrent lamellae; a central to eccentric, insinititious to subinsinititious stipe; ellipsoid to oblong, inamyloid, and hyaline basidiospores with white sporeprints; presence of caulocystidia; and coralloid or diverticulate terminal elements of pileipellis (Murrill 1915; Singer 1973; Antonín and Noordeloos 1993; Retnowati 2018; Oliveira et al. 2019). Owing to its relatively uncharacteristic basidiocarp and little variation in morphological characteristics, most gymnopoid/marasmioid species were previously placed within the genus **Collybia** Staude (1857) and **Marasmius** Fr. (1835) before molecular identification was introduced actively to taxonomy. However, recent molecular studies have clarified the phylogenetic relationship of gymnopoid/marasmioid species belonging to the family Omphalotaceae and family Marasmiaceae Roze ex Kühner (Wilson and Desjardin 2005; Oliveira et al. 2019).

Initial molecular studies have segregated **Collybia** and **Marasmius** and some species of both genera transferred into several genera such as **Gymnopus** Roussel, **Marasmiellus** Murril, **Rhodocollybia** Singer, etc. (Moncalvo et al. 2002; Mata et al. 2004b; Mata et al. 2004c; Wilson and Desjardin 2005; Hughes et al. 2010; Oliveira et al. 2019; Petersen and Hughes 2017, 2021). Five **Collybia** sections (Iocephalae Halling, Levipedes Quél, Striipedes Quél, Subfumosae Singer, and Vestipedes Quél) were subsumed into **Gymnopus** sensu lato (s.l.) (Mata et. al., 2004c). However, **Gymnopus** s. l. is polyphyletic, and there has been much debate on the delimitation of this genus (Mata et al, 2004c; Wilson and Desjardin 2005; Mata et al. 2006; Oliveira et al. 2019; Petersen and Hughes 2016). Prior to this debate, a monophyletic genus, **Marasmiellus** sensu stricto (s. str.), was proposed (Wilson and Desjardin 2005), with **Marasmiellus juniperinus** Murril as the monotype species (Wilson and Desjardin 2005; Sandoval-Leiva et al. 2016; Oliveira et al. 2019). A recent study showed that if judged congeneric, **Collybiopsis** Earle (1909) has priority over **Marasmiellus** Murril (1915) based on the nomenclature rule (Petersen and Hughes 2021). Hereupon, **Collybiopsis** has been redefined based on the type species, **Collybiopsis ramealis** Earle, with at least 44 closely related species (Petersen and Hughes 2021). All species of **Collybiopsis** and some species of **Gymnopus** sect. **Vestipedes**, as well as some species of **Marasmiellus**, are included in the genus **Collybiopsis** (Petersen and Hughes 2021).

**Collybiopsis** is morphologically similar and phylogenetically close to **Gymnopus** (Desjardin et al. 1999; Mata 2002; Dutta et al. 2015). Both genera are reported to be distinguishable through like types of the terminal element of pileipellis, attachment of lamellae, the character of stipe, basidiospores, and cheilocystidia. However, as the characteristics of each genus cannot be seen as absolute because exceptions exist, and some characteristics overlap, it is difficult to distinguish **Collybiopsis** from **Gymnopus** solely on morphology. Furthermore, the morphological characteristics of their basidiomata vary greatly depending on the environment and developmental stage. Therefore,
Seven new Collybiopsis species

Molecular data play an important role in distinguishing these genera (Antonín and Herink 1999; Hughes et al. 2014; Hughes and Petersen 2015).

Although there have been many taxonomic changes for gymnopoid/marasmioid species, these changes have not been reflected in the gymnopoid/marasmioid species in the Republic of Korea. Since the first report of Collybiopsis confluens (Pers.) R.H. Petersen, as its previous name Collybia confluens Fr. (Kaburagi 1940), nine current Collybiopsis species have been reported until recently (National list of species of Korea 2020). However, they were identified and classified as Collybia, Gymnopus, and Marasmiellus based on their macroscopic morphological features. Owing to the uncertain placement of previous morphologically identified collybioid collections, it was necessary to re-examine Korean collections of collybioids and marasmioids based on molecular data. In this study, we investigated gymnopoid/marasmioid specimens collected over 10 years and deposited in three Korean herbaria based on their molecular analysis. As a result, we provide a list of Collybiopsis species in the Republic of Korea with seven new species.

Methods

Collections of specimens

A total of 372 specimens deposited in three Korean fungal herbarium – Seoul National University Fungus Collection (SFC), Korea National Arboretum (KA), and the National Institute of Biological Resources (NIBR) – were used in this study. The specimens were collected from 2012 to 2021 and stored in dried condition. All specimens were identified based on their morphological characteristics by each herbarium. The collection information (e.g. collection date, collection site, collector, etc.) and the notes of fresh basidiomata of each specimen were provided from each herbarium.

Molecular analysis

Genomic DNA was extracted from each specimen using a modified CTAB DNA extraction protocol (Rogers and Bendich 1994). The primer set ITS1F/ITS4B (Gardes and Bruns 1993) was used to amplify the internal transcribed spacer (ITS) region for all specimens, and the primer set LR0R/LR5 (Vilgalys and Hester 1990; Rehner and Samuels 1994) was used to amplify the nuclear large subunit ribosomal RNA (nrLSU) region. PCR was conducted by a C1000 thermal cycler (Bio-Rad, Richmond, CA, USA) using AccuPower PCR master premix (Bioneer Co., Daejeon, the Republic of Korea). PCR conditions for ITS and nrLSU region 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 amplifications of the PCR products were verified by visualization using 1% agarose gels with EcoDye DNA staining solution (SolGent Co., Daejeon, the Republic of Korea). The PCR products were purified using the ExpinTM PCR Purification Kit (GeneAll Biotechnology, Seoul, the Republic of Korea).
of Korea) following the manufacturer’s instructions. The purified PCR amplicons were sequenced using an ABI Prism 3700 Genetic Analyzer (Life Technologies, Gaithersburg, MD, USA) at Macrogen (Seoul, the Republic of Korea).

All sequences generated in this study were proofread using MEGA version 7 (Kumar et al. 2016). The sequences used for analyses were deposited in GenBank (Table 1). We then selected the closely related sequences from NCBI databases mainly referred to Oliveira et al. (2019) and Petersen and Hughes (2021). After retrieving all published ITS and nrLSU sequences of all Collybiopsis species in GenBank, phylogenetic analyses were performed together with new sequences generated from specimens. The sequences were respectively aligned for each locus using Multiple Alignment Fast Fourier Transform (MAFFT ver. 7) with the L-NSI-I option algorithm (Katoh and Standley 2013). The aligned sequence data were manually checked and edited. The final sequence of each specimen was created as a concatemer by manually attaching the aligned sequences of the two loci. Maximum likelihood (ML) phylogenetic tree was constructed on the CIPRES Science Gateway (Miller et al. 2012) using the GTR+GAMMA model with 1000 bootstrap replicates. Rhodocollybia butyracea Lennox (TFB14382), Rhodocollybia dotae JL Mata and Halling (REH7007), and Rhodocollybia maculate Singer (TFB13989) were used as outgroups (Oliveira et al. 2019). Bootstraps higher than 70% were considered to support a clade and are shown in the tree (Figure 1).

Morphological observation

All specimens were preliminarily observed and macro/micro-structures of two to four representative specimens, which were in the best condition among the specimens, were presented in figures. Photographs and notes of fresh basidiomata taken at the time of collection were used for macro-morphological description. For micro-morphological observations, tissues of dried specimens were rehydrated in 5% (w/v) KOH and mounted in Congo red solution (Clémençon 1973) and Melzer’s reagent. The observation was performed by using a Nikon Eclipse 80i optical microscope (Nikon, Tokyo, Japan) at 20 × to 1000 × magnification. More than thirty basidiospores and more than twenty other microstructures (e.g., basidia, cheilocystidia, etc.) were measured to analyze the microstructures based on the microscopic pictures of specimens stained with Congo red. The Methuen Handbook of Colour (Kornerup and Wanscher 1978) was used for color indications. The following abbreviations and acronyms were used: Co = Collybiopsis; G = Gymnopus; Ma = Marasmiellus; L = the number of complete lamellae; I = the number of lamellulae tiers between neighboring complete lamellae; and Q = the values of the length divided by the width of basidiospores (Petersen and Hughes 2021; Ryoo et al. 2020).

Results

Through ITS sequence analysis of 372 gymnopoid/marasmioid specimens, 201 specimens were confirmed to belong to Collybiopsis. The remaining 160 specimens were
## Table 1. Information about the *Collybiopsis* specimens and published *Collybiopsis* sequences used in phylogenetic analysis. Species with an asterisk are those proposed as new species. Sequences newly produced in this study are presented in bold.

| Organisms              | Specimen       | Collection Date | Location                                      | GenBank Accession Number         |
|------------------------|----------------|-----------------|-----------------------------------------------|----------------------------------|
| **Collybiopsis albicantipes** | SFC20170725-35 | 25.7.2017       | Yeosu-si, Jeollanam-do, the Republic of Korea | OL467272 OL462811                 |
| **Co. bifrons**         | TFB14251       | USA: Tennessee, GSMNP | KJ416245 JI189567                           |
|                        | TFB13890       | USA: North Carolina | KJ416248 JI189570                           |
|                        | TFB13814       | USA: Tennessee   | KJ416249 JI189569                           |
| **Co. biformis**        | KA14-0526      | 15.7.2014       | Suncheon, Jeollanam-do, the Republic of Korea | OL467227 OL462784                 |
|                        | KA16-0526      | 13.7.2016       | Sunan-gun, Jeollanam-do, the Republic of Korea | OL467228 OL462785                 |
| **Co. bruneigracilis**  | SFC20180831-16 | 31.8.2018       | Jindo-gun, Jeollanam-do, the Republic of Korea | OL467230 OL462790                 |
| **Co. clavicystidiata** | SFC20180705-26 | 5.7.2018        | Haemam-gun, Jeollanam-do, the Republic of Korea | OL467250 OL462816                 |
| **Co. confluens**       | SFC20180705-84 | 5.7.2018        | Jindo-gun, Jeollanam-do, the Republic of Korea | OL467252 OL462817                 |
|                        | SFC20180705-92 | 5.7.2018        | Jindo-gun, Jeollanam-do, the Republic of Korea | OL467252 OL462817                 |
|                        | SFC20180713-09 | 13.7.2018       | Gwanak-gu, Seoul, the Republic of Korea       | OL467251 OL462819                 |
| **Co. confluens ssp. americana** | TFB14409 | Canada: New Brunswick | KJ710278 KJ189585                           |
|                        | TFB14075       | USA: North Carolina | KJ710281 KJ189581                           |
| **Co. dichroa**         | KA14-0969      | 19.8.2014       | Hwasan-gun, Jeollanam-do, the Republic of Korea | OL467254 OL462799                 |
| **Co. disjuncta**       | KA18-0389      | 10.7.2018       | Cheongdo-gun, Gyeongsangbuk-do, the Republic of Korea | OL467255 OL462864                 |
| **Co. eneficola**       | SFC20180712-16 | 12.7.2018       | Gwangju, Gyeonggi-do, the Republic of Korea   | OL467256 OL462800                 |
|                        | TEB9623        | USA: North Carolina | MW396865 MW396865                           |
|                        | TEB97920       | USA: North Carolina | JF313671                                    |
|                        | TEB9720        | USA: North Carolina | DQ500007                                    |
|                        | TEB99614c2     | USA: North Carolina | JF313672                                    |
|                        | TEB2028        | USA: North Carolina | DQ500008                                    |
|                        | TEB14115       | Germany, Thuringia | KJ710292                                    |
|                        | 110116MBPL0425 | China           | MW554401                                    |
|                        | HMAS 290186    | China           | M396541                                     |
| **Ca. confluens**       | TFB14409       | Canada: New Brunswick | KJ710278                                    |
|                        | TFB14075       | USA: North Carolina | KJ710281                                    |
| **Co. confluens ssp. americana** | TFB14409 | Canada: New Brunswick | KJ710278                                    |
|                        | TFB14075       | USA: North Carolina | KJ710281                                    |
| **Co. dichroa**         | KA14-0969      | 19.8.2014       | Hwasan-gun, Jeollanam-do, the Republic of Korea | OL467254 OL462799                 |
| **Co. disjuncta**       | KA18-0389      | 10.7.2018       | Cheongdo-gun, Gyeongsangbuk-do, the Republic of Korea | OL467255 OL462864                 |
| **Co. eneficola**       | SFC20180712-16 | 12.7.2018       | Gwangju, Gyeonggi-do, the Republic of Korea   | OL467256 OL462800                 |
|                        | TEB9623        | USA: North Carolina | MW396865 MW396865                           |
|                        | TEB9720        | USA: North Carolina | JF313671                                    |
|                        | TEB97920       | USA: North Carolina | DQ500007                                    |
|                        | TEB99614c2     | USA: North Carolina | JF313672                                    |
|                        | TEB2028        | USA: North Carolina | DQ500008                                    |
|                        | TEB14115       | Germany, Thuringia | KJ710292                                    |
|                        | 110116MBPL0425 | China           | MW554401                                    |
|                        | HMAS 290186    | China           | M396541                                     |
| **Co. confluens**       | TFB14409       | Canada: New Brunswick | KJ710278                                    |
|                        | TFB14075       | USA: North Carolina | KJ710281                                    |
| **Co. confluens ssp. americana** | TFB14409 | Canada: New Brunswick | KJ710278                                    |
|                        | TFB14075       | USA: North Carolina | KJ710281                                    |
| **Co. dichroa**         | KA14-0969      | 19.8.2014       | Hwasan-gun, Jeollanam-do, the Republic of Korea | OL467254 OL462799                 |
| **Co. disjuncta**       | KA18-0389      | 10.7.2018       | Cheongdo-gun, Gyeongsangbuk-do, the Republic of Korea | OL467255 OL462864                 |
| **Co. eneficola**       | SFC20180712-16 | 12.7.2018       | Gwangju, Gyeonggi-do, the Republic of Korea   | OL467256 OL462800                 |
|                        | TEB9623        | USA: North Carolina | MW396865 MW396865                           |
|                        | TEB9720        | USA: North Carolina | JF313671                                    |
|                        | TEB97920       | USA: North Carolina | DQ500007                                    |
|                        | TEB99614c2     | USA: North Carolina | JF313672                                    |
|                        | TEB2028        | USA: North Carolina | DQ500008                                    |
|                        | TEB14115       | Germany, Thuringia | KJ710292                                    |
|                        | 110116MBPL0425 | China           | MW554401                                    |
|                        | HMAS 290186    | China           | M396541                                     |
| **Co. confluens**       | TFB14409       | Canada: New Brunswick | KJ710278                                    |
|                        | TFB14075       | USA: North Carolina | KJ710281                                    |
| **Co. confluens ssp. americana** | TFB14409 | Canada: New Brunswick | KJ710278                                    |
|                        | TFB14075       | USA: North Carolina | KJ710281                                    |
| **Co. dichroa**         | KA14-0969      | 19.8.2014       | Hwasan-gun, Jeollanam-do, the Republic of Korea | OL467254 OL462799                 |
| **Co. disjuncta**       | KA18-0389      | 10.7.2018       | Cheongdo-gun, Gyeongsangbuk-do, the Republic of Korea | OL467255 OL462864                 |
| **Co. eneficola**       | SFC20180712-16 | 12.7.2018       | Gwangju, Gyeonggi-do, the Republic of Korea   | OL467256 OL462800                 |
|                        | TEB9623        | USA: North Carolina | MW396865 MW396865                           |
|                        | TEB9720        | USA: North Carolina | JF313671                                    |
|                        | TEB97920       | USA: North Carolina | DQ500007                                    |
|                        | TEB99614c2     | USA: North Carolina | JF313672                                    |
|                        | TEB2028        | USA: North Carolina | DQ500008                                    |
|                        | TEB14115       | Germany, Thuringia | KJ710292                                    |
|                        | 110116MBPL0425 | China           | MW554401                                    |
|                        | HMAS 290186    | China           | M396541                                     |
| Organisms        | Specimen     | Collection Date | Location                  | GenBank Accession Number |
|------------------|--------------|-----------------|---------------------------|--------------------------|
| Co. indoctus     | AWW04        | Unknown         |                           |                          |
| Co. istanbulensis| KATO Fungi 3596 | 21.7.2015       | Turkey                    |                          |
| Co. juniperina   | TFB9889      | USA: Louisiana  |                           |                          |
| Co. koreana      | SFC20120821-84 | 21.8.2012       | Boryeong-si, Chungcheongnam-do, the Republic of Korea | OL467269 OL546545 |
| Co. koreana      | SFC20130711-05 | 11.7.2013       | Pyeongchang-gun, Gangwon-do, the Republic of Korea | OL467270 OL462801 |
| Co. luxarienus   | NIBRFG0000502888 | 4.9.2018        | Ongjin-gun, Incheon, the Republic of Korea | OL467248 OL462803 |
| Co. melanopus    | TFB10350     | USA: North Carolina |                           |                          |
| Co. melanopus    | ZD16102301   | China           |                           |                          |
| Co. menehune     | TFB11005     | Costa Rica      |                           |                          |
| Co. mesoamericana| TENN 68165   | Hawaii          |                           |                          |
| Co. minor        | TFB11930     | USA: Tennessee, GSMNP |             |                          |
| Co. neotropica   | TFB10416     | Costa Rica      |                           |                          |
| Co. nonnulla     | KA13-0254    | Geochang-gun, Gyeongsangnam-do, the Republic of Korea | OL467242 OL462820 |
| Co. nonnulla     | KA13-0741    | Geochang-gun, Gyeongsangnam-do, the Republic of Korea | OL467243 OL462807 |
| Co. orientisubnuda* | NIBRFG0000500990 | 19.7.2016 | Ulleung-gun, Gyeongsangbuk-do, the Republic of Korea | OL467262 OL546546 |
| Co. orientisubnuda (as Gymnopus subnuda) | KUC20150911-19 | Korea |                           |                          |
| Co. parvula      | TFB10419     | Costa Rica      |                           |                          |
| Co. parvula      | TFB10422     | Costa Rica      |                           |                          |
### Seven new *Collybiopsis* species

| Organisms          | Specimen          | Collection Date | Location                                      | GenBank Accession Number |
|--------------------|-------------------|-----------------|-----------------------------------------------|--------------------------|
|                    |                   |                 |                                               |                          |
| Co. peronata       | TFB13743          |                 | Belgium                                       | KY026677                 |
|                    | LE-Bin1364        |                 | Russia                                        | KY026755                 |
|                    | CBS 223.37        |                 | unknown                                       | MH855896                 |
| Co. polygramma     | SFC20170807-35    | 7.8.2017        | Hapcheon-gun, Gyeongsangnam-do, the Republic of Korea | OL467245 OL546542 |
|                    | SFC20180905-63    | 5.9.2018        | Gwanak-gu, Seoul, the Republic of Korea       | OL467246 OL546544 |
|                    | SFC20210629-01    | 29.6.2021       | Gwanak-gu, Seoul, the Republic of Korea       | OL467247 OL546543 |
|                    | PR2542TN          |                 | Puerto Rico                                   | DQ450028                 |
|                    | CUH:AM082         |                 | India                                         | KJ778752                 |
|                    | URM 90015         | 7.8.2017        | Brazil: Amapa                                 | KY074640                 |
|                    | MHHNU 30912       |                 | China                                         | MK214392                 |
|                    | TFB9628           |                 | Puerto Rico                                   | KY026728                 |
|                    | SFC20120821-64    |                 | Korea                                         | KY026736                 |
|                    | HFJAU 0425        |                 | China: Jiangxi                                | MN258643                 |
|                    | KUC20140804-02    |                 | Korea                                         | KX513745                 |

(as *Gymnopus iscehalus*)

| Co. pseudoxarianus | TFB14290          |                 | USA: Mississippi                              | NR_137863                |
| Co. pseudomphalodes | PR24TN            |                 | Costa Rica                                    | AF505762                 |
| Co. quercophila    | TFB14570          |                 | Slovakia                                      | KY026728                 |
|                    | TFB14615          |                 | USA: California                               | KY026736                 |

| Co. namadisi       | NIBRFG00005088888 | 29.7.2020       | Jeongseon-gun, Gangwon-do, the Republic of Korea | OL467260 OL546549 |
|                    | TFB13769          |                 | Belgium                                       | MN413345 MN413345        |
|                    | TFB13770          |                 | Belgium                                       | MN413346 MW396882        |
|                    | DED4425           |                 | USA: North Carolina                           | DQ450031 AF402650        |
|                    | TFB14555          |                 | Slovakia                                      | WM405779 WM396884        |
|                    | BR 72_41          |                 | Belgium                                       | MW396875 WM396875        |
| Co. namadicola     | GDGM 43884        |                 | China                                         | KU577798                 |
|                    | GDGM 44256        |                 | China                                         | KU321529                 |
|                    | GDGM 50860        |                 | China                                         | KU321530                 |

| Co. readiae        | TFB7571           |                 | New Zealand                                   | DQ450034                 |
|                    | PDD-95844         |                 | New Zealand                                   | HQ533036                 |

| Co. stenophylla    | TFB13998          |                 | USA: Tennessee,                               | MN413331 MW396886        |
|                    | TFB4798           |                 | USA: Georgia                                  | MN413330 MW396887        |

| Co. subazathiformis| TFB9629           |                 |                                           |                          |
|                    | URM 90023         |                 | Brazil: Para                                  | KY404982                 |
|                    | URM 90022         |                 | Brazil: Para                                  | KY404983                 |

| Co. subnuda        | TFB12577          |                 | USA: Tennessee, GSNMP                         | KY026667 HJ502626        |
|                    | WWR 08-462        |                 | USA: West Virginia                            | KY026765 KY026765        |
|                    | TFB14043          |                 | USA: North Carolina                           | WM396876 WM396876        |

| Co. subpruinosus   | BRNM781138        |                 | Portugal: Madeira                             | MK646034                 |
|                    | TFB11063          |                 | USA                                           | DQ450025                 |

| Co. subumbilicata* | SFC20120802-03    | 2.8.2012        | Goseong-gun, Gangwon-do, the Republic of Korea | OL467231 OL462786        |
|                    | SFC20140701-03    | 1.7.2014        | Inje-gun, Gangwon-do, the Republic of Korea   | OL467232 OL462787        |
|                    | SFC20150902-50    | 2.9.2015        | Ulleung-gun, Gyeongsanghuk-do, the Republic of Korea | OL467234 OL546540 |
|                    | SFC20170822-14    | 22.8.2017       | Ulleung-gun, Gyeongsanghuk-do, the Republic of Korea | OL467233 OL462788 |
| Co. tregoides      | AWW51             |                 | Indonesia                                     | AY263428 AY639431        |

| Co. undulata*      | SFC20120821-04    | 21.8.2012       | Boryeong-si, Chongcheongnam-do, the Republic of Korea | OL467239 OL462813 |
|                    | SFC20130808-08    | 8.8.2013        | Sangju-si, Gyeongsanghuk-do, the Republic of Korea | OL467240 OL462814        |
|                    | SFC20150813-04    | 13.8.2015       | Goyang-si, Gyeonggi-do, the Republic of Korea   | OL467241 OL462815        |
identified as members of the following genera: *Gymnopus*, *Marasmius*, or *Rhodocollybia* and were excluded from this study. A total of 201 specimens were segregated into 16 putative taxa based on ITS phylogenetic analyses (Table 2). To confirm the species’ identity and to infer the phylogenetic relationships within *Collybiopsis*, the nrLSU region was amplified and sequenced from 47 representative specimens of 16 taxa (Table 1). The final phylogenetic analyses were conducted with datasets of two loci from 16 *Collybiopsis* species (Table 1). In ML analysis, 178 multigene sequences (110 for ITS and 68 for nrLSU) were retrieved from GenBank and used. The adjusted alignments comprised 535 to 794 bases for ITS and 324 to 904 bases for nrLSU. The phylogenetic analysis results of the two combined loci revealed that *Collybiopsis* specimens from the Republic of Korea were identified as 16 taxa (Fig. 1).

Of the 16 putative taxa, nine matched with previously described species – *Co. utriformis* (Peck) R.H. Petersen, *Co. confluens*, *Co. dichroa* (Berk. & M.A. Curtis) Earle, *Co. luxurians* (Peck) R.H. Petersen, *Co. menehune* (Desjardin, Halling & Hemmes) R.H. Petersen, *Co. nonnulla* (Corner) R.H. Petersen, *Co. polygramma* (Mont.) R.H. Petersen, *Co. ramealis* (Bull.) Earle, and *Marasmiellus koreanus* Antonín, Ryoo & H.D. Five species (*G. omphalodes* Halling & J.L. Mata, *G. pseudomphalodes* J.L. Mata, *G. ramulicola* T.H. Li & S.F. Deng, *Ma. istanbulensis* E. Sesli, Antonín and E.Aytaç, and *Ma. koreanus*), previously placed in *Gymnopus* section *Vestipedes*, were confirmed to be-

| Organisms | Specimen | Collection Date | Location | GenBank Accession Number |
|-----------|----------|----------------|----------|--------------------------|
| Co. utriformis | TFB14334h1 | USA: Connecticut | KY026708 KY026708 |
| WRW05-1170 | USA: West Virginia | KY026764 KY026764 |
| Co. vellerea | NIBRFG0000502858 | 4.9.2018 Ongjin-gun, Incheon, the Republic of Korea | OL467265 OL462791 |
| SFC20120708-02 | 8.7.2012 Seonan-si, Chungcheongnam-do, the Republic of Korea | OL467266 OL462809 |
| SFC20140821-29 | 21.8.2014 Gwanak-gu, Seoul, the Republic of Korea | OL467267 OL462810 |
| SFC20180705-90 | 5.7.2018 Jindo-gun, Jeollanam-do, the Republic of Korea | OL467268 OL462792 |
| Co. vallianti | TFB13739 | USA: Tennessee, GSMNP | KY026676 KY026676 |
| Co. villeippe | TFB9539 | USA | DQ590058 |
| TFB12836 | New Zealand: Fiordland | KJ416255 KJ750264 |
| Collybiopsis cf. ramealis | SFC20180829-20 | 29.8.2018 Shimon-gun, Jeollanam-do, the Republic of Korea | OL467261 OL546548 |
| Rhodocollybia butyracea | TFB 14382 | Canada: New Brunswick | KY026716 KY026716 |
| Rhodocollybia dotae | REH7007 | Costa Rica | AF505758 |
| Rhodocollybia maculata | TFB 13989 | USA: Mississippi | KY026688 KY026688 |
Seven new *Collybiopsis* species long to the genus *Collybiopsis*, and we thus propose to reclassify them as *Co. omphalodes* comb. nov., *Co. pseudomphalodes* comb. nov., *Co. ramulicola* comb. nov., *Co. istanbulensis* comb. nov., and *Co. koreana* comb. nov. respectively.
Figure 1. Phylogenetic tree based on maximum likelihood analysis using combined sequence data of ITS and nrLSU. ML bootstrap values greater than 70% are indicated at the nodes. Collybiopsis species that were newly sequenced in this study are represented in bold. Species with an asterisk are those proposed as new species.
Seven new *Collybiopsis* species

*Collybiopsis albicantipes* J.S. Kim & Y.W. Lim, sp. nov.

MycoBank No: 842053

Fig. 3A–B, Suppl. material 1: Fig. S1A

**Etymology.** Epithet “*albicantipes*” refers to having a whitish base of the stipe.

**Holotype.** The Republic of Korea, Jeollanam-do: Yeosu-si, Dolsan-eup, Hyangiram, 34°35'27"N, 127°47'55"E, alt. 183 m, 25 July 2017, Jae Young Park, Komsit Wisitrassameewong, SFC20170725–35 (GenBank accession no. ITS: OL467272; nrLSU: OL462811).

**Diagnosis.** This species notably has hemispherical to convex, 4–23 mm pileus, distant lamellae, central to eccentric, tomentose, 5–15 × 0.5–1.5 mm stipe with a white base; ellipsoid to ovoid, 5.8–7.4 × 2.8–4 μm basidiospores, clavate (often constricted), 25.5–34.8 × 4.8–6.7 μm basidium, broadly clavate, irregular, sometimes lobed, 26–49 × 5.4–10.6 μm cheilocystidia, and a habit of fruiting on branches.

**Description.** Pileus: 4–23 mm, eccentric, convex to hemispherical when young, becoming depressed and undulating with age; Surface smooth, brownish orange (5C3 to 6D4) at the center, becoming paler to the margin (4A3 to 3A2). Lamellae: distant,
Figure 3. Basidiomata and microscopic characters of the four new Collybiopsis species A, B Co. albicantipes (SFC20170725–35) C, D Co. clavicystidiata (SFC20180705–84) E, F Co. fulva (KA15–0210) G, H Co. orientisubnuda (NIBRFG0000502862). Scale bars: 1cm (A, C, E, G); 20 µm (B, D, F, H). Abbreviations: s basidiospores; b basidia; ch cheilocystidia; p pleurocystidia; ca caulocystidia.
Seven new Collybiopsis species

Collybiopsis clavicystidiata J.S. Kim & Y.W. Lim, sp. nov.
MycoBank No: 842054
Fig. 3C–D, Suppl. material 1: Fig. S1B

Etymology. Epithet “clavicystidiata” indicates that the new species has clavate cheilocystidia.

Holotype. The Republic of Korea, Jeollanam-do: Jindo-gun, Jodo-myeon, Donggeocha island, 34°23′34″N, 125°93′84″E, alt. 70 m, 05 July 2018, Jae Young Park, Tae Heon Kim, SFC20180705–84, (GenBank accession no. ITS: OL467252; nrLSU: OL462817).

Diagnosis. The prominent features of this species include a greyish orange to brownish, 6–45 mm pileus, whitish lamellae, a subinstitituous, tomentose, whitish, 15–

L = 10–16, l = 3–7, adnate, whitish to yellowish white (3A2). Stipe: 5–15 × 0.5–1.5 mm, central to eccentric, cylindrical, tomentose, apex brownish orange (5C3) to light brown (6D4), gradually becoming paler downwards (5B2 to 6C2), with whitish basal tomentum. Basidiospores: 5.8–7.4 × 2.8–4 μm (average 5.5 × 3.2 μm), Q = 1.6–2.1 (mean = 1.97), ellipsoid to ovoid, amygdaliform, smooth, hyaline, non-dextrinoid, with drops. Basidia: (23) 25.5–34.8 × 4.8–6.7 (7) μm, 4-spored, clavate, often constricted. Cheilocystidia: 26–49 × 5.4–10.6 (14) μm, broadly clavate, irregular, sometimes lobed. Pleurocystidia: 25.8–56.4 (62) × 6.2–12.5 μm, clavate, subulate, sometimes lobed. Trama hyphae: cylindrical, often sub-inflated, smooth, non-dextrinoid 1.7–9 (12) μm wide. Pileipellis: a cutis made up of cylindrical, often sub-inflated, with weak annular ornamentation, 2.0–7.5 μm wide hyphae; terminal elements adpressed, cylindrical, clavate, sometimes constricted or curved, 2.0–5 μm wide. Stipitipellis: a cutis of cylindrical, smooth, 2.7–9.7 (11) μm wide hyphae. Caulocystidia: 21.7–90 × 3.9–11.7 μm, cylindrical, flexuose, sometimes curved. Clamp connections: present in all tissues.

Other specimens examined. The Republic of Korea, Jeollanam-do: Jindo-gun, Maenggoldo island, 34°12′21″N, 125°51′41″E, alt. 24 m, 4 July 2018, Jae Young Park, SFC20180704–86.

Habit and habitat. Scattered to gregarious on the branch in mixed forest dominated by Camellia japonica Linne, in summer.

Distribution. The Republic of Korea.

Remark. Collybiopsis albicantipes is similar to Co. ramulicola and Co. koreana when comparing macro-morphological characteristics. Collybiopsis ramulicola is distinguishable from Co. albicantipes by a reddish pileus, fewer and buff lamellulae (1–4), a shorter and thinner stipe (12–23 × 2–3 mm), shorter and slightly elongated basidiospores (6.6–8.4 × 3.5–4.5 μm), shorter basidia (23–27 × 3.8–5.5 μm), and shorter cheilocystidia (23–27 × 3–6 μm) (Deng et al. 2016). Collybiopsis koreana differs from Co. albicantipes by having a larger pileus (27–60 mm), more lamellae (15–20) and lamellulae (2–3), longer and thicker stipe (14–70 × 2–3.5 μm), bigger and elongated basidiospores (7.5–10 × 4–5 μm), cheilocystidia with different shapes and sizes (25–55 × 4–10 μm), and incrustation dark brown in KOH (Antonín et al. 2010).
26 × 1.2–1.6 mm stipe, oblong to subcylindrical, 6.7–9.4 × 3.1–4.6 μm basidiospores, utriform, clavate, 20.1–37.5 × 6.8–12.2 μm cheilocystidia, and cylindrical, flexuose, irregular, 17–50 × 3.5–7 μm caulocystidia.

**Description.** Pileus: 6–45 mm, convex to hemispherical, becoming plano-convex to flat with an uplifted margin with age; Surface smooth, dull, hygrophanous, greyish orange (6B3) to brownish (7D8 to E8) at the center, being whitish at the margin (4A2 to 6C8), being paler with age. Lamellae: subdistant, L = 20–32, l = 1–7, adnexed, white. Stipe: 15–26 × 1.2–1.6 mm, cylindrical, tomentose, subinsititious, whitish to reddish grey (9B2). Basidiospores: 6.7–9.4 × 3.1–4.6 μm, average 8.13 × 3.62 μm, Q = 2–2.4 (mean = 2.26), oblong to cylindrical, smooth, hyaline, non-dextrinoid, with drops. Basidia: 18.3–30 × 4.1–8.8 μm, 4-spored, narrowly clavate, narrowly utriform, often curved. Cheilocystidia: 20.1–37.5 × 6.8–12.2 μm, utriform, clavate, sometimes with mucronate apex. Pleurocystidia: absent. Trama hyphae: cylindrical, often subinflated, smooth, branched, non-dextrinoid, 2–12 μm wide. Pileipellis: transition between cutis and trichoderm, composed of cylindrical, with heavy annular ornamentation, 4–12 μm wide hyphae; terminal elements adpressed to suberect, cylindrical, clavate, often incrusted (often incrusted), thin-walled, 3–6 μm wide. Stipitipellis: a cutis of cylindrical, smooth, 2–7 μm wide hyphae. Caulocystidia: 17–50 × 3.5–7 μm, cylindrical, flexuose, irregular or curved. Clamp connections: present in all tissues.

**Other specimens examined.** The Republic of Korea, Jeollanam-do: Haenam-gun, Mt. Duryun, 34°29'6"N, 126°38'54"E, alt. 169 m, 5 July 2018, Young Woon Lim, Abel Severin Lupala, Jun Won Lee, SFC20180705–26. The Republic of Korea, Seoul: Gwanak-gu, Gwanak-ro 1, Seoul National University, 37° 27' 37"N, 126° 56' 59"E, alt. 80m, 13 July 2018, Jae Young Park, SFC20180713–09.

**Habit and habitat.** Solitary to scattered on dead wood debris of conifers, in summer.

**Distribution.** The Republic of Korea

**Remark.** *Collybiopsis clavicystidiata* is morphologically similar to *G. omphalodes* and *Co. menehune*. *Collybiopsis omphalodes* differs in their larger pileus (2–30 mm), a darker colored stipe, smaller basidiospores (5–6 × 2.5–3 μm), and thinner hyphae in the pileipellis (5–8 μm wide). *Collybiopsis menehune* can be distinguished from *Co. clavicystidiata* by its larger pileus (8–30 mm), buff lamellae, longer stipe (15–60 mm), longer basidiospores (7.5–9.5 × 3.5–4.2 μm, Q = 2.2), and longer caulocystidia (16–67 × 3–5 μm) (Desjardins et al. 1999). *Co. clavicystidiata* is phylogenetically close to *Co. pseudomphalodes*. *Collybiopsis pseudomphalodes* has relatively few references for comparison, but differences can be found in the lengths of the stipe (3–4 mm) and cheilocystidia (40 × 3 μm) when compared with *Co. clavicystidiata* (Dennis 1961).

**Collybiopsis fulva** J.S. Kim & Y.W. Lim, sp. nov.
Mycobank No: 842055
Fig. 3E–F, Suppl. material 1: Fig. S1C

**Diagnosis.** This species has a pale orange to brownish-colored, 4–20 mm pileus, an orange white colored to light brownish colored, 7–30 × 0.7–1 mm stipe with pubescence,
Seven new *Collybiopsis* species

spheropedunculate, pleurocystidia, oblong to subcylindrical, 6.8–9.2 × 3.1–4.9 μm basidiospore, lobed, clavate with rostrate apex, 24.8–38.4 × 6.5–11.8 μm cheilocystidia.

**Etymology.** Epithet “fulva” referring to fox-colored pileus.

**Holotype.** The Republic of Korea, Gyeonggi-do: Pocheon-si, Soheul-eup, Gwangneungsumgwon-ro 415, 37°45'17"N, 127°9'59"E, alt. 101 m, Sang Kook Han, 21 July 2015, KA15–0210 (GenBank accession no. ITS: OL467259; nrLSU: OL462795).

**Description.** Pileus: 4–20mm, hemispherical, convex to plane, sometimes concave with slightly reflexed, wavy margin, hygrophanous, pale orange (6A3) to greyish orange, becoming more brownish to the center (5B4 to 7C4). Lamellae: distant, \( L = 16–28 \), \( l = 1–5 \), sinuate, broad, whitish to yellowish white (4A2) to brownish orange (6C4 to 7C4). Stipe: 7–30 × 0.7–1 mm, cylindrical, gradually widened towards the base, tomentose, apex orange white (5A2) to brownish orange (6C6), becoming dense downwards (6D8), covered with pubescence. Basidiospores: 6.8–9.2 × 3.1–4.9 μm (average 7.47 × 3.69 μm), \( Q = 2.05 \), oblong to cylindrical, smooth, colorless, non-dextrinoid, with drops. Basidia: 20.4–29.4 × 4.7–7.8 μm, 4-spored, narrowly clavate, sometimes constricted or curved. Cheilocystidia: (20.5) 24.8–38.4 × 6.5–11.8 μm, lobed, clavate, sometimes with rostrate apex. Pleurocystidia: 31.5–46.9 × 12–20.6 μm, spheropedunculate, obovoid, sometimes with mucronate apex. Trama hyphae: cylindrical to subinflated, irregular, thin-walled, smooth, branched, non-dextrinoid, 2.0–15 μm wide. Pileipellis: a cutis of cylindrical, thin-walled, 4–15 μm wide hyphae; terminal elements adpressed to suberect, narrowly clavate, thin-walled, with heavy annular ornamentation, 3–8 μm wide. Stipitipellis: a cutis of cylindrical, thin-walled, smooth, 5–15 μm wide hyphae. Caulocystidia: 45.6–108.3 (131) × 6.8–14.8 μm, cylindrical, irregular, curved. Clamp connections: present in all tissues.

**Other specimens examined.** The Republic of Korea, Gyeonggi-do: Pocheon-si, Soheul-eup, Gwangneung forest exhibition hall, 37°45'19"N, 127°9'58"E, alt. 99 m, 8 July 2016, Sang Kook Han, KA16–0428. The Republic of Korea, Gyeongsangnam-do: Geochang-gun, Mt. Gibaek, 35°43'6"N, 127°45'49"E, alt. 1095 m, 19 June 2013, Sang Kook Han, KA13–0216.

**Habit and habitat.** Scattered or gregarious on the bark of deciduous trees or on the rotting branch of both broadleaf trees and conifers, in summer.

**Distribution.** The Republic of Korea.

**Remark.** *Collybiopsis fulva* morphologically resembles *Co. menehune* and *Co. ramealis*. They can be distinguished based on several morphological differences. *Collybiopsis menehune* has a longer stipe (15–60 mm length), denser lamellae, and larger basidiospores (7.5–9.5 × 3.5–4.2 μm) (Desjardin et al. 1999). *Collybiopsis ramealis* has a smaller basidiocarp (2–20 mm), shorter basidiospores (7.8–11 × 2.5–4 mm) and different type of pileipellis (*Rameales*-structure) (Noordeloos 1983; Desjardin et al. 1997). Phylogenetically, *Co. fulva* is closely related to *Co. ramulicola*. *Collybiopsis ramulicola* differs in having a more yellowish pileus, fewer lamellae (9–12) that are brighter in color, a more reddish and thicker stipe (2–3 mm), and smaller sized cheilocystidia (23–27 × 3–6 mm) (Deng et al. 2016).
Collybiopsis orientisubnuda J.S. Kim & Y.W. Lim, sp. nov.
MycoBank No: 842056
Fig. 3G–H, Suppl. material 1: Fig. S1D

Etymology. Epithet “orientisubnuda” meaning the new species has originated from the East and is morphologically similar to Co. subnuda.

Holotype. The Republic of Korea, Gyeongsangbuk-do: Ulleung-gun, 37°31’21”N, 130°53’14”E, alt. 757 m, 19 July 2016, Changmu Kim, Jinsung Lee, Jae Young Park, NIBRFG0000500990 (GenBank accession no. ITS: OL467262; nrLSU: OL546546).

Diagnosis. It features a brownish, 15–50 mm pileus, orangish cream-colored lamellae, greyish to brownish orange, tomentose, 20–80 × 2.5–6 mm stipe, subcylindrical to fusoid, 6.7–8.6 × 1.8–3.2 μm basidiospores, and cylindrical, flexuose, sometimes irregular or curved, 26.3–52 (63) × 3.5–6.5 μm caulocystidia. This species is morphologically similar to Co. subnuda.

Description. Pileus: 15–50 mm, convex to plano-convex, sometimes subumbonate; Surface smooth, brownish orange (6C5 to 7C4), becoming paler to the margin (5A2). Lamellae: distant, L = 16‒28, l = 3‒7, adnexed, pale yellow (4A3) to orange white (5A2). Stipe: 20–80 (100) × 2.5–6 mm, central to eccentric, cylindrical, tomentose, often twisted, greyish orange (6B4) to brownish orange(7C4), becoming paler and thinner to the base. Basidiospores: 6.7–8.6 × 1.8–3.2 μm (average 7.5 × 2.5 μm), Q = 2.5–3.2 (mean = 2.92), cylindrical to fusoid, smooth, hyaline, non-dextrinoid, with drops. Basidia: (17) 19.8–28.7 (29) × 3.7–7.3 μm, 4-spored, narrowly clavate, often constricted. Cheilocystidia: variable in shape and size, 21–33.3 × 4.7–8.2 μm, lobed, clavate, slightly sphaeropendunculate, sometimes constricted or with rostrate apex. Pleurocystidia: 24.7–52.3 × 5.1–9.1 μm, narrowly utriform, clavate, sometimes clavate with rostrate apex. Trama hyphae: cylindrical, often subinflated, smooth, branched, non-dextrinoid, 2.0–7.0 μm wide. Pileipellis: a cutis made up of cylindrical, 2–8 μm wide hyphae; terminal elements adpressed, cylindrical, often subinflated, with weak annular ornamentation, 3–6 μm wide. Stipitipellis: a cutis of cylindrical, smooth, 2.5–7 μm wide hyphae. Caulocystidia: 26.3–52 (63) × 3.5–6.5 μm, cylindrical, flexuose, sometimes irregular or curved. Clamp connections: present in all tissues.

Other specimens examined. The Republic of Korea, Chungcheongnam-do: Yesan-gun, Mt. Gaya, 35°48’14”N, 128°5’49”E, alt. 863 m, 23 August 2017, Hae Jin Cho, Ki Hyeong Park, SFC20170823–39. The Republic of Korea, Gangwon-do: Pyeongchang-gun, Mt. Odae, 37°43’54”N, 128°35’42”E, alt. 683 m, 8 July 2017, Nam Kyu Kim, SFC20170708–14. The Republic of Korea, Gyeongsangbuk-do: Ulleung-gun, 37°31’30”N, 130°52’21”E, alt. 718 m, 2 September 2015, Jae Young Park, SFC20150902-01.

Habit and habitat. Scattered to gregarious on the ground covered with dead and decaying leaves of broadleaf forest, from summer to autumn.

Distribution. The Republic of Korea.
**Remark.** *Collybiopsis orientisubnuda* is morphologically similar to *Co. peronata* (Bolton) R.H. Petersen and *Co. subnuda* (Ellis ex Peck) R.H. Petersen. *Collybiopsis peronata* can be distinguished from *Co. orientisubnuda* by fewer and buff lamellulae (1–3), a thicker stipe (3–8 mm), smaller Q value (2.3), longer basidia (20–40 μm), and longer cheilocystidia (25–90 × 5–10 μm) (Noordeloos et al. 1999). *Collybiopsis subnuda* differs from *Co. orientisubnuda* with thinner stipe (~3 mm), larger basidiospores (8–11 × 3–4.5 μm) and the absence of pleurocystidia (Tekpinar and Acar 2020).

*Collybiopsis subumbilicata* J.S. Kim & Y.W. Lim, sp. nov.

MycoBank No: 842057

Fig. 4A, B, Suppl. material 1: Fig. S1E

**Etymology.** Epithet “*subumbilicata*” referring to having a small depressed center in pileus.

**Holotype.** The Republic of Korea, Seoul, Gwanak-gu, Mt. Gwanak, 37°12’39”N, 128°19”E, alt. 877 m, 01 July 2014, Young Woon Lim, SFC20140701–03 (GenBank accession no. ITS: OL467232; nrLSU: OL462787).

**Diagnosis.** The distinctive features include a brownish, 10–35 mm pileus, white colored lamellae, a brownish, 25–60 × 1–3 mm stipe covered with pubescence, ellipsoid to oblong basidiospores, narrowly clavate and cylindrical, 17–24.3 × 3.5–5.1 μm basidia, and cylindrical, flexuose, sometimes curved, 12.6–38.2 × 2.4–6.6 μm caulocystidia.

**Description.** Pileus: 10–35 mm, plano-convex to plano-concave, subumbilicate, becoming undulate and uplifted in age; Surface smooth, greyish orange (5B3) to brown (6E5). Lamellae: subdistant, L = 22–38, l = 3–7, free to adnexed, white. Stipe: 25–60 × 1–3 mm, cylindrical, tomentose, hollow, light brown (7D4) to dark brown (9F8), becoming paler to the apex, covered with pubescence. Basidiospores: 5.5–7.5 × 2.5–3.6 μm (average 6.47 × 3.0 μm), Q = 1.8–2.2 (mean = 2), oblong to fusiform, smooth, hyaline, non-dextrinoid, with drops. Basidia: (15.6) 17–24.3 (27.6) × 3.5–5.1 (5.9) μm, 4-spored, narrowly clavate, cylindrical. Cheilocystidia: 17.6–38.4 × 5–7.8 μm, various in shape, lobed. Pleurocystidia: 20.3–30.7 × 6.8–9.5 μm, clavate, fusiform, slightly sphaeropedunculate. Trama hyphae: cylindrical, subinflated, branched, smooth, non-dextrinoid, 1.5–8 μm wide. Pileipellis: a cutis made up of cylindrical, often incrusted, with heavy annular ornamentation, 5.0–15 μm wide hyphae; terminal elements adpressed to suberect, fusoid, clavate, 6.0–16 μm wide. Stipitipellis: a cutis of cylindrical, smooth, thin-walled, 2.0–6.0 μm wide hyphae. Caulocystidia: 12.6–38.2 × 2.4–6.6 μm, cylindrical, flexuose, sometimes irregular or curved. Clamp connections: present in all tissues.

**Other specimens examined.** The Republic of Korea, Gangwon-do: Goseong-gun, Hwajinpo, Hwajinpo Condominium, 38°28’24”N, 128°26’30”E, alt. 7 m, 2 August 2012, Young Woon Lim, SFC20120802–03. The Republic of Korea, Gyeongsangbuk-do: Ulleung-gun, Ulleung island, 37°30’38”N, 130°51’44”E, alt. 429 m, 22 August 2017, Jae Young Park, Nam Kyu Kim, SFC20170822–14.
Habit and habitat. Scattered to gregarious on the ground covered with dead leaves in temperate mixed forests, from summer to autumn.

Distribution. The Republic of Korea.

Remark. *Collybiopsis subumbilicata* appears similar to *Co. villosipes* (Cleland) R.H. Petersen. *Collybiopsis villosipes* is distinguished from *Co. subumbilicata* by fewer and brownish lamellae (also lamellulae), a noninsititious, light-colored stipe, larger basidiospores (6.5–10.5 × 3.5–4.5 μm) and basidia (25–34 × 6.5–7.5 μm) (Desjardin et al.
Seven new *Collybiopsis* species

Furthermore, *Co. subumbilicata* is phylogenetically close to *Co. biformis* and *Co. disjuncta* (R.H. Petersen & K.W. Hughes) R.H. Petersen & K.W. Hughes. *Collybiopsis biformis* is morphologically similar to *Co. subumbilicata* but can be distinguished by elongated basidiospores (6.4‒9.2 × 2.4‒4.8 μm), thicker basidia (6–7 μm thick) and cheilocystidia (6–12 μm thick) (Morgan 1905; Mata 2002). *Collybiopsis disjuncta* can be distinguished from *Co. subumbilicata* by a smaller pileus (7‒12 mm) with olivaceous tint, pinkish lamellae, slender stipe (0.5–1 mm thick), bigger basidiospores (6‒7.5 × 3‒3.5 μm), bigger basidia (22‒34 × 5‒7 μm), and a seldom incrusted pileipellis (Petersen and Hughes 2014).

*Collybiopsis undulata* J.S. Kim & Y.W. Lim, sp. nov.

MycoBank No: 842058

Fig. 4C–D, Suppl. material 1: Fig. S1F

**Etymology.** Epithet “*undulata*” referring to having an undulate margin of pileus.

**Holotype.** The Republic of Korea, Chungcheongnam-do, Boryeong-si, recreation forest of Mt Sungju, 36°20’4”N, 126°39’50”E, alt. 241 m, 21 August 2012, Jae Young Park, SFC20120821–04 (GenBank accession no. ITS: OL467239; nrLSU: OL462813).

**Diagnosis.** It is characterized by having 10‒23 mm sized pileus that is particularly brown in the middle with a wavy margin, subdistant and creamy lamellae, a dark brown, 35‒55 × 0.8‒2 mm stipe that becomes lighter to the apex, subcylindrical, broadly clavate or irregular, sometimes lobed, 16.7–28 × 4.8–8 μm cheilocystidia, and 27–60 × 3.5–6 μm sized caulocystidia which has a morphology similar to cheilocystidia and sometimes grows in bundles.

**Description.** Pileus: 10‒23 mm, convex to concave, margin becoming undulate with age; Surface smooth, hygrophanous, brown (7D2 to 7E6) in the center, becoming paler to the margin (5A2–5B3 to 7B2). Lamellae: subdistant, L = 15‒30, l = 3–9, adnexed, cream. Stipe: 35‒55 × 0.8‒2 mm, cylindrical, tomentose, dark brown (7F5 to 8F8), gradually becoming paler to apex (7B2 to 7C2). Basidiospores: 5.6‒9.5 × 2‒3.4 μm (average 7.3 × 2.8 μm), Q = 2‒3.1 (mean = 2.58), cylindrical, smooth, hyaline, non-dextrinoid, with drops. Basidia: 15‒22.3 × 3.6‒6.8 μm, 4-spored, cylindrical, narrowly clavate to utriform, often curved. Cheilocystidia: 16.7–28 × 4.8–8 μm, subcylindrical, broadly clavate or irregular, sometimes lobed. Pleurocystidia: absent. Trama hyphae: cylindrical, sometimes subinflated, smooth, branched, non-dextrinoid, 2‒8 μm wide. Pileipellis: a cutis made up of cylindrical, often incrusted, slightly brownish, with heavy annular ornamentation, 2.4–7 μm wide hyphae; terminal elements adpressed to suberect, cylindrical to clavate, 3–6 μm wide. Stipitipellis: a cutis of cylindrical, smooth, 2.0–3.5 μm wide hyphae. Caulocystidia: 27–60 × 3.5–6 μm, irregularly cylindrical, narrowly utriform, seldom apically lobed, sometimes gathered in a bunch. Clamp connections: present in all tissues.

**Other specimens examined.** The Republic of Korea, Gyeonggi-do: Goyang-si, Deogyang-gu, Seooreung, 37°37’26”N, 126°54’4”E, alt. 35 m, 13 August 2015, Jae Young Park,
Habit and habitat. Scattered to gregarious on leaf litter in mixed forest dominated by broadleaf trees, in summer.

Distribution. The Republic of Korea.

Remark. Collybiopsis undulata is morphologically similar to Co. subpruinosa (Murrill) R.H. Petersen. Collybiopsis subpruinosa has differences in having small central papilla on pileus, fewer lamellulae (3–4 series), vivid colored lamellae, thicker basidiospores (4.5–5.2 μm wide), larger basidia (30–36 × 7.5–8.5 μm) and cheilocystidia (25–80 × 5–16 μm), thick-walled trama hyphae (0.5–1 μm), caulocystidia with a wider size range, and a habit of growing solitary on rotten twigs or logs (Desjardin et al. 1999). Collybiopsis undulata is phylogenetically close to Co. villosipes but Co. villosipes can be differentiated by having fewer lamellulae (2–3 series), vivid colored lamellae, thicker stipe (1.5–4.0 mm), slightly thicker basidiospores (3.5–4.5 μm wide), and basidia (25–34 × 6.5–7.5 μm) (Desjardin et al. 1997).

Collybiopsis vellerea J.S. Kim & Y.W. Lim, sp. nov.

MycoBank No: 842059
Fig. 4E–F, Suppl. material 1: Fig. S1G

Etymology. Epithet “vellerea” refers to having a velvety stipe.

Holotype. The Republic of Korea, Seoul: Gwanak-gu, Mt. Gwanak, 37°27′32″N, 126°56′49″E, alt. 90 m, 21 August 2014, Young Woon Lim, SFC20140821–29 (GenBank accession no. ITS: OL467267; nrLSU: OL462810).

Diagnosis. It has a dull, greyish orange, 18–45 mm pileus with darker center, a tomentose (like velvet), insititious, orangish, 15–55 × 3–5 mm stipe, sphaeropendunculate, subovoid, 23.4–49 × 7.5–13.4 μm pleurocystidia, oblong to subcylindrical basidiospores, narrowly clavate with rostrate apex, sometimes lobed, 7.7–49.7 × 3.8–14.6 μm cheilocystidia.

Description. Pileus: 18–45 mm, hemispherical, appendiculate to convex, subumbonate with an uplifted margin when old; Surface smooth, dull, hygrophanous, orange white (5A2) to greyish orange (6E8 to 7F8) on the center, gradually becoming paler to the edge (5A1 to 5B2). Lamellae: crowded to close, L = 38–52, l = 3–7, furcate, white. Stipe: 15–55 × 3–5 mm, cylindrical, finely tomentose, insitious, pale orange (5A3) to reddish grey (7B2), becoming darker to the base (6A2 to 7C2). Basidiospores: 5.2–7 × 2.5–3.8 μm (average 6.17 × 3.06 μm), Q = 1.8–2.4 (mean = 2.03), oblong to subcylindrical, smooth, hyaline, non-dextrinoid, with drops. Basidia: 16.2–24.8 x 3.3–5.3 μm, 4-spored, (narrowly) clavate, often curved or constricted. Cheilocystidia: 7.7–49.7 × 3.8–14.6 μm, narrowly clavate with rostrate apex, sometimes lobed. Pleurocystidia: 23.4–49 × 7.5–13.4 μm, sphaeropendunculate, subovoid. Trama hyphae: cylindrical, often subinflated, thin-walled, smooth, branched, non-dextrinoid, 2–5 μm wide. Pileipellis: a cutis made up of cylindrical, thin-walled, with weak annular ornamentation, 3–10 μm wide hyphae; terminal elements adpressed to suberect, cylindrical, fusoid, clavate, 5–11 μm wide. Stipitipellis: a cutis of cylindrical, thin-walled, smooth,
Seven new Collybiopsis species  

2.0–6.0 μm wide hyphae. Caulocystidia: 12–38 × 2.4–6.6 μm, cylindrical, narrowly utriform, sometimes irregular, or curved. Clamp connections: present in all tissues.

Other specimens examined. The Republic of Korea, Chungcheongnam-do: Seosan-si, Mt. Gaya, 36°41′0″ N, 126°35′19″ E, alt. 260 m, 20 August 2012, Jae Young Park, SFC20120820–02. The Republic of Korea, Incheon: Ongjin-gun, 37°13′10″ N, 126°10′4″ E, alt. 6 m, 4 September 2018, Changmu Kim, Jin Sung Lee, NIBRFG0000502858. The Republic of Korea, Jeollanam-do: Jindo-gun, Seogeocha island, 34°15′22″N, 125°55′11″ E, alt. 38 m, 5 July 2018, Jae Young Park, Tae Heon Kim, SFC20180705–90.

Habit and habitat. Scattered to gregarious on the ground covered with dead and decaying conifer needles, from summer to autumn.

Distribution. The Republic of Korea.

Remark. Collybiopsis vellerea is morphologically similar to Co. menehune and G. spongiosus Halling. Collybiopsis menehune has a paler stipe, a smaller pileus (8–30 mm), and fewer lamellulae (4–6 series) (Desjardin et al. 1999). Gymnopus spongiosus has a smaller pileus (8–20 mm) and longer stipe (20–55 mm). Micromorphologically, Co. menehune has larger basidiospores, basidia, and caulocystidia (Desjardin et al. 1999). Gymnopus spongiosus differs from Co. vellerea in that its pilepellis is a Dryophila-type cutis and its color changes in alkalies. Furthermore, its basidia (18–25 × 6–9 μm) and trama hyphae (3.5–17 μm) are thicker and its caulocystidia (3.5–10.5 μm broad) are smaller (Halling 1996). Collybiopsis vellerea is phylogenetically close to Co. omphalodes. Collybiopsis omphalodes differs in having smaller basidiomata (20–30 mm) and its habit on logs (Dennis 1951).

Proposal for Collybiopsis recombination

In this study, many epithets were found that required an additional transfer of species from Marasmiellus to Collybiopsis apart from the study done by Petersen and Hughes (2021). Oliveira et al. (2019) had previously suggested to replace these species from Gymnopus to Marasmiellus s. str., but this study suggests that these species should be further transferred from Marasmiellus s. str. to Collybiopsis.

Collybiopsis istanbulensis (E.Sesli, Antonín & E.Aytaç) J.S. Kim & Y.W. Lim, comb. nov.  
MycoBank No: 842060

Basionym. Marasmiellus istanbulensis E. Sesli, Antonín & E.Aytaç. Pl. Biosystems 152(4): 669. 2018.

Collybiopsis koreana (Antonín, Ryoo & H.D.Shin) J.S. Kim & Y.W. Lim, comb. nov.  
MycoBank No: 842061

Basionym. Marasmiellus koreanus Antonín, Ryoo and H.D.Shin. Mycotaxon 112: 190. 2010.
**Collybiopsis omphalodes** (Berk.) J.S. Kim & Y.W. Lim, comb. nov.
MycoBank No: 842062

Chamaeceras omphalodes (Berk.) Kuntze, Revis. gen. pl. (Leipzig) 3(3): 456. 1898.
Collybia omphalodes (Berk.) Dennis, Trans. Br. mycol. Soc. 34(4): 443. 1951.
Marasmiellus omphalodes (Berk.) Singer. Sydowia 9(1–6): 385. 1955.
Gymnopus omphalodes (Berk.) Halling & J.L. Mata, in Mata, Halling, and Petersen, Fungal Diversity 16: 122. 2004.

**Basionym.** Marasmius omphalodes Berk., Hooker’s J. Bot. Kew Gard. Misc. 8: 138. 1856.

**Collybiopsis pseudomphalodes** (Dennis) J.S. Kim & Y.W. Lim, comb. nov.
MycoBank No: 842063

Gymnopus pseudomphalodes (Dennis) J.L. Mata, in Mata, Hughes, and Petersen, Sydowia 58(2): 289. 2006, as “pseudo-omphalodes”.
Marasmiellus pseudomphalodes (Dennis) J.S. Oliveira, in Oliveira, Vargas-Isla, Cabral, Rodrigues and Ishikawa, Mycol. Progr. 18(5): 735. 2019, as “pseudomphalioides”.

**Basionym.** Collybia pseudomphalodes Dennis, Kew Bull. 15(1): 74 (1961).

**Collybiopsis ramulicola** (T.H. Li & S.F. Deng) J.S. Kim & Y.W. Lim, comb. nov.
MycoBank No: 842064

**Basionym.** Gymnopus ramulicola T.H. Li & S.F. Deng, in Deng, Li, Jiang and Song, Mycotaxon 131(3): 665. 2016.

**Taxonomic key to Collybiopsis in Korea**

1. Pileus < 25 mm diam ................................................................. 2
   – Pileus > 25 mm diam .......................................................... 11
2. Lamellae subdistant to distant (10–30) ............................... 3
   – Lamellae close to crowded (> 30) ........................................ 9
3. Basidiomes on bark, branch, or woody debris ...................... 4
   – Basidiomes on duff or on soil ............................................. 8
4. Pleurocystidia present ......................................................... 5
   – Pleurocystidia absent ........................................................ 7
5. Stipe base covered with dense whitish basal tomentum ....... Co. albicantipes
   – Stipe base not covered with whitish basal tomentum ........ 6
6. Pileipellis composed of a coarse Rameales-structure hyphae ...... Co. ramealis
   – Pileipellis composed of a cylindrical, often sub-inflated hyphae, not a Rameales-structure ........................................... Co. fulva
| Seven new Collybiopsis species |
|--------------------------------|
| Pileus distinctly sulcate. Stipe base covered with dense whitish basal tomentum ................................................................. Co. koreana |
| - Pileus slightly sulcate. Stipe base covered with weak whitish basal tomentum ................................................................. Co. nonnulla |
| 8 Stipe < 2 cm long. Q value of basidiospores 1.6–2.2 ............................................................ Co. dichroa |
| - Stipe > 2 cm long. Q value of basidiospores 2.0–3.1 ............................................................. Co. undulata |
| 9 Lamellae crowded (> 100) ................................................................................................................. Co. confluens |
| - Lamellae close to crowded (< 100) ................................................................................................. 10 |
| 10 Basidia > 22 μm long ......................................................................................................................... Co. biformis |
| - Basidia < 22 μm long ........................................................................................................................ Co. libidoles |
| 11 Lamellae subdistant to distant (10–38) ......................................................................................... 12 |
| - Lamellae close (> 38) ......................................................................................................................... 15 |
| 12 Pleurocystidia present ..................................................................................................................... 13 |
| - Pleurocystidia absent ....................................................................................................................... 14 |
| 13 Q value of basidiospores > 2.2 .............................................................................................. Co. orientisubnuda |
| - Q value of basidiospores < 2.2 ................................................................................................. Co. subumbilicata |
| 14 Pileus convex, hemispherical, plano-convex to flat. Cheilocystidia utriform and clavate ......................................................... Co. clavicyclidiata |
| - Pileus convex to broad-convex. Cheilocystidia narrowly clavate .......................................................... Co. polygramma |
| 15 Pleurocystidia present ..................................................................................................................... Co. vellerea |
| - Pleurocystidia absent ....................................................................................................................... Co. luxurians |

**Discussion**

Of the 372 gymnopoid/marasmioid specimens, we confirmed 201 specimens (54%) to belong to *Collybiopsis*. These results indicate that the species of *Collybiopsis* can be confused with those of similar genera as well as with other *Collybiopsis* members when identification is based solely on morphological information. This is because some characteristics are overlapped between species (Suppl. material 2: Fig. S2) and the characteristics can be different depending on developmental stage or environmental conditions. Further, the high misidentification ratio may be caused by the slow rate of adoption of the current names. Sequence-based taxonomy has introduced rapid changes in the classification of gymnopoid/marasmioid species (Mata 2002; Mata et al. 2004a; Mata et al. 2004c; Hughes et al. 2010; Oliveira et al. 2019; Petersen and Hughes 2017, 2021). As such, taxonomic confusion has been resolved in taxa that have been well researched based on molecular data (Desjardin et al. 1999; Mata 2002; Lee et al. 2019).

Nine of the sixteen *Collybiopsis* species were identified as already known species. Of the nine described species, seven species were identified as the species previously recorded in the Republic of Korea: *Collybiopsis biformis*, *Co. confluens*, *Co. koreana*, *Co. luxurians*, *Co. menehune*, *Co. polygramma*, and *Co. ramealis*. Two species, *Co. dichroa* and *Co. nonnulla*, were reported for the first time in the Republic of Korea. Most of the nine described species formed a monophyletic clade with each corresponding species. However, sequence
variations by continent were detected in *Co. biformis*, *Co. confluens*, *Co. dichroa*, and *Co. nonnulla*. Asian samples, including our specimens, were clearly separated from those of Europe, North America, and Africa. These results have also been reported in previous studies on *Collybiopsis biformis* (Mata 2002; Petersen and Hughes 2014; Razaq et al. 2020) and *Co. confluens* (Hughes and Petersen 2015). Especially, *Co. confluens* is known as a representative example of intra-specific variation between continents. Percent ITS sequence divergence of this species was reported to be 3.25% when comparing the sequences of the North America and Europe (Hughes and Petersen 2015). We confirmed that percent ITS sequence divergence of Asian *Co. confluens* (our Korean samples and Chinese sequences) were each about 3% when compared to American and European sequences.

Similarly, *Co. dichroa* showed sequence variations that were previously reported in association with intraspecific hybridization and dramatic sequence variations including frequent nucleotide substitutions of Adenine and Guanine (Hughes et al. 2015). The Korean *Co. dichroa* was closely related to *Co. dichroa* taxa 2 mentioned in Hughes et al. 2015. Similarly, the intraspecific genetic variation depending on environmental conditions or geographical distribution has been reported in many other fungal species (Manian et al. 2001; Kauserud et al. 2007; Seierstad et al. 2013). For the last, Korean *Co. nonnulla* showed high intra-specific divergence when matching with sequences of *Co. nonnulla* of America and Cameroon. According to the phylogenetic analysis results, there is a slight sequence variation, but it forms a clade supported by a high bootstrap and morphologically almost coincides with the reference. Therefore, we view this sequence variation as due to different environments by continent and identify the specimens as *Co. nonnulla*. Nevertheless, compared to the fact that it was reported as a new species a long time ago, only seven sequences were deposited in the NCBI, so further study on this species is necessary.

Morphologically, the morphological characteristics of the seven described species were also in agreement with the previous descriptions (Suppl. material 2: Fig. S2). However, *Co. luxurians* and *Co. polygramma* found in the Republic of Korea showed few differences compared to the Western descriptions in the previous literature (Mata 2003; Noordeloos et al. 1999). In the case of the *Co. luxurians*, Korean sequences formed a slightly distinct clade in the phylogenetic tree, along with the Chinese sequence (ZD16102301), from European sequences. In this study, direct morphological comparison studies with European and Chinese samples were difficult and there was no significant morphological difference from the references. For these reasons, we identified Korean specimens as *Co. luxurians*, but further studies are needed with more samples from other countries for this species.

Seven new species have common characteristics of *Collybiopsis* such as insititious to subinsititious stipe, ellipsoid to oblong, inamyloid basidiospores, and presence of caulocystidia. However, it is difficult to distinguish them from other *Collybiopsis* species based on morphological characteristics alone. Upon molecular phylogenetic analyses, each of them clearly formed a distinct clade clearly in the ML phylogenetic tree (Fig. 1). Their morphological features may or may not be distinguished from their phylogenetically close relatives. The morphological differences between new species and morphologically similar or phylogenetically close species are discussed in the remarks for each species.
Two species previously reported in the Republic of Korea, *Co. peronata* (Cho & Lee, 1979) and *Co. subnuda* (National list of species of Korea 2020), were not confirmed in this study. *Co. peronata* and *Co. subnuda*, which are typical collybioid mushrooms, have been reported in Asia based on their morphological characteristics (Cho and Lee 1979; Kim et al. 1991; Park and Cho 1992; Yoshida and Muramatsu 1998; Tolgor and Yu 2000). Molecular analyses showed that none of the Korean specimens examined in this study could be identified as *Co. peronata* nor *Co. subnuda*. Instead, the specimens labelled as *Co. peronata* or *Co. subnuda* were identified as different species – *Gymnopus similis* Antonín, Ryoo & Ka and *Co. orientisubnuda*. *Collybiopsis peronata* were originally mostly reported from Europe and America and *Co. subnuda* were originally reported from America (Desjardin et al. 1999; Mata et al. 2006). Furthermore, there have been no recent sequence uploads to GenBank or reports of *Co. peronata* and *Co. subnuda* from Asia, making it difficult to confirm whether they exist in the Republic of Korea. Although *Co. orientisubnuda* is closely related to *Co. peronata* and *Co. subnuda*, there are clear differences in the ITS regions of these three species (Suppl. material 3: Fig. S3). Morphologically, *Co. orientisubnuda* is highly similar to *Co. subnuda* and considerably different from *Co. peronata*. The detailed comparisons of the morphological features are provided in the remarks for each species.

In conclusion, we identified 16 *Collybiopsis* species in the Republic of Korea through morphological and molecular analyses and we update the Korean inventory of *Collybiopsis*. Our study showed that the identification of *Collybiopsis* species requires both morphological and molecular analyses. Further, this study has the following significance as in the previous study conducted by Petersen and Hughes (2021): additional combinations of *Marasmiellus* species under *Collybiopsis*, detailed morphological characterization of *Collybiopsis* species in the Republic of Korea along with photographs and drawings, and specific approaches to species differentiation and identification through morphological and molecular analyses. Furthermore, we believe that this study will be helpful for further studies such as research of *Collybiopsis* distribution worldwide as it provides additional molecular information about *Collybiopsis* in the Republic of Korea and proposes seven new species identified from the Republic of Korea. These data will be useful for the identification and taxonomic arrangement of gymnopoid/marasmioid mushrooms.

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**References**

Antonín V, Herink J (1999) Notes on the variability of *Gymnopus luxurians* (Tricholomataceae). Czech Mycology 52(1): 41–49. https://doi.org/10.33585/cmy.52103
Antonín V, Noordeloos ME (1993) A Monograph of Marasmius, Collybia, and Related Genera in Europe: Marasmius, Setulipes, and Marasmiellus. Libri botanici 8: 1–229.

Antonín V, Ryoo R, Shin HD (2010) Two new marasmielloid fungi widely distributed in the Republic of Korea. Mycotaxon 112(1): 189–199. https://doi.org/10.5248/112.189

Cho DH, Lee JY (1979) Higher fungi in the Northern area of Kyungsangbuk-do. The Korean Journal of Mycology 7: 1–7.

Clémençon H (1973) Zwei verbesserte Präparierlösungen für die mikroskopische Untersuchung von Pilzen. Pilzkunde 38: 49–53.

Deng SF, Li TH, Jiang ZD, Song B (2016) Gymnopus ramulicola sp. nov., a pinkish species from southern China. Mycotaxon 131(3): 663–670. https://doi.org/10.5248/131.663

Dennis R (1951) Some Agaricaeae of Trinidad and Venezuela. Leucosporae: Part I. Transactions of the British Mycological Society 34(4): 411–482. https://doi.org/10.1016/S0076-1536(51)80030-5

Dennis R (1961) Fungi venezuelani: IV. Agaricales. Kew Bulletin 15(1): 67–156[+ii]. https://doi.org/10.2307/4115784

Desjardin DE, Halling RE, Perry BA (1997) Gymnopus villipes—a common collybioid agaric from California. Mycotaxon 64: 141–148.

Desjardin DE, Halling RE, Hemmes DE (1999) Agaricales of the Hawaiian Islands. 5. The genera Rhodocollybia and Gymnopus. Mycologia 91(1): 166–176. https://doi.org/10.2307/3761206

Dutta AK, Wilson AW, Antonín V, Acharya K (2015) Taxonomic and phylogenetic study on gymnopoid fungi from Eastern India. I. Mycological Progress 14(10): 1–18. https://doi.org/10.1007/s11557-015-1094-3

Earle FS (1909) The genera of the North American gill fungi. Bulletin of the New York Botanical Garden 5: 373–451.

Gardes M, Bruns TD (1993) ITS primers with enhanced specificity for basidiomycetes-application to the identification of mycorrhizae and rusts. Molecular Ecology 2(2): 113–118. https://doi.org/10.1111/j.1365-294X.1993.tb00005.x

Halling RE (1996) Notes on Collybia V. Gymnopus section Levipedes in tropical South America with comments on Collybia. Brittonia 48(4): 487–494. https://doi.org/10.2307/2807862

Hughes K, Petersen RH (2015) Transatlantic disjunction in fleshy fungi III: Gymnopus confusens. MycoKeys 9: 37–63. https://doi.org/10.3897/mycokeys.9.4700

Hughes KW, Mather DA, Petersen RH (2010) A new genus to accommodate Gymnopus acervatus (Agaricales). Mycologia 102(6): 1463–1478. https://doi.org/10.3852/09-318

Hughes KW, Segovia AR, Petersen RH (2014) Transatlantic disjunction in fleshy fungi. I. The Sparassis crispa complex. Mycological Progress 13(2): 407–427. https://doi.org/10.1007/s11557-013-0927-1

Hughes K, Morris SD, Reboredo-Segovia AL (2015) Cloning of ribosomal ITS PCR products creates frequent, non-random chimeric sequences — A test involving heterozygotes between Gymnopus dichrous taxa I and II. MycoKeys 10: 45–56. https://doi.org/10.3897/mycokeys.10.5126

Kaburagi Y (1940) Korean and Manchurian practical manual of forest. Korea Forest Experiment Station, Tokyo, 339–367.

Katoh K, Standley DM (2013) MAFFT multiple sequence alignment software version 7: Improvements in performance and usability. Molecular Biology and Evolution 30(4): 772–780. https://doi.org/10.1093/molbev/ms010
Seven new *Collybiopsis* species

Kauserud H, Hofton TH, Saetre GP (2007) Pronounced ecological separation between two closely related lineages of the polyporous fungus *Gloeoporus taxicola*. Mycological Research 111(7): 778–786. https://doi.org/10.1016/j.mycres.2007.03.005

Kim KS, Park WH, Min KH (1991) The higher fungal Flora in the areas of Mt. Daesung and Mt. Daeduck. The Korean Journal of Mycology 19: 167–174.

Kornerup A, Wanscher JH (1978) Methuen handbook of colour. 3rd edn. Methuen, London.

Kumar S, Stecher G, Tamura K (2016) MEGA7: Molecular Evolutionary Genetics Analysis version 7.0 for bigger datasets. Molecular Biology and Evolution 33(7): 1870–1874. https://doi.org/10.1093/molbev/msw054

Lee H, Wissitrassameewong K, Park MS, Verbeken A, Eimes J, Lim YW (2019) Taxonomic revision of the genus *Lactarius* (Russulales, Basidiomycota) in Korea. Fungal Diversity 95(1): 275–335. https://doi.org/10.1007/s13225-019-00425-6

Manian S, Sreenivasaprasad S, Bending G, Mills P (2001) Genetic diversity and interrelationships among common European *Suillus* species based on ribosomal DNA sequences. FEMS Microbiology Letters 204(1): 117–121. https://doi.org/10.1111/j.1574-6968.2001.tb10873.x

Mata JL (2002) Taxonomy and systematics of *Lentinula, Gymnopus* and *Rhodocollybia* (Agaricales, Fungi) with emphasis on oak forests of southern Costa Rica. PhD Thesis, University of Tennessee, Knoxville.

Mata JL (2003) Type studies of neotropical *Collybia* species. Mycotaxon 86: 303–316.

Mata JL, Halling RE, Hughes KW, Petersen RH (2004a) *Rhodocollybia* in neotropical montane forests. Mycological Progress 3(4): 337–352. https://doi.org/10.1007/s11557-006-0104-x

Mata JL, Halling RE, Petersen RH (2004b) New species and mating system reports in *Gymnopus* (Agaricales) from Costa Rica. Fungal Diversity 16: 113–129.

Mata JL, Hughes KW, Petersen RH (2004c) Phylogenetic placement of *Marasmiellus juniperinus*. Mycoscience 45(3): 214–221. https://doi.org/10.1007/S10267-004-0170-3

Mata JL, Hughes KW, Petersen RH (2006) An investigation of *omphalotaceae* (Fungi: Euagarics) with emphasis on the genus *Gymnopus*. Sydowia 58: 191–289.

Miller MA, Pfeiffer W, Schwartz T (2012) The CIPRES science gateway: enabling high-impact science for phylogenetics researchers with limited resources. Proceedings of the 1st Conference of the Extreme Science and Engineering Discovery Environment: Bridging from the extreme to the campus and beyond. https://doi.org/10.1145/2335755.2335836

Moncalvo JM, Vilgalys R, Redhead SA, Johnson JE, James TY, Aime MC, Hofstetter V, Verduin SJ, Larsson E, Baroni TJ (2002) One hundred and seventeen clades of euagarics. Molecular Phylogenetics and Evolution 23(3): 357–400. https://doi.org/10.1016/S1055-7903(02)00027-1

Morgan AP (1905) North American species of *Marasmius*. Journal of Mycology 11(5): 201–212. https://doi.org/10.2307/3752425

Murrill W (1915) Agaricaceae (pars). Flora of North America 9: 286–296.

National list of species of Korea (2020) National Institute of Biological Resources. http://kbr.go.kr [Accessed on 14.10.2021]

Noordeloos ME (1983) Notulae as Floram agaricinam neerlandicam – I–III. *Marasmiellus, Macrocystidia* and *Rhodocybe*. Persoonia-Molecular Phylogeny and Evolution of Fungi 12: 31–49.

Noordeloos ME, Kuyper TW, Vellinga E (1999) Flora Agaricina Neerlandica Vol 4. CRC Press, Florida.
Oliveira JJ, Vargas-Isla R, Cabral TS, Rodrigues DP, Ishikawa NK (2019) Progress on the phylogeny of the Omphalotaceae: Gymnopus s. str., Marasmiellus s. str., Paragymnopus gen. nov. and Pusillomyces gen. nov. Mycological Progress 18(5): 713–739. https://doi.org/10.1007/s11557-019-01483-5

Park SS, Cho DH (1992) The Mycoflora of Higher Fungi in Mt. Paekdu and Adjacent Areas (I). The Korean Journal of Mycology 20: 11–28.

Petersen R, Hughes K (2014) New North American species of Gymnopus. North American Fungi 9(0): 1–22. https://doi.org/10.2509/naf2014.009.003

Petersen RH, Hughes KW (2016) Micromphale sect. Perforantia (Agaricales, Basidiomycetes); expansion and phylogenetic placement. MycoKeys 18: 1–122. https://doi.org/10.3897/mycokeys.18.10007

Petersen RH, Hughes KW (2017) An investigation on Mycetinis (Euagarics, Basidiomycota). MycoKeys 24: 1–139. https://doi.org/10.3897/mycokeys.24.12846

Petersen RH, Hughes KW (2021) Collybiopsis and its type species, Co. ramealis. Mycotaxon 136(2): 263–349. https://doi.org/10.5248/136.263

Razaq A, Ilyas S, Khalid AN (2020) Molecular systematics and evolutionary relationships of some inland gilled basidiomycetes from the Himalayan moist temperate forests of Pakistan based on rDNA marker. Pakistan Journal of Botany 52(3): 1055–1063. https://doi.org/10.30848/PJB2020-3(3)

Rehner SA, Samuels GJ (1994) Taxonomy and phylogeny of Gliocladium analysed from nuclear large subunit ribosomal DNA sequences. Mycological Research 98(6): 625–634. https://doi.org/10.1016/S0953-7562(09)80409-7

Retnowati A (2018) The species of Marasmiellus (Agaricales: Omphalotaceae) from Java and Bali. Gardens'. Bull, Singapore 70(1): 191–258. https://doi.org/10.26492/gbs70(1).2018-17

Rogers SO, Bendich AJ (1994) Extraction of total cellular DNA from plants, algae, and fungi. In: Plant molecular biology manual. Springer, 183–190. 10.1007/978-94-011-0511-8_12

Ryoo R, Antonín V, Ka KH (2020) Marasmioid and Gymnopedoid Fungi of the Republic of Korea. 8. Gymnopus Section Levipedes. Mycobiology 48(4): 252–262. https://doi.org/10.1080/12298093.2020.1769541

Sandoval-Leiva PA, McDonald JV, Thorn RG (2016) Gymnopanella nothofagi, a new genus and species of gymnopoid fungi (Omphalotaceae) from Chilean Nothofagus forest. Mycologia 108(4): 820–827. https://doi.org/10.3852/15-303

Seierstad KS, Carlsen T, Sætre GP, Miettinen O, Hofton TH, Kauzerud H (2013) A phyleogeographic study of a circum boreal polypore indicates introgression among ecologically differentiated cryptic lineages. Fungal Ecology 6(1): 119–128. https://doi.org/10.1016/j.funeco.2012.09.001

Singer R (1973) The genera Marasmiellus, Crepidotus and Simocybe in the neotropics. Nova Beih Nova Hedwigia 44: 1–517. https://doi.org/10.2307/3758379

Staud F (1857) Die Schwämme Mitteldeutschlands, insbesondere des Herzogthums Coburg. Dietz, Coburg.

Tekpinar A, Acar İ (2020) Fungal Systematics and Evolution: FUSE 6. Sydowia: 231–356. https://doi.org/10.1290/0380.sydowia72-2020-0271

Tolgor LI, Yu LI (2000) Study on fungal flora diversity in Daqinggou Nature Reserve. Shengwu Duoyangxing 8(1): 73–80. https://doi.org/10.17520/biods.2000010
Seven new *Collybiopsis* species

Vilgalys R, Hester M (1990) Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several *Cryptococcus* species. Journal of Bacteriology 172(8): 4238–4246. https://doi.org/10.1128/jb.172.8.4238-4246.1990

Wilson AW, Desjardin DE (2005) Phylogenetic relationships in the gymnopoid and marasmioid fungi (Basidiomycetes, euagarics clade). Mycologia 97(3): 667–679. https://doi.org/10.1080/15572536.2006.11832797

Yoshida S, Muramatsu Y (1998) Concentrations of alkali and alkaline earth elements in mushrooms and plants collected in a Japanese pine forest, and their relationship with 137Cs. Journal of Environmental Radioactivity 41(2): 183–205. https://doi.org/10.1016/S0265-931X(97)00098-2

**Supplementary material 1**

**Figure S1**
Authors: Ji Seon Kim, Yoonhee Cho, Ki Hyeong Park, Ji Hyun Park, Minkyeong Kim, Chang Sun Kim, Young Woon Lim
Data type: Jpg file.
Explanation note: Pileipellis elements of seven new species. **A** *Collybiopsis albicantipes* **B** *Co. clavicystidiata* **C** *Co. fulva* **D** *Co. orientisubnuda* **E** *Collybiopsis subumbilicata* **F** *Co. undulata* **G** *Co. vellerea*. Scale bars: 10 µm.

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Link: https://doi.org/10.3897/mycokeys.88.79266.suppl1

**Supplementary material 2**

**Figure S2**
Authors: Ji Seon Kim, Yoonhee Cho, Ki Hyeong Park, Ji Hyun Park, Minkyeong Kim, Chang Sun Kim, Young Woon Lim
Data type: Jpg file.
Explanation note: Comparison of the morphological characters of 16 Korean *Collybiopsis* species.

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Link: https://doi.org/10.3897/mycokeys.88.79266.suppl2
Supplementary material 3

Figure S3
Authors: Ji Seon Kim, Yoonhee Cho, Ki Hyeong Park, Ji Hyun Park, Minkyeong Kim, Chang Sun Kim, Young Woon Lim
Data type: Jpg file.
Explanation note: Sequence difference between the three species in the ITS region.
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Link: https://doi.org/10.3897/mycokeys.88.79266.suppl3