Morphological and Molecular Evidence Reveal Eight New Species of Gymnopus from Northeast China

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Abstract: Gymnopus is a widely distributed genus consisting of about 300 species thus far, including Gymnopus fusipes as a generic type. A total of nine species from China belong to the sect. Levipedes, including eight new species—Gymnopus longisterigmaticus, Gymnopus longus, Gymnopus macrosporus, Gymnopus striatus, Gymnopus changbaiensis, Gymnopus tomentosus, Gymnopus tilicola, and Gymnopus globulosus—which were delimited and proposed based on morphological and molecular evidence; and one new record from Jilin Province, China—Gymnopus erythropus. Detailed descriptions and illustrations are presented, as well as comparisons to similar species. Overall, our results broaden the morphological characterization of the genus. The pileipellis of sect. Levipedes typically takes on the “Dryophila structure”, while, in our findings, pileipellis terminal hyphae inflated to spherical to prolate were observed, in addition to extremely long basidia sterigma. The phylogenies inferred from the ITS and nLSU dataset supported the Gymnopus, which was defined by Oliveira et al. as a monophyletic genus, and the novel species as separate lineages within. A key to all species described in this study is also provided.

Keywords: Gymnopus sect. Levipedes; Gymnopus erythropus complex; new species; Northeast China; phylogenetic analysis

1. Introduction

The genus Gymnopus (Pers.) Roussel belongs to the family Omphalotaceae, according to Antonin and Noordeloos [1]. There is a long taxonomic research history on this genus, beginning with its proposal by Persoon in 1801 as a tribe of Agaricus L. [2]. Later, Fries [3] established Agaricus trib. Collybia Fr., transferring the species of Agaricus trib. Gymnopus Pers. into it accordingly. This perspective was widely accepted by other mycologists, until Staude [4] established the genus Collybia (Fr.) Staude. Singer [5–7] divided the genus Collybia into nine sections—sect. Stripedes (Fr.) Quél., sect. Dictyoplocae (Mont.) Singer, sect. Ioeffalae Sing. ex Halling, sect. Levipedes (Fr.) Quél., sect. Vestipedes (Fr.) Quél., sect. Subfulmosae Sing., sect. Cyistiatae Sing., sect. Isotrima Sing., and sect. Collybia Sing.—in his book, The Agaricales in Modern Taxonomy. It is the embryonic form of the modern taxonomy of the genus Collybia (Gymnopus). Based on their research [8–10], Halling, Antonin and Noordeloos pointed out that the genus Collybia had a problematic and controversial taxonomy and, thus, lacked a clear definition; then Antonin et al. [11] shifted the section and species into Gymnopus and Rhodocollybia Singer, leaving three species in the genus Collybia. The members of Gymnopus, in the conception of Antonin and Noordeloos [1,12], are mainly characterized by basidiomata, usually collybioid, marasmioid, and gymnopoid, stipes only
rarely arising from the sclerotia, which is a white spore print with smooth basidiospores that are commonly ellipsoid to oblong, typically the presence of clamp connections, a cutis-type pileipellis, ixocutis or similar to a trichoderm, terminal elements mostly coralloid to diverticulate, and usually encrusted pigments.

With the advent and development of molecular technologies, the phylogenetic analysis of marasmioid and collybioid fungi based on sequences of nuclear ribosomal DNA is just beginning to help clarify generic and infrageneric circumscriptions. Moncalvo et al. [13] pointed out that the genus *Gymnopus* was multiphyletic. Mata et al. [14], who found similar conclusions, stated that *Gymnopus* is more closely related to *Marasmiellus* Murrill. The type specimen of *Marasmiellus*, *Marasmiellus juniperinus* Murrill, was confirmed within *Gymnopus* sect. *Levipedes* (Fr.) Antonín, Halling and Noordel. [12]. More recently, Oliveira et al. [15] redefined the genus *Gymnopus* more strictly standard based on their combined ITS + nLSU phylogenetic analysis. In its conception, the key features of the genus *Gymnopus* are collybioid (rarely tricholomatoid or marasmioid) basidiomata, free, emarginate, or adnate lamellae that are usually crowded, an insititious stipe or not, usually with a strigose base; a white spore print, basidiospores ellipsoid to short-oblong, inamyloid; cheilocystidia usually present, or a variety of cheilocystidia, a cutis or ixocutis pileipellis with radially arranged cylindrical hyphae or interwoven more akin to a trichoderm or ixotrichoderm, made up of irregular coralloid terminal elements (“Dryophila structures”)—often incrusted, diverticulate hyphal elements, mixed with broom cells and coralloid hyphae; and clamp connections present in all tissues. As a result, *Gymnopus* sect. *Vestipedes* (Fr.) Antonín, Halling and Noordel. is segregated and placed within *Marasmiellus* s. str, and *Gymnopus* sect. *Perforanita* (Singer) R.H. Petersen is considered a new independent genus *Paragymnopus* J.S. Oliveira. In addition, some *Gymnopus* species were transferred to two new genera [16].

Most species of *Gymnopus* sect. *Levipedes* (Quél.) Halling have smooth, polished, or pubescent stipe; pileipellis mostly as an entangled trichoderm (never radially oriented), composed of inflated, often lobed elements or coralloid (“Dryophila structures”); non-dextrinoid trama and elements, with some species turning green in alkali [1,17]. *Gymnopus erythropus* (Pers.) Antonín, Halling and Noordel. is one of the most confusing species in this section. This species was named by Persoon as *Agaricus erythropus* Pers. [2], and then transferred to *Gymnopus* [11]. However, Persoon had a broad conception of this species. Singer [18] selected a neotype from the herbarium of Persoon, labeled *Agaricus erythropus*, which was confirmed to be a *Mycena* (Pers.) Roussel species later on. There remained more specimens labeled *Agaricus erythropus* in the herbarium of Persoon, until Jansen [19] studied the material and found that one specimen fit well with the current concept of *Collybia erythropus* (Pers.) P. Kumm. (≡ *Gymnopus erythropus*); considering this, Singer’s choice was rejected. Prior to the current study, only two red stipe species had been reported in this section *Gymnopus erythropus*, and *Gymnopus fagiphilus* (Velen.) Antonín, Halling, and Noordel. These two species are morphologically very similar, with the clear distinguishing factor being the tomentose stipe. Specifically, *Gymnopus erythropus* have a smooth stipe, while those with a dense tomentose at the base of the stipe are *Gymnopus fagiphilus*.

Approximately 300 species have been validly published in the genus *Gymnopus* [20], with most species having been reported from Europe and America. However, research on *Gymnopus* in China is lacking. Teng [21] was the first to report a *Gymnopus* species in China; based on the genus *Collybia*, four taxa were reported. Later, Tai [22] reported eight taxa. Deng [23], a preliminary study on the resources of the genus *Gymnopus* in Southern China, reported 19 taxa. Recently, three new species and 11 new records were recorded from China [23–29]. Until now, 24 species of *Gymnopus* s. str. have been recognized from China.

This paper aims to describe and illustrate nine species of *Gymnopus* sect. *Levipedes*—eight species new to science, and one new record from Jilin Province, China—based on morphology and molecular studies.
2. Materials and Methods

2.1. Sampling and Morphological Studies

The studied specimens were photographed in situ. The size of the basidiomata was measured when fresh. After examination and description of the fresh macroscopic characteristics, the specimens were dried in an electric drier at 40–45 °C.

Descriptions of the macroscopic characteristics were based on field notes and photographs, with the colors corresponding to the Flora of British fungi: Color identification chart [30]. The dried specimens were rehydrated in 94% ethanol for microscopic examination, and then mounted in 3% potassium hydroxide (KOH), 1% Congo red dissolved in 10 mL distilled water, and Melzer’s reagent (1.5 g potassium iodide, 0.5 g crystalline iodine and 22 g chloral hydrate dissolved in 20 mL distilled water) [31]; they were then examined with a Zeiss Axio lab. A1 microscope at magnifications up to 1000×. All measurements were taken from the sections mounted in the 1% Congo red. For each specimen, a minimum of 40 basidiospores, 20 basidia, 20 cheilocystidia, and 20 widths of pileipellis were measured from two different basidiocarps. When reporting the variation in the size of the basidiospores, basidia, cheilocystidia, and width of the pileipellis, 5% of the measurements were excluded from each end of the range, and are given in parentheses. The basidiospores measurements are given as length × width (L × W). Q denotes the variation in the ratio of L to W among the studied specimens, and Qm denotes the average Q value of all the basidiospores ± standard deviation. “I” refers to the number of lamellulae between every two complete lamellae, and “L” refers to the number of complete lamellae. The specimens examined are deposited in the Herbarium of Mycology of Jilin Agricultural University (HMJAU).

2.2. DNA Extraction, PCR Amplification, and Sequencing

The total DNA was extracted from dried specimens by using the NuClean Plant Genomic DNA Kit (Kangwei Century Biotechnology Company Limited, Beijing, China), according to the manufacturer’s instructions. Sequences of the internal transcribed spacer (ITS) region, and nuclear large ribosomal subunits (nLSU) were used for phylogenetic analysis. The ITS sequence was amplified by using the primer pair ITS1-F (CTT GGT CAT TTA GAG GAA GTA A) and ITS4-B (CAG GAG ACT TGT ACA CGG TCC AG) [32], and the nLSU sequence was amplified by using the primer pair LROR (GTA CCC GCT GAA CTT AAC) and LR7 (TAC TAC CAC CAA GAT CT) [33,34]. PCR reactions (25 µL) contained 8 µL 2 × EasyTaq® PCR SuperMix (TransGen Biotech Co., Ltd., Beijing, China), 1 µL 10 µM primer L, 1 µL 10 µM primer R, 3 µL DNA solution, and 12 µL dd H2O. The reaction programs were as follows: for the ITS, initial denaturation at 94 °C for 4 min, followed by 30 cycles at 94 °C for 1 min, 54 °C for 1 min and 72 °C for 1 min, and a final extension of 72 °C for 10 min [35]; for the nLSU, initial denaturation at 95 °C for 3 min, followed by 30 cycles at 94 °C for 30 s, 47 °C for 45 s, and 72 °C for 90 s, and a final extension of 72 °C for 10 min [36]. The PCR products were visualized via UV light after electrophoresis on 1% agarose gels stained with ethidium bromide and purified by using the Genview High-Efficiency Agarose Gels DNA Purification Kit (Gen-View Scientific Inc., Galveston, TX, USA). The purified PCR products were then sent to Sangon Biotech Limited Company (Shanghai, China) for sequencing, using the Sanger method. The new sequences were deposited in GenBank (http://www.ncbi.nlm.nih.gov/genbank (accessed on 17 November 2021); see Table 1).

2.3. Data Analysis

Based on the results of BLAST and morphological similarities, the sequences obtained and related to these samples were collected and are listed in Table 1. We used a dataset of ITS and nLSU resign comprising sequences from this study, with 49 representative sequences showing the highest similarity to Gymnopus spp. This dataset included all Gymnopus s. str. section (sect. Androcacei (Kühner) Antonín and Noordel., sect. Levipedes (Quél.) Halling, sect. Impudicae (Antonín and Noordel.) Antonín and Noordel., and sect. Gymnopus
(Pers.) Roussel) to further explore the relationships of the newly sequenced Chinese specimens within the genus Gymnopus. Moreover, the species within this genus and those in allied genera, including Lentinula Earle, Rhodocollybia Singer, Mycetinis Earle, Marasmiellus Murrill, Collybiopsis (J. Schröt.) Earle, and Paragymnopus J.S. Oliveira were included. The sequences of Marasmius sect. Globulares Kühner, Marasmius stenophyllus Mont., Marasmius aurantiomaculatus Hongo, Marasmius brunneoaspermus Har. Takah., Marasmius maximus Hongo, and Marasmius nivicola Har. Takah., were selected as the outgroup taxa [15].

For the dataset, each gene region was aligned by using ClustalX [37], MACSE V2.03 [38], or MAFFT 7.490 [39], and then manually adjusted in BioEdit 7.0.5.3 [40]. The datasets first were aligned, and then the ITS and nLSU sequences were combined with Phylosuit V1.2.2 [41]. The best-fit evolutionary model was estimated by using Modelfinder [42]. Following the models, Bayesian inference (BI) algorithms were used to perform the phylogenetic analysis. Specifically, BI was calculated with MrBayes 3.2.6 with a general time-reversible DNA substitution model and a gamma distribution rate variation across the sites [43]. Four Markov chains were run for two runs from random starting trees for two million generations until the split deviation frequency value was <0.01; the trees were sampled every 100 generations. The first 25% of the sampled trees were discarded as burn-in, while all remaining trees were used to construct a 50% majority consensus tree and for calculating the Bayesian posterior probabilities (BPPS). RaxmlGUI 2.0.5 [44] was used for maximum likelihood (ML) analysis, along with 1000 bootstraps (BS) replicates, using the GTRGAMMA algorithm to perform a tree inference and search for the optimal topology [45]. Then the FigTree v1.3.1 was used to visualize the resulting trees.

Table 1. Voucher/specimen numbers, country, and GenBank accession numbers of the specimens included in this study. Sequences produced in this study are in bold.

| Scientific Name                | Country       | Voucher/SPECimen Numbers | GenBank Accession Numbers | References |
|--------------------------------|---------------|--------------------------|---------------------------|------------|
| Collybiopsis dichroa           | USA           | TENN56726                 | AY256702                  | [46]       |
| Co. filamentipes               | USA           | TENN-F-065861             | MN897832                  |            |
| Co. furtiva                    | USA           | SFSU: DED4425             | DQ450031                  | [47]       |
| Co. hasanskyensis              | Russia        | TENN-F-060730             | MN897829                  | [47]       |
| Co. juniperina                 | USA           | TENN59540                 | AY256708                  | [14]       |
| Co. melanopus                  | Indonesia     | SFSU: A.W. Wilson 54      | NR_137539                 | NG_060624  | [48]       |
| Co. melanoporus                | China         | LF1758                    | KU529307                  | [23]       |
| Co. mesoamericana              | Costa Rica    | TENN 058613               | NR_119583                 | KY019632   | [49,50]    |
| Co. minor                      | USA           | TENN-F-059993             | MN413334                  | MW396880   | [47]       |
| Co. parvula                    | USA           | TENN-F-059993             | MN41334                   | Unpublished |
| Co. stonophylla                | USA           | TENN59449                 | DQ450033                  | [46]       |
| Gymnopus alkalivirens          | USA           | TENN51249                 | DQ450000                  | [46]       |
| G. allifoliotrichodactylus      | China         | GDGM76695                 | MT023344                  | MT017526   | [25]       |
| G. alpinus                     | Latvia        | CB16251                   | JX536168                  | [51]       |
| G. androsaceus                 | Russia        | TENN-F-59594              | KY026663                  | KY026663   | [50]       |
| G. androsaceus                 | France        | CBS239.53                 | MH857174                  | MH868713   | [52]       |
| G. aurantipes                  | Czech Republic| BRNM665362                | JX536172                  | [51]       |
| G. aureus                      | USA           | AWW116                    | AY263432                  | AY639410   | [48]       |
| G. bicolor                     | USA           | AWW116                    | AY263423                  | AY639411   | [48]       |
| G. bifurcatus                  | USA           | TENN58541                 | DQ450054                  | [48]       |
| G. brunneiraciulus             | USA           | AWW01                     | AY263434                  | AY639412   | [48]       |
| G. changbaiensis               | China         | HMJA060300                | OM030272                  | OM033387   | this study |
| G. changbaiensis               | China         | HMJA060301                | OM030273                  | OM033388   | this study |
| G. changbaiensis               | China         | HMJA060302                | OM030274                  | OM033389   | this study |
| Scientific Name       | Country       | Voucher/Specimen Numbers | GenBank Accession Numbers | References |
|----------------------|---------------|--------------------------|---------------------------|------------|
| G. collybioides      | Costa Rica    | TENN58020                | AF505772                  | [46]       |
| G. confusus          | Sweden        | TENN50524                | DQ450044                  | [46]       |
| G. confusus          | USA           | TENN55695                | DQ450050                  | [46]       |
| G. cylindricus       | Costa Rica    | TENN-058097              | NR_119464                 | [49]       |
| G. densiramellatus   | Republic of Korea | BRNM714984            | KP336686 KP336695         | [36]       |
| G. dryophilus        | Czech Republic | BRNM695586              | JX536143                  | [51]       |
| G. dryophilus        | Germany       | BRNM737691              | JX536139                  | [51]       |
| G. dryophilus        | China         | HMAS290095              | MK966542 Unpublished      |            |
| G. dryophilus        | Japan         | Duke31                  | DQ480099                  | [46]       |
| G. dryophioides      | Republic of Korea | BRNM781447            | MH589967 MH589985         | [53]       |
|                      | USA           | TENN59141               | AF505778                  | [46]       |
| G. erythrophorus     | Czech Republic | BRNM714784              | JX536136                  | [51]       |
|                      | USA           | JFA12910                | DQ449998                  | [46]       |
| G. erythrophorus     | Austria       | TENN59329               | AF505786                  | [46]       |
| G. erythropus         | China         | HMJAU60313              | OM030281 OM033395         | this study |
| G. erythropus         | China         | HMJAU60315              | OM030280 OM033396         | this study |
|                      | Czech Republic | BRNM707079            | JX536129                  | [51]       |
| G. fusipes           | Austria       | TENN59300               | AF505777                  | [46]       |
|                      | France        | TENN59217               | AY256710 AY256710         | [14]       |
| G. globulosus        | China         | HMJAU60307              | OM030269 OM033406         | this study |
| G. globulosus        | China         | HMJAU60308              | OM030270 OM033407         | this study |
| G. globulosus        | China         | HMJAU60308              | OM030271 OM033408         | this study |
| G. hybridus          | Italy         | BRNM695773              | JX536177                  | [51]       |
| G. inexpectatus      | Italy         | BRNM70709               | EU622905 EU622906         | [54]       |
| G. inusitatus        | Spain         | SCM B-4058              | JN247553 JN247557         | [51]       |
| G. junquilleus       | USA           | TENN55224               | NR_119582                 | [49]       |
| G. lanipes           | Spain         | BRNM670686              | JX536137                  | [51]       |
| G. longisterigmaticus| China         | HMJAU60288              | OM030282 OM033403         | this study |
| G. longisterigmaticus| China         | HMJAU60289              | OM030283 OM033404         | this study |
| G. longisterigmaticus| China         | HMJAU60290              | OM030284 OM033405         | this study |
| G. longus            | China         | HMJAU60291              | OM030285 OM033400         | this study |
| G. longus            | China         | HMJAU60292              | OM030286 OM033401         | this study |
| G. longus            | China         | HMJAU60293              | OM030287 OM033402         | this study |
| G. macrosporus       | China         | HMJAU60294              | OM030266 OM033397         | this study |
| G. macrosporus       | China         | HMJAU60295              | OM030267 OM033398         | this study |
| G. macrosporus       | China         | HMJAU60296              | OM030268 OM033399         | this study |
| G. ocior             | Czech Republic | BRNM699795            | JX536166                  | [51]       |
| G. pullipes          | China         | GDGM81513               | MW582856                  | [24]       |
| G. ramulicola        | China         | GDGM44256               | KU321529                  | [27]       |
| G. similis           | Republic of Korea | BRNM766739            | KP336692 KP336699         | [36]       |
| G. similis           | China         | GDGM78308               | MT023352 MT017530         | [25]       |
| G. striatus          | China         | HMJAU60297              | OM030263 OM033384         | this study |
| G. striatus          | China         | HMJAU60298              | OM030264 OM033385         | this study |
| G. striatus          | China         | HMJAU60299              | OM030265 OM033386         | this study |
| G. tiliicola         | China         | HMJAU60305              | OM030275 OM033393         | this study |
| G. tiliicola         | China         | HMJAU60306              | OM030276 OM033394         | this study |
| G. tiliicola         | China         | HMJAU60307              | OM030277 OM033392         | this study |
| G. tomentosus        | China         | HMJAU60303              | OM030278 OM033390         | this study |
| G. tomentosus        | China         | HMJAU60304              | OM030279 OM033391         | this study |
Table 1. Cont.

| Scientific Name            | Country          | Voucher/Specimen Numbers | GenBank Accession Numbers | References |
|----------------------------|------------------|--------------------------|---------------------------|------------|
| Letinula aciculospora      | Costa Rica       | TENN37996                | AY016443                  | [55]       |
| L. boryana                 | Brazil           | TENN58368                | AY016440                  | [55]       |
| L. edodes                  | China            | STCL125                  | AF031183                  | [56]       |
| Marasmius aurantiocurrugineus | Republic of Korea | BRNM714752               | FJ904962                  | MK278334   | [57]       |
| M. bruneospermus           | Republic of Korea | KPM-NC0005011            | FJ904969                  | FJ904951   | [57]       |
| M. maximus                 | Republic of Korea | BRNM714570               | FJ904976                  | FJ904958   | [57]       |
| M. nivicola                | Republic of Korea | KPM-NC0006038            | FJ904973                  | FJ904955   | [57]       |
| Marasmiellus ramealis      | Sweden           | TENN50324                | DQ450030                  | [46]       |
| Mycetinis alliaceus        | Russia           | TENN-F-55630              | KY696784                  | KY696752   | [58]       |
| My. curraniae              | New Zealand      | PDD95301                 | KY696778                  | [58]       |
| My. opacus                 | USA              | TENN-F-59451              | KY696755                  | [58]       |
| My. scorodonius            | Switzerland      | TENN-F-59451              | KY696725                  | [58]       |
| Paragymnopus foliophilus   | USA              | TENN-F-68183              | KY026705                  | KY026705   | [50]       |
| P. perforans               | Sweden           | TENN-F-50319              | KY026625                  | KY026625   | [50]       |
| P. pinophilus              | USA              | TENN-F-69207              | KY026725                  | KY026725   | [50]       |
| Rhodocollyba butyracea     | Sweden           | TENN53580                | AY313293                  | [46]       |
| R. butyracea               | China            | HFJAU0269                | MN258680                  | Unpublished |
| R. maculata                | Dominican Republic | TFB11720                | KT205402                  | [59]       |
| R. maculata                | USA              | TENN59459                | AY313296                  | [46]       |

3. Results

3.1. Phylogenetic Analyses

In the dataset, 143 sequences derived from two gene loci (ITS and nLSU) from 92 samples were used to build phylogenetic trees; 50 of these were newly generated, with 25 ITS sequences and 25 nLSU sequences. The phylogenetic construction performed via ML and BI analysis for the two combined datasets showed a similar topology. The combined ITS and nLSU dataset represented 63 taxa and 2600 characters after being trimmed. The Bayesian analysis was run for two million generations and resulted in an average standard deviation of split frequencies of 0.004989. The same dataset and alignment were analyzed by using the ML method. In the phylogenetic tree, six clades corresponding to Gymnopus, Rhodocollybia, Lentinula, Marasmiellus, Marasmius, Mycetina, Collybiopsis, and Paragymnopus were revealed (Figures 1 and 2). Twenty-one sampled specimens formed eight new species and were clustered in a clade comprising the species of Gymnopus sect. (Figure 2). At the same time, two sampled specimens—clustered with Gymnopus erythropus with strong support—were confirmed as new records from Jilin Province, China.

The phylogeny inferred from the dataset of ITS and nLSU region recovered Gymnopus s. str. as a monophyletic genus divided into four clades, sect. Androcei clade, sect. Levipedes clade, sect. Impudicae clade, and sect. Gymnopus clade, formed a sister clade to Rhodocollybia, Paragymnopus, and Lentinula (Figure 1). The sect. Levipedes clade was mainly divided into three clades, the red stipe species formed an independent clade, and the Gymnopus dryophilus complex species formed an independent clade. These two clades mentioned above are near the species Gymnopus alkalivirens (Singer) Halling that turns green in KOH, representing Gymnopus sect. Levipedes subsect. Alkalivirentes Antonín and Noorde.
3.2. Taxonomy

**Gymnopus longisterigmaticus** J.J. Hu, B. Zhang and Y. Li sp. nov.

Figures 3a and 4

MycoBank: MB 842333

Etymology: The epithet “longisterigmaticus” refers to the extremely long sterigmata of the basidia.

Diagnosis: This species is distinguished from closed species by pileus brown at the center, light brown to yellow towards the margin, margin light yellow to yellowish white, stipe reddish brown, covered with white to light reddish brown density hairs at base, basidia four-spored, sterigmata extremely long, pileipellis wider than *Gymnopus longus* and *Gymnopus macrosporus*, branched, pigment yellowish brown incrusting in pileipellis, and larger basidiospores.

Type: China. Jilin Province: Yanbian Korean Autonomous Prefecture, Antu County, Erdaobaihe Town, 42.39° N, 128.11° E, 4 September 2018, Jia-Jun Hu and Bo Zhang, HMJAU 60288, holotype (GenBank accession no.: ITS = OM030282, nLSU = OM033403).

Basidiomata small-to-medium-sized, scattered to gregarious. Pileus convex to applanate, 1.5–3.2 cm diameter, smooth, hygrophanus, brown at the center, light brown to yellow towards the margin, margin light yellow to yellowish white, entire. Context thin, fleshy, light reddish brown, odorless. Stipe center, cylindrical, 3.2–5.0 cm long and 0.2–0.3 cm wide, reddish brown, smooth, covered with white to light reddish brown density hairs at base, fistulose, fibrous. Lamellae subfree to adnate, white to light yellow, I = 1–3, L = 15–18, crowded.
Figure 2. Cont.
Figure 2. Maximum likelihood phylogenetic tree generated from the ITS and nLSU dataset. Bootstraps values (BS) ≥ 70% from ML analysis and Bayesian posterior probabilities (BPPS) ≥ 0.90 are shown on the branches. Newly sequenced collections are indicated in bold, and the type specimens are denoted by (T).

Basidiospores elliptic, (6.2) 6.7–9.0 × (3.0) 3.1–4.3 (5.0) µm, Q = (1.40) 1.67–2.25 (2.26), Qm = 1.93 ± 0.20, smooth, hyaline, inamyloid, thin-walled. Basidia clavate, (18) 19–27 (28) × (5) 6–10 µm, four-spored, thin-walled, smooth, hyaline; sterigmata extremely long, up to 40 µm. Cheilocystidia abundant, clavate, with obtuse on the top, or branched, (16) 18–27 × (4) 5–8 (9) µm, thin-walled, smooth, hyaline. Pileipellis a cutis, made up of irregularly branched hyphae, inflated, 10–27 (35) µm wide, hyaline to light yellow, smooth or pigment yellowish brown incrusting in pileipellis, thin-walled, clamps present.

Ecology: Grows on the deciduous layer or rotten branches in coniferous and broad-leaved mixed forest.

Distribution: China (Jilin Province).

Other specimen examined: China. Jilin Province: Yanbian Korean Autonomous Prefecture, Antu County, Erdaobaihe Town, 42.39° N, 128.11° E, 13 September 2019, Jia-Jun Hu and Bo Zhang, HMJAU 60289 (GenBank accession no.: ITS = OM030283, nLSU = OM033404); Yanbian Korean Autonomous Prefecture, Antu County, Erdaobaihe Town, 42.39° N, 128.11° E, 13 September 2019, Jia-Jun Hu and Bo Zhang, HMJAU 60290 (GenBank accession no.: ITS = OM030284, nLSU = OM033405).

Note: Morphologically, *Gymnopus longisterigmaticus* is similar to *Gymnopus erythropus* and *Gymnopus fagiphilus* with its reddish brown stipe. However, *Gymnopus longisterigmaticus* differs from *Gymnopus erythropus* with its light reddish brown density hairs on the stipe, extremely long sterigmata of basidiomata (up to 40 µm), different shape of cheilocystidia—cheilocystidia of *Gymnopus erythropus* is clavate to subclavate or somewhat flexuous, coralloid at apex sometimes [1], while clavate of *Gymnopus longisterigmaticus*, and quite larger basidiospores [(6.2) 6.7–9.0 × (3.0) 3.1–4.3 (5.0) µm].
Gymnopus longisterigmaticus and Gymnopus fagiphilus are both covered with hairs on the stipe, but the lamellae of Gymnopus longisterigmaticus is white to light yellow, while that of Gymnopus fagiphilus is pinkish brown to pinkish yellow; on the other hand, Gymnopus longisterigmaticus has extremely long sterigmata of the basidia and lack of chaulocystidia. Moreover, the different shape and size of cheilocystidia can differentiate Gymnopus longisterigmaticus from Gymnopus fagiphilus. The cheilocystidia of Gymnopus fagiphilus is usually irregularly clavate, often with lobed apex or with short-to-long rostrum, sometimes very slender and lageniform and quite larger [15–40 (60) × 4.0–8.0 (10) µm] [1], while cheilocystidia of Gymnopus longisterigmaticus is clavate, branched or obtuse.

Figure 3. Fresh basidiomata of Gymnopus species: (a) Gymnopus longisterigmaticus (Holotype, HMJAU 60288), (b) Gymnopus longus (Holotype, HMJAU 60291), (c) Gymnopus macrosorpus (Holotype, HMJAU 60294), (d) Gymnopus tiliicola (Holotype, HMJAU 60304), (e) Gymnopus globulosus (Holotype, HMJAU 60308), (f) Gymnopus changbaiensis (HMJAU 60300), (g) Gymnopus striatus (Holotype, HMJAU 60297), (h) Gymnopus erythropus (HMJAU 60315), and (i) Gymnopus tomentosus (Holotype, HMJAU 60303). Scale bars = 1 cm.
Figure 4. Morphological characteristics of Gymnopus longusterigmaticus (HMJAU 60288, holotype): (a) basidiomata, (b) pileipellis, (c) basidiospores, (d) basidia, and (e) cheilocystidia. Scale bars: 1 cm (a), 25 µm (b), and 5 µm (c–e).

Gymnopus longus J.J. Hu, B. Zhang and Y. Li sp. nov.
Figures 3b and 5
MycoBank: MB 842334
Etymology: The epithet “longus” refers to the extremely long sterigmata of the basidia.
Diagnosis: Gymnopus longus can be easily differentiated from closely-related species Gymnopus fagiphilus by its pileus reddish brown, stipe reddish brown, with brown farinose on the upper part and white to light reddish brown tomentose at the base, basidia 2- or 4-spored, sterigmata extremely long, and smaller basidiospores.
Type: China. Jilin Province: Yanbian Korean Autonomous Prefecture, Antu County, Erdaobaihe Town, 42.39° N, 128.11° E, 4 September 2018, Jia-Jun Hu, Bo Zhang, and Gui-Ping Zhao, HMJAU 60291, holotype (GenBank accession no.: ITS = OM030285, nLSU = OM033400).
Basidiomata small-to-medium-sized, scattered to gregarious. Pileus 1.7–3.7 cm in diameter, convex to applanate or revolute, smooth, hygrophanous, reddish brown at the center, towards margin light reddish brown to brown; margin white to light yellow or light brown, entire. Context thin, fleshy, light reddish brown, odorless. Stipe central, cylindrical to clavate, 3.7–4.3 cm long and 0.3–0.6 cm wide, reddish brown, with brown farinose on the upper part, and white to light reddish brown tomentose at the base, hollow, filiform. Lamellae adnate, white to light yellow, I = 5–7, L = 19–24, crowded. Spores print unknown.
Basidiospores (5.6) 6.0–8.0 × (3.0) 3.1–4.1 (4.9) µm, Q = (1.27) 1.47–2.19 (2.58), Qm = 1.8 ± 0.24, oblong, smooth, hyaline, thin-walled, inamyloid. Basidia (19) 20–28 (29) × 6–9 µm, two- or four-spored, hyaline, thin-walled, clavate; sterigmata extremely long, up to 33 µm long. Cheilocystidia (21) 22–29 (30) × 5–7 µm, mass, clavate, with obtuse on the top, hyaline, thin-walled, smooth. Pileipellis a translation between a cutis and a trichoderm, made up of irregularly interwoven, repent or ascending, inflated hyphae with inflated and irregularly branched terminal elements, hyaline to light brown, (6) 7–13 (15) µm wide, smooth or pigment yellowish brown incrusting in pileipellis.
Ecology: Grows on the deciduous layer or rotten branches in coniferous and broad-leaved mixed forest.
Other specimen examined: China. Jilin Province: Yanbian Korean Autonomous Prefecture, Antu County, Erdaobaihe Town, 42.39° N, 128.11° E, 4 September 2018, Jia-Jun Hu, Bo Zhang, and Gui-Ping Zhao, HMJAU 60292 (GenBank accession no.: ITS = OM030286, nLSU = OM033401); Yanbian Korean Autonomous Prefecture, Antu County, Erdaobaihe
Note: *Gymnopus longus* is closed to *Gymnopus erythropus*, *Gymnopus fagiphilus*, and *Gymnopus longisterigmaticus* in morphological, because of the red pileus and stipe. However, *Gymnopus longus* differs from *Gymnopus erythropus* by being covered with brown farinose on the upper part, white to light reddish brown tomentose at the base, slight thin basidiospores, smaller Qm [1], and extremely long sterigmata (up to 33 µm long).

A deeper color pileus, covered with brown farinose on the stipe, smaller basidiospores, clavate with obtuse cheilocystidia, and pileipellis a translation between a cutis and a trichoderm differs *Gymnopus longisterigmaticus* from *Gymnopus longus*. *Gymnopus longus* differs from *Gymnopus fagiphilus* by a farinose stipe, deep color pileus and stipe, white lamellae, smaller basidiospores, lack of caulocystidia, and uncoralloid pileipellis [1].

**Figure 5.** Morphological characteristics of *Gymnopus longus* (HMJAU 60291, holotype): (a) basidiomata, (b) pileipellis, (c) basidiospores, (d) basidia, and (e) cheilocystidia. Scale bars: 1 cm (a), 25 µm (b), and 5 µm (c–e).

*Gymnopus macrosporus* J.J. Hu, B. Zhang and Y. Li sp. nov.

Figures 3c and 6

MycoBank: MB 842335

Etymology: the epithet “*macrosporus*” refers to the big basidiospores of this species.

Diagnosis: This species is distinguished from closed species by a convex to applanate pileus that is deep reddish brown at the center and reddish brown to yellowish brown toward the margin, with the margin beige to light yellow, striped; a deep reddish brown to reddish brown stipe with smooth, light yellow to light reddish brown tomentose at the base, coralloid pileipellis, bigger basidiospores, and extremely long basidia sterigmata.

Type: China. Jilin Province: Yanbian Korean Autonomous Prefecture, Antu County, Erdaobaihe Town, 42.39° N, 128.11° E, 4 September 2018, Jia-Jun Hu and Bo Zhang, HMJAU 60294, holotype (GenBank accession no.: ITS = OM030266, nLSU = OM033397).

Basidiomata small-to-medium-sized, gregarious. Pileus convex to applanate, 1.2–4.6 cm diameter, smooth, hygrophanus, deep reddish brown at the center, reddish brown to yellowish brown towards margin; margin beige to light yellow, striped, entire, wavy. Context thin, fleshy, light reddish brown to light yellowish brown, odorless. Stipe center, cylindrical, 7.8–9.5 cm long and 0.2–0.5 cm wide, deep reddish brown to reddish brown,
smooth, fistulose, fibrous, and light yellow to light reddish brown tomentose at the base. Lamellae adnexed to adnate or near free, light yellow, I = 1–3, L = 13–17, crowded.

Basidiospores elliptic, (6.0) 6.8–7.9 (8.3) × (3.0) 3.1–4.2 (4.3) µm, Q = (1.63) 1.67–2.32 (2.37), Qm = 1.88 ± 0.18, smooth, hyaline, inamyloid, thin-walled. Basidia clavate, 20–29 × 6–9 µm, two- or four-spored, thin-walled, smooth, hyaline; sterigmata extremely long, up to 32 µm. Cheilocystidia abundant, clavate, with obtuse on the top, 20–28 (30) × 5 (6)–9 µm, thin-walled, smooth, hyaline. Pileipellis a cutis, made up of irregular branched or weakly coralloid hyphae, inflated, 10–27 (35) µm wide, hyaline to light yellow, smooth, thin-walled, clamps present.

Ecology: Grows on the deciduous layer or rotten branches in coniferous and broad-leaved mixed forest.

Distribution: China (Jilin Province)

Other specimen examined: China. Jilin Province: Yanbian Korean Autonomous Prefecture, Erdaobaihe Town, 42.39° N, 128.11° E, 4 September 2018, Jia-Jun Hu and Bo Zhang, HMJAU 60295 (GenBank accession no.: ITS = OM030267, nLSU = OM033398); Yanbian Korean Autonomous Prefecture, Antu County, Erdaobaihe Town, 42.39° N, 128.11° E, 13 September 2019, Jia-Jun Hu and Bo Zhang, HMJAU 60296 (GenBank accession no.: ITS = OM030268, nLSU = OM033399).

Note: Gymnopus macrosporus is morphologically similar to Gymnopus longisterigmaticus and Gymnopus longus because of its reddish brown, tomentose stipe, and long sterigmata of basidia. Gymnopus macrosporus differs from Gymnopus longus due to its pileus in a darker color—pileus deep reddish brown at center, reddish brown to yellowish brown towards margin; margin beige to light yellow, striped characteristics, and smooth texture on the upper part of the stipe, coralloid and without pigment incrusting pileipellis. These two Gymnopus species have a similar basidiospore size; however, the Qm of Gymnopus macrosporus is larger than Gymnopus longus. Gymnopus longisterigmaticus differs in smooth, pale color, and unstriped pileus; pileipellis a bit wider and pigment yellowish brown incrusting in pileipellis, and it has bigger basidiospores [(6.2) 6.7–9.0 × (3.0) 3.1–4.3 (5.0) µm].

Figure 6. Morphological characteristics of Gymnopus macrosporus (HMJAU 60294, holotype): (a) basidiomata, (b) pileipellis, (c) basidiospores, (d) basidia, and (e) cheilocystidia. Scale bars: 1 cm (a), 25 µm (b), and 5 µm (c–e).
*Gymnopus striatus* J.J Hu, B. Zhang and Y. Li sp. nov.

Figures 3g and 7

MycoBank: MB 842336

Etymology: the epithet “striatus” refers to the striped stipe of this species.

Diagnosis: This species is distinguished from closed species by a cinnamon pileus, with a lighter color toward the margin and a white to light yellow margin, striped; yellow to light brown lamellae, a deep reddish brown stipe, longitudinal striped stipe up to 1/3 covered with yellow to light brown hairs (from the base upward), short sterigmata of basidia, and smaller basidiospores.

Type: China. Jilin Province: Yanbian Korean Autonomous Prefecture, Antu County, Erdaobaihe Town, 42.39° N, 128.11° E, 9 September 2019, Jia-Jun Hu, Gui-Ping Zhao, and Bo Zhang, HMJAU 60297, holotype (GenBank accession no.: ITS = OM030263, nLSU = OM033384).

Basidiomata small-to-medium-sized, gregarious. Pileus convex to applanate, depressed when old, 2.3–4.1 cm diameter, smooth, hygrophanus, cinnamon at the center, brown to light brown towards margin; margin white to light yellow, striped, entire, wavy. Context thin, fleshy, light yellowish brown, odorless. Stipe center, cylindrical to clavate, 5.5–7.0 cm long and 0.3–0.8 cm wide, deep reddish brown to reddish brown, smooth in the upper part, longitudinal striped, covered with yellow to light brown hairs up to 1/3 (from the base upwards), fistulose, fibrous. Lamellae adnate, yellow to light brown, I = 3–9, L = 17–23, crowded.

Basidiospores elliptic, 6.0–8.0 (9.0) × 3.0–4.0 µm, Q = (1.50) 1.58–2.50 (2.60), Qm = 2.01 ± 0.25, smooth, hyaline, inamyloid, thin-walled. Basidia clavate, 20 (21)–34 (37) × 5–10 µm, two- or four-spored, thin-walled, smooth, hyaline. Cheilocystidia abundant, clavate, with obtuse on the top, (17) 20–30 × 4–8 (10) µm, thin-walled, smooth, hyaline. Pileipellis a cutis, made up of irregular branched or weakly coralloid hyphae, inflated, 10–30 (35) µm wide, hyaline to light yellow, smooth, thin-walled, clamps present.

Ecology: Grows on the deciduous layer or rotten branches in coniferous and broad-leaved mixed forest.

Distribution: China (Jilin Province)

Other specimen examined: China. Jilin Province: Yanbian Korean Autonomous Prefecture, Antu County, Erdaobaihe Town, 42.39° N, 128.11° E, 18 September 2020, Jia-Jun Hu, Gui-Ping Zhao, and Bo Zhang, HMJAU 60298 (GenBank accession no.: ITS = OM030264, nLSU = OM033385); Yanbian Korean Autonomous Prefecture, Antu County, Erdaobaihe Town, 42.39° N, 128.11° E, 18 September 2020, Jia-Jun Hu, Gui-Ping Zhao, and Bo Zhang, HMJAU 60299 (GenBank accession no.: ITS = OM030265, nLSU = OM033386).

Note: *Gymnopus striatus* is easily confused with *Gymnopus longisterigmaticus*, *Gymnopus longus*, and *Gymnopus macrosorus* due to their highly similar morphology. However, *Gymnopus striatus* differs from those three species by its deeper color lamellae, longitudinal stripes on the stipe and stripes on the margin of pileus, bigger Qm, and short basidia sterigmata. *Gymnopus striatus* can be easily differentiated from *Gymnopus fagiphilus* by its deeper color pileus, uniform colored and longitudinally striped stipe, lack of caulocystidia, uncoralloid cheilocystidia, without pigment incrusting in pileipellis, and smaller basidiospores.
Gymnopus changbaiensis J.J. Hu, B. Zhang and Y. Li sp. nov.
Figures 3f and 8
MycoBank: MB 842337
Etymology: the epithet “changbaiensis” refers to Mt. Changbai, the location of the holotype.
Diagnosis: This species is distinguished from closed species by a reddish brown pileus and depressed when mature at the center, light pink to white outwards and margin, striped; fresh to pink lamellae, and a reddish brown stipe up to 1/3 covered with light yellow to brown hairs (from the base upwards), short sterigmata of basidia, lack of caulocystidia, uncoralloid cheilocystidia and smaller basidiospores.

Type: China. Jilin Province: Baishan City, Changbai Korean Autonomous County, Wάntian’е Scenic Spot, 41.56°N, 127.95°E, 17 September 2020, Jia-Jun Hu, Gui-ping Zhao, and Bo Zhang, HMJAU 60300, holotype (GenBank accession no.: ITS = OM030272, nLSU = OM033387).
Basidiomata small-to-medium-sized, gregarious. Pileus hemispherical, deep reddish brown when young, convex or slightly depressed sometimes when mature, 2.1–3.4 cm diameter, smooth, hygrophanus, reddish brown at the center, light pink towards margin; margin white to light pink, striped, entire. Context thin, fleshy, light yellowish brown, odorless. Stipe center, cylindrical, 4.2–5.3 cm long and 0.2–0.3 cm wide, deep reddish brown to reddish brown, smooth in the upper part, covered with light yellow to brown hairs up to 1/3 (from the base upwards), fistulose, fibrous. Lamellae adnate, fresh to pink, I = 1–5, L = 19–24, crowded.

Basidiospores elliptic, (5.8) 6.0–8.1 (9.0) × 3.0–4.1 (4.2) μm, Q = (1.41) 1.53–2.40 (2.50), Qm = 1.98 ± 0.24, smooth, hyaline, inamylloid, thin-walled. Basidia clavate, (19) 20–29 (32) × 5–8 μm, two- or four-spored, thin-walled, smooth, hyaline. Cheilocystidia abundant, clavate, with obtuse on the top, (23) 24–34 (39) × (5) 6–7 (9) μm, thin-walled, smooth, hyaline. Pileipellis a cutis, made up of irregular branched or weakly coralloid hyphae, inflated, 8–23 (25) μm wide, hyaline to light yellow, smooth, thin-walled, clamps present.

Ecology: Grows on the deciduous layer or rotten branches in coniferous and broad-leaved mixed forest.
Distribution: China (Jilin Province)
Other specimen examined: China. Jilin Province: Baishan City, Changbai Korean Autonomous County, Wangtian’e Scenic Spot, 41.56° N, 127.95° E, 9 September 2019, Jia-Jun Hu, Gui-ping Zhao, and Bo Zhang, HMJAU 60301 (GenBank accession no.: ITS = OM030273, nLSU = OM033388); Baishan City, Changbai Korean Autonomous County, Wangtian’e Scenic Spot, 41.56° N, 127.95° E, 9 September 2019, Jia-Jun Hu, Gui-ping Zhao, and Bo Zhang, HMJAU 60302 (GenBank accession no.: ITS = OM030274, nLSU = OM033389).

Note: Gymnopus changbaiensis is significantly related to Gymnopus fagiphilus and Gymnopus striatus based on its reddish brown and tomentose stipe, and short basidia sterigmata. Gymnopus changbaiensis can be distinguished from Gymnopus fagiphilus by its lighter and depressed pileus, denser and fresh to pink lamellae, and, in terms of microscopic characteristics, smaller basidiospores, uncoralloid cheilocystidia, and lack of caulocystidia. Gymnopus changbaiensis differs from Gymnopus striatus by its pale color, striped, and depressed pileus, fresh-to-pink lamellae, non-striped stipe, a bit longer cheilocystidia, coralloid pileipellis.

Figure 8. Morphological characteristics of Gymnopus changbaiensis (HMJAU 60300, holotype): (a) basidiomata, (b) pileipellis, (c) basidiospores, (d) basidia, and (e) cheilocystidia. Scale bars: 1 cm (a), 25 µm (b), and 5 µm (c–e).

Gymnopus tomentosus J.J. Hu, B. Zhang and Y. Li sp. nov. Figures 3i and 9
MycoBank: MB 842338
Etymology: the epithet “tomentosus” refers to the tomentose margin of pileus.
Diagnosis: This species is distinguished from closed species by a near white pileus with a tomentose margin, yellowish green lamellae, and a reddish brown stipe up to 1/4 covered with reddish brown hairs (from the base upwards), smaller basidiospores, clavate cheilocystidia, and inflated to bulbous pileipellis.
Type: China: Jilin Province, Jiaohe City, Lafa Mountain National Forest Park Red Leaf Valley Scenic Spot, 43.71° N, 127.08° E, 7 September 2019, Jia-Jun Hu, Gui-ping Zhao, and Bo Zhang, HMJAU 60303, holotype (GenBank accession no.: ITS = OM030278, nLSU = OM033390).
Basidiomata small-to-medium-sized, scattered. Pileus convex, 1.6–3.0 cm diameter, smooth, tan at the center, light brown towards margin; margin white, tomentose, entire. Context thin, fleshy, white to light yellow, odorless. Stipe center, cylindrical, 3.3–4.3 cm long and 0.2–0.5 cm wide, blackish green at apex, reddish brown below, covered with reddish
brown hairs up to 1/4 (from the base upwards), fistulose, fibrous. Lamellae adnexed, yellowish green, I = 3–7, L = 19–25, crowded.

Basidiospores elliptic, (6.0) 6.2–8.2 (9.0) × 3.0–4.1 (4.2) µm, Q = (1.50) 1.59–2.33 (2.40), Qm = 1.92 ± 0.23, smooth, hyaline, inamyloid, thin-walled. Basidia clavate, 20–30 (31) × 5–8 µm, two- or four-spored, thin-walled, smooth, hyaline. Cheilocystidia abundant, clavate, with obtuse on the top sometimes, (20) 22–30 (32) × 5–7 µm, thin-walled, smooth, hyaline. Pileipellis a cutis, made up of irregular branched to weakly coralloid or bulbous hyphae, inflated, 10–18 (21) µm wide, light brown, smooth, thin-walled, clamps present.

Ecology: Grows on the deciduous layer in broad-leaved forest.

Distribution: China (Jilin Province)

Note: The reddish brown and tomentose stipe makes Gymnopus tomentosus similar to Gymnopus fagiphilus, Gymnopus longisterigmaticus, Gymnopus longus, Gymnopus macrosporus, Gymnopus striatus, and Gymnopus changbaiensis. However, its white-to-pale-yellow pileus with a tomentose margin and inflated bulbous terminal hyphae of the pileipellis differentiates Gymnopus tomentosus from Gymnopus longisterigmaticus, Gymnopus longus, Gymnopus macrosporus, Gymnopus striatus, and Gymnopus changbaiensis. Gymnopus tomentosus can be distinguished from Gymnopus fagiphilus by its near-white pileus with a tomentose margin, coralloid-to-bulbous pileipellis, smaller basidiospores, and lack of caulocystidia [1].

Gymnopus tiliicola J.J. Hu, B. Zhang and Y. Li sp. nov.
Figures 3d and 10
MycoBank: MB 842339
Etymology: the epithet “tiliicola” refers to this species grows at the base of Tilia sp.

Diagnosis: This species is distinguished from closed species by a deep rose-red pileus that is pale color outward, light pink to fresh lamellae, with a deep reddish brown and smooth stipe that is longitudinally striped, grows at the base of Tilia sp., uncoralloid cheilocystidia, two- or four-spored basidia, and a bit bigger basidiospores.

Type: China. Jilin Province: Yanbian Korean Autonomous Prefecture, Antu County, Erdaobaihe Town, 42.39° N, 128.11° E, 13 September 2019, Jia-Jun Hu, Gui-Ping Zhao, and Bo Zhang, HMJAU 60304, holotype (GenBank accession no.: ITS = OM030275, nLSU = OM033392).

Basidiomata medium-to-large-sized, gregarious. Pileus convex, 3.0–6.7 cm diameter, smooth, deep rose-red at the center, yellowish pink towards margin; margin white to light yellow, striped, entire, wavy. Context thin, fleshy, white to pink, odorless. Stipe center,
cylindrical, 2.2–4.5 cm long and 0.3–0.7 cm wide, deep reddish brown, smooth, fistulose, fibrous. Lamellae adnexed to adnate, light pink to fresh, I = 1–3, L = 19–24, crowded.

Basidiospores elliptic, (6.0) 6.9–8.0 (8.2) × (3.0) 3.1–4.0 (4.2) µm, Q = (1.70) 1.75–2.26 (2.33), Qm = 1.93 ± 0.17, smooth, hyaline, inamyloid, thin-walled. Basidia clavate, 20–30 × 6–8 µm, two- or four-spored, thin-walled, smooth, hyaline. Cheilocystidia abundant, clavate, with obtuse on the top, (20) 21–27 (28) × 5–7 µm, thin-walled, smooth, hyaline. Pileipellis a cutis, made up of irregular branched to weakly coralloid hyphae, inflated, (5) 6–15 (17) µm wide, light brown, smooth, thin-walled, clamps present.

Ecology: Grows at the base of *Tilia* sp.

Distribution: China (Jilin Province)

Other specimen examined: China. Jilin Province: Yanbian Korean Autonomous Prefecture, Antu County, Erdaobaihe Town, 42.39° N, 128.11° E, 31 August 2020, Jia-Jun Hu, Gui-Ping Zhao, and Bo Zhang, HMJAU 60305 (GenBank accession no.: ITS = OM030277, nLSU = OM033393); Yanbian Korean Autonomous Prefecture, Antu County, Erdaobaihe Town, 42.39° N, 128.11° E, 27 August 2021, Jia-Jun Hu, Gui-Ping Zhao, and Bo Zhang, HMJAU 60304 (GenBank accession no.: ITS = OM030276, nLSU = OM033394).

Note: Morphologically, the rose-red to dark red pileus and stipe make *Gymnopus tiliicola* closed to *Gymnopus erythropus*. *Gymnopus tiliicola* differs from *Gymnopus erythropus* in a lighter color and striped pileus, light pink to fresh and denser lamellae. Besides, *Gymnopus tiliicola* grows at the base of *Tilia* sp., while *Gymnopus erythropus* grows on the deciduous layer or rotten branches. In regard to microfeatures, *Gymnopus tiliicola* differs from *Gymnopus erythropus* by a weakly coralloid pileipellis, uncoralloid cheilocystidia, bigger basidiospores, and two- or four-spored basidia.

*Gymnopus globulosus* J.J. Hu, Y.L. Tuo, B. Zhang and Y. Li sp. nov.

Figures 3e and 11

MycoBank: MB 842340

Etymology: the epithet “globulosus” refers to pileipellis terminal hyphae inflated to spherical to prolate.

Diagnosis: This species is distinguished from closed species by a convex to aplnate pileus that is deep reddish brown at the center, lighter-colored outwards, and light yellow margin, striped; white to light yellowish green lamellae, with a reddish brown and smooth
stipe, pileipellis two layers and the terminal hyphae inflated to spherical to prolate, and a bit bigger basidiospores.

Type: China. Jilin Province: Tonghua City, Ji’an County, Wunvfeng National Forest Park, 41.28° N, 126.14° E, 28 August 2019, Yong-Lan Tuo and Jia-Jun Hu, HMJAU 60307, holotype (GenBank accession no.: ITS = OM030269, nLSU = OM033406).

Basidiomata medium-sized, gregarious. Pileus convex to applanate, 4.5–5.5 cm diameter, smooth, deep reddish brown at the center, yellowish brown towards margin; margin white to light yellow, striped, entire, wavy. Context thin, fleshy, brown, odorless. Stipe center, clavate, 4.8–6.0 cm long and 0.6–0.8 cm wide, deep reddish brown, paler at apex, smooth, fistulose, fibrous. Lamellae adnexed to adnate, white to light yellowish green, I = 1–3, L = 9–15, crowded.

Basidiospores elliptic, (6.8) 7.0–8.8 (9.0) × (3.1) 3.3–4.2 (4.8) µm, Q = (1.63) 1.75–2.20 (2.26), Qm = 1.93 ± 0.16, smooth, hyaline, inamyloid, thin-walled. Basidia clavate, (23) 25–32 (33) × 6–9 (11) µm, two- or four-spored, thin-walled, smooth, hyaline. Cheilocystidia abundant, clavate, with obtuse on the top, (22) 24–38(39) × 5–9 (10) µm, thin-walled, smooth, hyaline. Pileipellis layered, the upper layer inflated to spherical to prolate hyphae, 15–33 (47) µm wide, brown, smooth, thin-walled; down layer made up of branched and inflated hyphae, pigment light brown to brown incrusting in pileipellis, thin-to-thick-walled.

Ecology: Grows on rotten wood.

Distribution: China (Jilin Province)

Other specimen examined: China. Jilin Province: Tonghua City, Ji’an County, Wunvfeng National Forest Park, 41.28° N, 126.14° E, 3 September 2021, Yong-Lan Tuo and Jia-Jun Hu, HMJAU 60308 (GenBank Accession no.: ITS = OM030270, nLSU = OM033407).

Note: In terms of morphology, Gymnopus globulosus resembles Gymnopus erythropus and Gymnopus tiliicola in its red to dark red pileus and stipe. However, Gymnopus globulosus is distinguishable from Gymnopus erythropus due to its deeper-colored pileus, light yellowish green lamellae, which is light yellow of Gymnopus erythropus. In terms of microfeature, the pileipellis of Gymnopus erythropus is between a cutis and a trichoderm, while the pileipellis of Gymnopus globulosus is layered, with the upper layer inflated to spherical to prolate hyphae and the down layer made up of branched and inflated hyphae, and bigger basidiospores. Gymnopus globulosus differs from Gymnopus tiliicola with its deeper-colored pileus, light yellowish green lamellae, grows on rotten wood, pileipellis two layers and the terminal hyphae inflated to spherical to prolate, and bigger basidiospores.

Figure 11. Morphological characteristics of Gymnopus globulosus (HMJAU 60307, holotype): (a) basidiomata, (b) pileipellis, (c) basidiospores, (d) basidia, and (e) cheilocystidia. Scale bars: 1 cm (a), 25 µm (b), and 5 µm (c-e).
New record from Jilin Province, China

_Gymnopus erythropus_ (Pers.) Antonin, Halling and Noordel.

Figures 3h and 12

Basidiomata small-to-medium sized, scattered to gregarious. Pileus convex to applanate, 1.1–3.2 cm diameter, smooth, hygrophanous, reddish brown to brown at the center, light reddish brown to yellowish brown towards margin; margin beige to light yellow, entire, wavy sometimes. Context thin, fleshy, light brown, odorless. Stipe central, cylindrical, 4.1–10.0 cm long and 0.2–0.5 cm wide, deep reddish brown to light reddish brown, paler at apex, smooth, covered with scattered light yellow to brown hairs hairy at base, fistulose, fibrous. Lamellae adnate, fresh-pink, I = 3–5, L = 14–27, crowded.

Basidiospores elliptic, (5.0) 6.0–8.2 (10.0) × (2.1) 3.0–5.0 (6.0) µm, Q = (1.20) 1.48–2.33 (3.00), Qm = 1.87 ± 0.27, smooth, hyaline, inamyloid, thin-walled. Basidia clavate, (17) 21–33 (38) × (4) 5–9 (10) µm, two- or four-spored, thin-walled, smooth, hyaline. Cheilocystidia abundant, clavate, with obtuse on the top, (15) 21–33 (39) × (3) 4–8 (9) µm, thin-walled, smooth, hyaline. Pileipellis a cutis, made up of irregular branched or weakly coralloid hyphae, inflated, (6) 8–20 (20) µm wide, hyaline to light yellow, smooth, thin-walled, clamps present.

Ecology: Grows on the deciduous layer or rotten branches in coniferous and broad-leaved mixed forest.

Distribution: China (Jilin Province)

Specimen examined: China. Jilin Province: Baishan City, Changbai Korean Autonomous County, Wangtian’e Scenic Spot, 41.56° N, 127.95° E, 8 September 2019, Jia-Jun Hu, Gui-ping Zhao, and Bo Zhang, HMJAU 60309; Baishan City, Changbai Korean Autonomous County, Wangtian’e Scenic Spot, 41.56° N, 127.95° E, 8 September 2019, Jia-Jun Hu, Gui-ping Zhao, and Bo Zhang, HMJAU 60315 (GenBank Acc. no.: ITS = OM030280, nLSU = OM033395); Baishan City, Fusong County, Lushuihe Town, 42.53° N, 127.80° E, 8 September 2019, Jia-Jun Hu, Gui-ping Zhao, and Bo Zhang, HMJAU 60313 (GenBank Acc. no.: ITS = OM030281, nLSU = OM033396); Yanbian Korean Autonomous Prefecture, Antu County, Edaobaihe Town, 42.39° N, 128.11° E, 4 September 2018, Jia-Jun Hu and Bo Zhang, HMJAU 60310; HMJAU 60311; HMJAU 60312; Liaoning Province: Jinzhou City, Yi County, Mt. Yiwuul, 24 September 2013, Di Wang, HMJAU 28892, Jinzhou City, Yi County, Mt. Yiwuul, 25 September 2013, Di Wang, HMJAU 28839.

Figure 12. Morphological characteristics of _Gymnopus erythropus_ (HMJAU 60315). (a) Basidomata, (b) pileipellis, (c) basidiospores, (d) basidia, and (e) cheilocystidia. Scale bars: 1 cm (a), 25 µm (b), and 5 µm (c–e).
| Scientific Name     | Pileus                                                                 | Lamellae                                      | Stipe                                                                 |
|--------------------|------------------------------------------------------------------------|-----------------------------------------------|----------------------------------------------------------------------|
| \textit{G. longisterigmaticus} | 1.5–3.2 cm diameter, smooth, brown at center, light brown to yellow towards the margin, margin light yellow to yellowish white, entire | Lamellae subfree to adnate, white to light yellow, \( I = 1–3, \ L = 15–18 \), crowded | 3.2–5.0 × 0.2–0.3 cm, reddish brown, smooth, covered with white to light reddish brown density hairs at base, white to light reddish brown, with brown farinose on the upper part, and white to light reddish brown tomentose at the base |
| \textit{G. longus} | 1.7–3.7 cm diameter, smooth, reddish brown at center, towards margin light reddish brown to brown; margin white to light yellow or light brown | Adnate, white to light yellow, \( I = 5–7, \ L = 19–24 \), crowded | 3.7–4.3 cm × 0.3–0.6 cm, reddish brown, with brown farinose on the upper part, and white to light reddish brown tomentose at the base |
| \textit{G. macrosporus} | 1.2–4.6 cm diameter, smooth, deep reddish brown at center, reddish brown to yellowish brown towards margin; margin beige to light yellow, striped, wavy | Adnexed to adnate or near free, light yellow, \( I = 1–3, \ L = 13–17 \), crowded | 7.8–9.5 × 0.2–0.5 cm, deep reddish brown to reddish brown, smooth, and light yellow to yellowish brown tomentose at the base |
| \textit{G. striatus} | Depressed when old, 2.3–4.1 cm diameter, smooth, cinnamon at center, brown to light brown towards margin; margin white to light yellow, striped, wavy | Adnate, yellow to light brown, \( I = 3–9, \ L = 17–23 \), crowded | 5.5–7.0 cm × 0.3–0.8 cm, deep reddish brown to reddish brown, longitudinal striped, covered with yellow to light brown hairs up to 1/3 (from the base upwards), fistulose, fibrous |
| \textit{G. changbaensis} | 2.1–3.4 cm diameter, smooth, hygrophanus, reddish brown at the center, light pink towards margin; margin white to light pink, striped | Adnate, fresh to pink, \( I = 1–5, \ L = 19–24 \), crowded | 4.2–5.3 cm × 0.2–0.3 cm, deep reddish brown to reddish brown, covered with light yellow to brown hairs up to 1/3 (from the base upwards) |
| \textit{G. tomentosus} | 1.6–3.0 cm diameter, smooth, tan at the center, light brown towards margin; margin white, tomentose | Adnexed, yellowish green, \( I = 3–7, \ L = 19–25 \), crowded | 3.3–4.3 cm × 0.2–0.5 cm, blackish green at apex, reddish brown below, covered with reddish brown hairs up to 1/4 (from the base upwards) |
| \textit{G. tiliicola} | 3.0–6.7 cm diameter, smooth, deep rose-red at the center, yellowish pink towards margin; margin white to light yellow, striped | Adnexed to adnate, light pink to fresh, \( I = 1–3, \ L = 19–24 \), crowded | 2.2–4.5 cm × 0.3–0.7 cm, deep reddish brown, smooth |
| \textit{G. globulosus} | 4.5–5.5 cm diameter, smooth, deep reddish brown at the center, yellowish brown towards margin; margin white to light yellow, striped | Adnexed to adnate, white to light yellowish green, \( I = 1–3, \ L = 9–15 \), crowded | 4.8–6.0 cm × 0.6–0.8 cm, deep reddish brown, paler at apex, smooth |
| \textit{G. erythropus} | 1.1–3.2 cm diameter, smooth, hygrophanus, reddish brown to brown at the center, light reddish brown to yellowish brown towards margin; margin beige to light yellow | Adnate, fresh-pink, \( I = 3–5, \ L = 14–27 \), crowded | 4.1–10.0 cm × 0.2–0.5 cm, deep reddish brown to light reddish brown, paler at apex, smooth, covered with scattered light yellow to brown hairs hairy at base 20–40 (70) × 1–3 mm, orange-brown to red-brown, sometimes paler at apex, dark red-brown towards base, covered with fine, white or yellow hairs up to 2/3 of length (from base upwards) |
| \textit{G. fagiphilus} | (7) 15–25 (35) mm broad, when moist slightly translucently striate at margin, yellow-brown or reddish brown, paler at margin | Moderately distant, \( I = 18–21 \), \( I = 3–7 \) (15), free or narrowly adnate, rarely adnate, pinkish brown or pinkish cream, darker with age or tinged gray | Note: The description of \textit{Gymnopus fagiphilus} is based on Antonin and Noordeloos [1]. |
Table 3. Microcharacteristics comparison between our new species, *Gymnopus erythropus* and *Gymnopus fagiphilus*.

| Scientific Name         | Pileipellis                                                                 | Q          | Qm         | Basidiospores                          | Basidia                              | Chlorocystidia | Caulocystidia |
|-------------------------|------------------------------------------------------------------------------|------------|------------|----------------------------------------|--------------------------------------|----------------|--------------|
| *G. longisterigmaticus* | Cutis, irregularly branched hyphae, inflated, 10–27 (35) µm wide, hyaline to light yellow, smooth or pigmented yellowish brown incrusting in pileipellis | (1.40) 1.67–2.25 (2.26) | 1.93 ± 0.20 | (6.2) 6.7–9.0 × (3.0) 3.1–4.3 (5.0) µm | Clavate, (18) 19–27 (28) × (5) 6–10 µm, four-spored; sterigmata extremely long, up to 40 µm | Clavate, with obtuse on the top, or branched, (16) 18–27 × (4) 5–8 (9) µm | None          |
| *G. longus*             | Cutis, made up of irregular branched or weakly coralloid hyphae, inflated, 10–18 (21) µm wide, hyaline to light yellow, smooth | (1.27) 1.47–2.19 (2.58) | 1.80 ± 0.24 | (5.6) 6.0–8.0 × (3.0) 3.1–4.1 (4.9) µm | Clavate, 20–28 (29) × 6–9 µm, two- or four-spored, clavate; sterigmata extremely long, up to 33 µm long | Clavate, (21) 22–29 (30) × 5–7 µm, with obtuse on the top | None          |
| *G. macrosporus*        | Cutis, made up of irregular branched or weakly coralloid hyphae, inflated, 10–27 (35) µm wide, hyaline to light yellow, smooth | (1.63) 1.67–2.32 (2.37) | 1.88 ± 0.18 | (6.0) 6.8–7.9 (8.3) × (3.0) 3.1–4.2 (4.3) µm | Clavate, 20–29 × 6–9 µm, two- or four-spored, thin-walled; sterigmata extremely long, up to 32 µm | Clavate, with obtuse on the top, 20–28 (30) × 5 (6)–9 µm | None          |
| *G. striatus*           | Cutis, made up of irregular branched or weakly coralloid hyphae, inflated, 10–30 (35) µm wide, hyaline to light yellow, smooth | (1.50) 1.58–2.50 (2.60) | 2.01 ± 0.25 | 6.0–8.0 (9.0) × 3.0–4.0 µm | Clavate, 20 (21)–34 (37) × 5–10 µm, two- or four-spored | Clavate, with obtuse on the top, (17) 20–30 × 4–8 (10) µm | None          |
| *G. changxiensis*       | Cutis, made up of irregular branched or weakly coralloid hyphae, inflated, 8–23 (25) µm wide, hyaline to light yellow, smooth | (1.41) 1.53–2.40 (2.50) | 1.98 ± 0.24 | (5.8) 6.0–8.1 (9.0) × 3.0–4.1 (4.2) µm | Clavate, 19 (20)–29 (32) × 5–8 µm, two- or four-spored | Clavate, with obtuse on the top, (23) 24–34 (39) × 5 (6)–7 (9) µm | None          |
| *G. tomentosus*         | Cutis, made up of irregular branched to weakly coralloid or bulbous hyphae, inflated, 10–18 (21) µm wide, light brown | (1.50) 1.59–2.33 (2.40) | 1.92 ± 0.23 | (6.0) 6.2–8.2 (9.0) × 3.0–4.1 (4.2) µm | Clavate, 20–30 (31) × 5–8 µm, two- or four-spored | Clavate, with obtuse on the top sometimes, (20) 22–30 (32) × 5–7 µm | None          |
| *G. tiitica*            | Cutis, made up of irregular branched to weakly coralloid hyphae, inflated, (5)–15(17) µm wide, light brown, smooth | (1.70) 1.75–2.26 (2.33) | 1.93 ± 0.17 | (6.0) 6.9–8.0 (8.2) × (3.0) 3.1–4.0 (4.2) µm | Clavate, 20–30 × 6–8 µm, two- or four-spored | Clavate, with obtuse on the top, (20) 21–27 (28) × 5–7 µm | None          |
| *G. globulosus*         | Layered, the upper layer inflated to spherical to prolate hyphae, 15–33 (47) µm wide, brown, smooth, thin-walled; down layer made up of branched and inflated hyphae, pigment light brown to brown incrusting in pileipellis, thin-to-thick-walled | (1.63) 1.75–2.20 (2.26) | 1.93 ± 0.16 | (6.8) 7.0–8.8(9) × (3.1) 3.3–4.2 (4.8) µm | Clavate, (23) 25–32 (33) × 6–9 (11) µm, two- or four-spored | Clavate, with obtuse on the top, (22) 24–38 (39) × 5–9 (10) µm | None          |
| *G. erythropus*         | Cutis, made up of irregular branched or weakly coralloid hyphae, inflated, (6) 8–20 (20) µm wide, hyaline to light yellow, smooth | (1.20) 1.48–2.33 (3.00) | 1.87 ± 0.27 | (5.0) 6.0–8.2 (10.0) × (2.1) 3.0–5.0 (6.0) µm | Clavate, (17) 21–33 (38) × (4) 5–9 (10) µm, two- or four-spored | Clavate, with obtuse on the top, (15) 21–33 (39) × (3) 4–8 (9) µm, thin-walled, smooth, hyaline, 15–40 (60) × 4.5–8.0 (10) µm, irregularly clavate, often with lobed apex or with short to long, up to 10 µm long rostrum, sometimes very slender lagenaiform | None          |
| *G. fagiphilus*         | Cutis with transitions to a trichoderm, made up of irregularly shaped, 4.0–15 (25) µm-wide coralloid elements ("Dryophila-structure"); pigment brown-yellow, incrusted in pileipellis | 1.7–2.3 | 2.1 | (6.0) 7.0–9.0 × (3.0) 3.5–4.5 µm | 21–31 × 6.0–8.5 µm, 4-spored | None          | None          |

Note: The description of *Gymnopus fagiphilus* is based on Antonín and Noordeloos [1].
Key to the species reported in this study

1 Stipe covered with dense hairs at the base .................................................. 2
2 Stipe smooth, or covered with sparse hairs at the base ................................. Gymnopus erythropus
2 Basidia sterigmata extremely long ................................................................. 3
3 Basidia sterigmata short .................................................................................. 5
4 Stipe smooth in upper part ............................................................................. 4
5 Stipe covered with brown farinose on the upper part ................................... Gymnopus longus
5 Pileus pale color, stipe color uneven ............................................................... Gymnopus longisterigmaticus
5 Growing on the deciduous layer or rotten branches ...................................... Gymnopus macrosporus
6 Pileus dark color, stipe color uniform .............................................................. Gymnopus tiliicola
6 Pileus pale color, near white ......................................................................... emph Gymnopus tomentosus
6 Pileus deep color ............................................................................................. 7
7 Stipe covered with longitudinally stripes ....................................................... Gymnopus striatus
8 Stipe without longitudinally stripes ............................................................... 8
8 Pileipellis a cuits, typically “Dryophila type” ................................................. Gymnopus changbaiensis
8 Pileipellis layered, hyphae inflated to spherical to prolate ............................. Gymnopus globulosus

4. Discussion

4.1. New Sights on Morphological Characteristics

The genus Gymnopus is geographically widely distributed; however, in China, its species diversity is poorly known. Moreover, in China, only three species were originally described with molecular evidence. One of these is Gymnopus ramulicola T.H. Li and S.F. Deng [27] from Hainan Province, China; the second one is Gymnopus alliifoetidissimus T.H. Li and J.P. Li [25] from Guangdong Province, China; and the third is Gymnopus pallipes J.P. Li and Chun Y. Deng [25] from Guangdong and Guizhou Province, China. In our study, eight new species of Gymnopus from China are described as new species. They are well-supported by molecular phylogenetic and morphological evidence. Our newly recognized and delimited species are distributed in the broad-leaved and mixed forests, and occur in early autumn in Northeast China. The species we described here are hardly seen in the wild mushroom market; thus, their edibility is not yet known.

The description of these new species also broadens the morphological characterization of the genus Gymnopus. In the previous study, the pileipellis of the species in this genus was a cuits to trichoderm. Moreover, the pileipellis in the species of sect. Levipedes was an entangled, not radially oriented trichoderm of inflated, often lobed or coralloid elements of the “Dryophila type” [1,17]. In this study, the pileipellis of Gymnopus globulosus was divided into two layers, with the upper layer comprising hyphae inflated to spherical to prolate, differing from that of all known species in the genus, while the second layer was typical of the “Dryophila type”. To our knowledge, the sterigmata of the basidia are usually not too long; however, the species Gymnopus longisterigmaticus, Gymnopus longus, and Gymnopus macrosporus had extremely long sterigmata, up to 40 µm. Thus, the structure of extremely long basidia sterigmata is traceable in our species. In addition, all the species described from this study are detailed compared in macro- and micro-features (Tables 2 and 3).

4.2. Phylogenetic Relationships of Gymnopus s.l. with Related Genera

Phylogenetic analyses of the species of Gymnopus s.l. and the related genera presented in this study confirmed that the genus Gymnopus defined by Antonín and Noordeloos, as well as Halling, is not monophyletic in a strongly supported clade. Similar results were observed with our phylogenetic analysis. Our results, thus, support the finding of Oliveira et al., promoting sect. Perforanita to the genus level, Paragymnopus, and share a close affinity with Lentinula. Moreover, sect. Vestipedes was clearly separated from Gymnopus s. str [12,15], and were closed to Marasmiellus, Collybiopsis, and Rhodocollybia. However, in their study, the species of Gymnopus sect. Vestipes was involved with
Levipedes was mainly divided into four clades. Sect.
from China. However, probably due to the lacking of species sampling or the
Gymnopus Vizzini, Anton Gymnopus dryophilus would becoming synonyms of
Lentinula lead to a deeper understanding of the relationships within and among these genera.

need for a deeper and more extensive study on sect. Levipedes.

result, it is clear that Gymnopus lanipes Gymnopus dryophilus
is not considered an independent species, then Gymnopus dryophioides and Gymnopus inexpectatus should equally be treated as Gymnopus dryophilus. Moreover, Gymnopus erythropus complex, a subclade (defined here as/erythropus), includes Gymnopus erythropus, Gymnopus fagophilus, and our new species (characterized by a red to reddish brown color, a smooth or scattered-to-dense tomentose stipe, and occurring in early autumn). The above results imply the need for a deeper and more extensive study on sect. Levipedes.

some species within the genus, were advised to be relocated to Collybiopsis [47]. Thus, the boundaries between Gymnopus, Marasmiellus, and Collybiopsis would be more blurred, especially between Marasmiellus and Collybiopsis, as well as if these species were transferred to Collybiopsis; then it would be multiplyetic, with Rhodocollybia, Paragymnopus, and Lentinula would becoming synonyms of Gymnopus.

4.3. Nova Suggestions of Phylogenetic Relationships within Gymnopus s. str.

In our phylogenetic results, the genus Gymnopus, which was defined by Oliveira et al. [15], was mainly divided into four clades. Sect. Levipedes, sect. Gymnopus, and sect. Androsaceli are somewhat more closely related, whereas they are distant from the sect. Impudicae. Before 2010, both sect. Impudicae and sect. Levipedes were subsections below the same section. However, from our results, sect. Impudicae and sect. Levipedes are more distantly related, probably due to similar environments, causing a similar appearance. In addition, the genus Mycetines and sect. Impudicae, with a strong odor, are not closely related to each other, and this is consistent with the result that they have a different pileipellis structure of pileus.

Thus, sect. Levipedes being split into two sections was supported by the phylogenetic analysis. Sect. Levipedes subsect. Levipedes was also divided into two subclades: one is Gymnopus dryophilus complex, a subclade (defined here as/dryophila) that includes all the Gymnopus dryophilus complex species reported around the world (characterized by a Gymnopus dryophilus–like appearance and arises in early spring or later in the autumn). From the result, the East Asia sequences of Gymnopus dryophilus were not clustered with the European sequences, while they were clustered with the new species—Gymnopus dryophioides—that Antonin, Ryoo and Ka reported from Korea in 2020. Antonin et al. [51] do not accept Gymnopus lanipes (Malençon and Bertault) Vila and Llimona as a separate species and consider it to be a variant of Gymnopus dryophilus. From our phylogenetic result, it is clear that Gymnopus lanipes clusters with Gymnopus inexpectatus, which Consiglio, Vizzini, Antonin and Contu described from Europe, which, if Gymnopus lanipes is not considered an independent species, then Gymnopus dryophioides and Gymnopus inexpectatus should equally be treated as Gymnopus dryophilus. Moreover, Gymnopus erythropus complex, a subclade (defined here as/erythropus), includes Gymnopus erythropus, Gymnopus fagophilus, and our new species (characterized by a red to reddish brown color, a smooth or scattered-to-dense tomentose stipe, and occurring in early autumn). The above results imply the need for a deeper and more extensive study on sect. Levipedes.

Based on the current study’s findings, we increased the species diversity of the genus Gymnopus from China. However, probably due to the lacking of species sampling or the inadequate genetic variation in the DNA loci in our study, the deep phylogenetic relationships within the genus Gymnopus and between the related genera—Lentinula, Rhodocollybia, Mycetinis, Collybiopsis, etc.—remain unresolved. Thus, in future work, more species of this genus and similar genera will be discovered, which will provide new evidence and, thus, lead to a deeper understanding of the relationships within and among these genera.

Marasmiellus; therefore, Oliveira et al. [15] proposed to transfer Gymnopus sect. Vestipedes to Marasmiellus and redefined the genus Gymnopus more strictly.

However, in our phylogenetic analyses, a different result was obtained. In our results, sect. Vestipedes did not group into one clade with Marasmiellus to form an independent clade, forming a sister clade to genus Collybiopsis. Furthermore, the taxonomic status of Collybiopsis minor R.H. Petersen still needs to be clarified; in our study, C. minor was separated far away from Collybiopsis, while being clustered with sect. Vestipedes within a single clade.

Some species of sect. Vestipedes and genus Marasmiellus have been proposed for transfer to other genera in recent years. Gymnopus cylindricus J.L. Mata and Gymnopus brunneigracilis (Corner) A.W. Wilson, Desjardin and E. Horak were suggested to be switched into Marasmiellus. The type species of Marasmiellus, Marasmiellus juniperinus, and some other species within the genus, were advised to be relocated to Collybiopsis [47].
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