Morpho-Molecular Evidence Reveals Four Novel Species of Gymnopus (Agaricales, Omphalotaceae) from China

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Abstract: Nine collections of gymnopoid fungi were studied based on morpho-molecular characteristics. The macromorphology was made according to the photograph of fresh basidiomata and field notes, while the micromorphology was examined via an optical microscope. Simultaneously, the phylogenetic analyses were performed by maximum likelihood and Bayesian inference methods based on a combined dataset of nrITS1-nr5.8S-nrITS2-nrLSU sequences. Integrated analysis of these results was therefore, G. efibulatus belonging to sect. Androsacei, G. iodes and G. sinopolyphyllus belonging to sect. Impudicae and G. strigosipes belonging to sect. Levipedes are proposed as new to science. The detailed descriptions, colour photos of basidiomata and line-drawings of microscopic structures are provided. The comparisons with closely related species and a key to known species of Gymnopus s. str. reported with morpho-molecular evidence in China is also given.

Keywords: fungal taxonomy; Holarctic regions; morphology; phylogeny; saprotrophic fungi; sect. Androsacei; sect. Impudicae; sect. Levipedes

1. Introduction

Gymnopus (Pers.) Roussel is a group of white-spored macrofungi with collybioid, rarely tricholomatoid, marasmioid or omphalinoid habit and distributed worldwide [1–22]. Its habit, causing the similarity in macromorphology, is the main reason for the confusion in taxonomy in the past. When revisiting the history of the genus, it is clear that the materials from Holarctic regions, comprised of Palaearctic and Nearctic subregions, were well studied [1–8,23,24]. Morphological studies on samples from Europe and northern Africa, a part of the Palaearctic subregion, and a few samples from North America, belonging to the Nearctic subregion, dominated the major revision of the generic concept [1,2,23–25]. However, the highly phenotypic plasticity that causes the close species often forms a complex, such as the G. dryophilus complex, making classification in the species level hard if only depends on morphology [26,27]. The taxonomic study was improved following the use of the polyphasic method. Studies on mating systems and isozymes were used to distinguish the G. dryophilus complex, confirming the morphological results [26,27]. The molecular–phylogenetic analysis plays a critical role in species recognition and generic revision as a tool for evolutionary inferences. Based on the morphological study and multigene phylogeny, the concepts of G. dryophilus (Bull.) Murrill and G. ocior (Pers.) Antonín and Noordel. were clarified [4]. Additionally, several results inferred from this method inspired mycologists to reconsider the inter- and infrageneric taxonomic position [7,28,29].
Therewith, G. sect. Androsacei (Kühner) Antonín and Noordel. was proposed [30]. Gymnopus sect. Vestipes subsect. Impudicae and subsect. Vestipes were raised, representing two distinct sections now [2]. In addition to that, G. sect. Vestipes (Fr.) Antonín, Halling and Noordel. was transferred to Marasmiellus Murrill but is currently called Collybiopsis Earle according to the nomenclature argument [31,32]. Lately, the monotypic section, G. sect. Gymnopus, was revised by including two additional small-sized species based on the polyphasic method of combined morpho-molecular evidence [18].

Currently, the study within the additional component of the Palaeartic subregion, the Asian north of the Himalayan mountains, is less covered that only 15 new taxa within Gymnopus sensu stricto (s. str.) were described therein [10–13,33]. Emending the type section of Gymnopus implied the importance of Chinese materials [18]. The reports regarding the Chinese individual(s) of Gymnopus s str. were at least beginning in 1892; Karsten reported a collection from Gansu Province, China, representing Marasmius dryophilus (Bull.) P. Karst. (=Gymnopus dryophilus (Bull.) Murrill; author’s name printed as (Bolt.) Karst. by typographical errors) [34]. However, only 15 species were reported based on morpho-molecular evidence in China to date [16–18,33], which reveals that the knowledge of the genus is still deprived in this region. In this study, four new species of Gymnopus from China, including one Holarctic taxon, were proposed based on the polyphasic method, viz. combined macro- and micro-morphology and multi-gene (nrITS1-nr5.8S-nrITS2-nrLSU) phylogenetic analyses. Colour photos of basidiomata and line-drawings of their microstructures are present. Discussions about phylogenetic relationships, comparisons with close species and a key to known species within Gymnopus s. str. reported by morpho-molecular evidence, are also given.

2. Materials and Methods
2.1. Abbreviations for Specific Names and Additional Mycological Glossary

G. = Gymnopus; Ma. = Marasmius; My. = Mycetinis; Pa. = Paragymnopus; nom. prov. = nomen provisorium; s. str. = sensu stricto.

2.2. Specimen

Nine new collections of gymnopoid fungi from China were included in this study. Samples were photographed in the field and dried by a portable drier operated at 45 °C. The specimens were deposited in HMJAU (Herbarium of Mycology, Jilin Agricultural University, Changchun, China), HGAS-MF (Herbarium of Guizhou Academy of Sciences, Guiyang, China) and HMAS (Fungarium of the Institute of Microbiology, Chinese Academy of Sciences, Beijing, China), respectively. The herbarium abbreviations follow Index Herbariorum [35].

2.3. Morphological Studies

Macromorphological features were described based on photographs of fresh basidiomata and field notes. The colours terminology and code follow Kornerup and Wanscher [36]. Two types of lamellae were counted, of which the number of full-length lamellae is represented by ‘L’, and the number of lamellulae tiers is represented by ‘l’.

Tiny tissue was cut from the dried basidiomata using a sharp blade and then mounted in 5% KOH on a glass slide for microscopic observation via a light microscope (ZEISS Axioscope 5). When needed, the Congo Red solution was used to highlight the outline of microscopic structures, and Melzer’s reagent was used to test amyloid or dextrinoid reactions. In microscopic description, ‘n’ refers to the number of measured elements. Measurements of basidiospores are given as (a)b–c(d), of which ‘b–c’ refers to the minimum of 90% of the measured values. The main body excluding sterigmata or excrescences of basidia, basidioles and cystidia were measured.
2.4. DNA Extraction, Amplification and Sequencing

The dried tissue was used for genomic DNA extraction using NuClean Plant Genomic DNA Kit (Cowin Biotech Co., Ltd., Taizhou, China). The nuclear ribosomal internal transcribed spacer (nrITS) and nuclear ribosomal large subunit (nrLSU) sequences were amplified using primer pairs of ITS5/ITS4 and LR0R/LR5, respectively [37–39]. The polymerase chain reaction (PCR) programs were followed according to Li et al. [18], and the PCR products were sent to Sangon Biotech (Changchun, Jilin, China) for sequencing.

2.5. Phylogenetic Analyses

Sequences generated in this study were combined with those obtained from GenBank by Basic Local Alignment Search Tool (BLAST) and then added to the matrix used by Li et al. [18], which covered all the sections of Gymnopus s. str. Based on two overlapping reads, targeted sequences were assembled and trimmed via BioEdit v.7.0.9 [40]. Quality control, such as degenerate bases checking, was completed before depositing the sequences to be used in GenBank (see Table 1) [41]. The ML (Maximum Likelihood) and BI (Bayesian Inference) analyses follow Li et al. [18]. The Bootstrap Proportions ≥70% for ML analysis (ML-BP) and Posterior Probability ≥0.95 for Bayesian Inference analysis (BI-PP) were considered a significant value. The alignment file of the combined dataset used for phylogenetic analyses and both the two phylograms generated from two methods was deposited in Treebase (https://www.treebase.org/treebase-web/home.html (accessed on 18 March 2022).

Table 1. Species names, collection numbers and corresponding GenBank accession numbers used in this study.

| Species Name | Collection No. | GenBank Accession No | References |
|--------------|----------------|----------------------|------------|
| G. adventitius nom. prov. | SFSU: DED8813 | KY026760 KY026760 | [42] |
| G. alliifoetidissimus * | GDGM 76695 | MT023348 MT017526 | [16] |
| G. androsaceus | CULTENN5609 | KY026750 KY026750 | [42] |
| G. androsaceus | CBS 240.53 | MH857175 MH868714 | [43] |
| G. androsaceus | CBS 239.53 | MH857174 MH868713 | [43] |
| G. androsaceus | CULTENN5021h2 | KY026748 KY026748 | [42] |
| G. androsaceus | TENN: F-59594 | KY026663 KY026663 | [42] |
| G. atlanticus * | URM 87728 | KT222654 KY302698 | [21] |
| G. aurantiipes | SFSU: AWW118 | AY263432 AY639410 | [15] |
| G. brunneiniger | XAL: Cesar50 | MT232388 MW187069 | [9] |
| G. brunneodiscus | BRNM 714974 | MH589973 MH589988 | [10] |
| G. cremeostipitatus * | BRNM 747547 | KP251071 KP251091 | [11] |
| G. densilamellatus | BRNM 714927 | KP336685 KP36694 | [12] |
| G. dryophiloides * | BRNM 781447 | MH589967 MH589985 | [10] |
| G. dryophilus | TENN: F-57012 | DQ241781 AY640619 | [29] |
| G. dysodes | TENN: F-61125 | KY026666 FJ750265 | [42] |
| G. dysodes | BRNM 766741 | KP336693 KP336701 | [12] |
| G. efibulatus * | HGASMF01-7052 haplotype1 | OM970865 | OM970865 This study |
| G. efibulatus * | HGASMF01-7052 haplotype2 | OM970866 | OM970866 This study |
| G. efibulatus | HGASMF01-11995 | OM970873 | OM970877 This study |
| Species Name          | Collection No. | GenBank Accession No | References |
|-----------------------|----------------|----------------------|------------|
|                       |                | ITS                  | LSU        |            |
| G. foetidus           | TENN: F-69323  | KY026739             | KY026739   | [42]       |
| G. frigidomarginatus  | TENN: F-55679  | KY026648             | KY026648   | [42]       |
| G. fusipes            | TENN: F-59217  | AY256710             | AY256710   | [44]       |
| G. impudicus          | BRNM 714849    | LT594119             | LT594119   | [12]       |
| G. inflatotrama nom.  | TENN: F-48143  | KY026619             | KY026619   | [42]       |
| G. inflatotrama nom.  | TFB 4529       | KY026744             | KY026744   | [42]       |
| G. inflatotrama nom.  | TENN: F-53490  | KY026640             | KY026640   | [42]       |
| G. inflatotrama nom.  | TENN: F-51233  | KY026612             | KY026632   | [42]       |
| G. inusitatus *       | BCN: SCM B-4058| JN24753              | JN247557   | [3]        |
| G. iocephalus         | Duke RV94154   | DQ449986             | unavailable| [7]        |
| G. iocephalus         | TENN: F-52970  | DQ449984             | KY019630   | [7]        |
| G. iodes              | HGASMF01-10068 | OM970868             | OM970868   | This study |
| G. iodes *            | HGASMF01-10068 | OM970869             | OM970869   | This study |
| G. iodes              | HMJAU 60388    | OM970870             | OM970870   | This study |
| G. irresolatus *      | SFSU: DED 8209 | MF100973             | unavailable| [22]       |
| G. montagnei          | JMCR 143       | DQ449988             | AF261327   | [7]        |
| G. neobrevipes        | TENN: F-14505  | MH673474             | MH673477   | [8]        |
| G. novae-angliae nom. | CULTENN4975    | KY026745             | KY026745   | [42]       |
| G. novomundi nom.     | SFSU-DED5097   | KY026799             | KY026799   | [42]       |
| G. octor              | TENN: F-65135  | KY026678             | KY026678   | [42]       |
| G. omphalinoides *    | GDGM 78318     | MW134044             | MW134730   | [18]       |
| G. pallipes *         | GDGM 81513     | MW582856             | OK087327   | [17,18]    |
| G. polyphyllus        | TENN62814-H1   | FJ596894             | unavailable| [45]       |
| G. polyphyllus        | TENN62814-H2   | FJ596895             | unavailable| [45]       |
| G. schizephyllus *    | GDGM 77165     | MW134043             | MW134729   | [18]       |
| G. semihirtipes       | TENN: F-07595  | OK376741             | unavailable| GenBank    |
| G. similis            | BRNM 714981    | KP336690             | KP336690   | [12]       |
| G. sinopolyphyllus    | HMJAU 60387    | OM970871             | OM970871   | This study |
| G. sinopolyphyllus *  | HMJAU 60386    | OM970872             | OM970872   | This study |
| G. sp.                | WCS023         | AB968433             | unavailable| [46]       |
| G. sp.                | Ta-BL62        | LC505290             | LC505290   | [47]       |
| G. spongiosus         | TENN: F-65912  | KY026687             | KY026687   | [42]       |
| G. spongiosus         | TENN: F-65912  | KY026686             | KY026686   | [42]       |
| G. strigosipes *      | HMAS 295796    | OM970874             | OM970874   | This study |
| G. strigosipes        | HMAS 295797    | OM970867             | OM970867   | This study |
| G. subsupinus         | PDD: 96595     | KM975399             | KM975375   | GenBank    |
| G. varicolor          | BRNM 714959    | LT394121             | KP348011   | [12]       |
Table 1. Cont.

| Species Name | Collection No. | GenBank Accession No. | References |
|--------------|----------------|-----------------------|------------|
| *Ma. androsaceus* | Sara Landvik: NN008037 | JN943605 JN941145 | [11] |
| *Ma. otagensis* | PDD: 106823 | MT974597 MT974601 | [18] |
| *Ma. sp.* | Sw5-1 | LC504952 unavailable GenBank |
| *My. alliaceus* | TENN: F-55630 | KY696752 KY696752 | [48] |
| *My. scorodonius* | TENN: F-53474 | KY696748 KY696748 | [48] |
| *Pa. perforans* | TENN: F-50319 | KY026625 KY026625 | [42] |

Newly generated sequences are highlighted in bold and sequences derived from type specimen are marked with an asterisk (*). The haplotypes were deduced from forward and reverse sequences.

3. Results

A combined dataset of two markers, including 1712 bases, comprising 64 nrITS sequences and 56 nrLSU sequences, was used to calculate ML and BI analyses. Amongst the dataset, 1237 were constant sites, 128 were variable and parsimony–uninformative sites, and 347 (≈20.27%) were parsimony–informative sites. According to the BIC criterion, the GTR+F+I+G4, K2P, HKY+F+G4 and HKY+F+I+G4 models were selected as the best-fit model for the nrITS1 region, 5.8S marker, nrITS2 region and nrLSU gene, respectively. Only the tree with a better topology generated by the ML method was shown (Figure 1).

In the newly produced phylogram, the clade *Paragymnopus* helps to separate the *Gymnopus* s. str., forming a monophyletic clade with high support (BI-PP/ML-BP = 1.00/100%). Sequences of the nine studied samples were restricted in the *Gymnopus* s. str. clade forming four distinct lineages. Amongst them, the lineage of the collections HGASM01-11995 and HGASM01-7052 is highly supported (BI-PP/ML-BP = 1.00/98%) and nested in an unsolved clade representing *G.* sect. *Androsacei.* Moreover, the lineage of the collections HGASM01-10068, HGASM01-10069 and HMAU 60388 is highly supported (BI-PP/ML-BP = 1.00/100%) within a well-supported clade, namely, *G.* sect. *Impudicae* (BI-PP/ML-BP = 1.00/96%). Furthermore, the lineage of the collections HMAS 295796 and HMAS 295797 belongs to the clade of *G.* sect. *Levipedes,* and both are strongly supported by the two methods analyses (BI-PP/ML-BP = 1.00/100%). Besides, collections HMAU 60386–60387 are clustered in the clade of *G.* sect. *Impudicae,* and their sequences only differ by having two degenerate bases but including the same nucleotide in the corresponding site.
supported (BI-PP/ML-BP = 1.00/100%) within a well-supported clade, namely, *G. sect. Impudicae* (BI-PP/ML-BP = 1.00/96%). Furthermore, the lineage of the collections HMAS 295796 and HMAS 295797 belongs to the clade of *G. sect. Levipedes*, and both are strongly supported by the two methods analyses (BI-PP/ML-BP = 1.00/100%). Besides, collections HMJAU 60386–60387 are clustered in the clade of *G. sect. Impudicae*, and their sequences only differ by having two degenerate bases but including the same nucleotide in the corresponding site.

**Figure 1.** Phylogram inferred from the combined dataset (ITS1-5.8S-ITS2-LSU region) by ML analysis. ML-BP ≥ 70% and BI-PP ≥ 0.95 are shown above and below the branches, respectively. Sequences produced in this study are highlighted in bold, and sequences from type materials are marked with a five-pointed star.

**4. Taxonomy**

*Gymnopus efibulatus* J.P. Li, Chang-Tian Li, Chun Y. Deng and Y. Li, sp. nov. (Figures 2A,B and 3).

MycoBank number: MB843239

*Etymology:* The specific name ‘efibulatus’ (Latin), referring to the absence of clamp-connections.
Type: China, Guizhou Province, Tongren City, Fanjingshan National Nature Reserve, 27°54’37” N, 108°41’53” E, elev. 2058 m, on dead broadleaves, 28 April 2020, H. Gao, J. Zhang, Z.Q. Shu, D.J. Ou, HGASMF01-7052 (holotype).

Diagnosis: This species is characterized by its brownish grey to dark-brown pileus, whitish to yellowish white rhizomorphs and ellipsoid to oblong basidiospores 7–9 × (3.5–)4–4.5(–5.5) µm in size.

Description: Basidiomata: solitary to gregarious. Pileus: 5.4–8.8 mm in diam., hemispherical when young, then gradually planate, shallowly depressed at centre or not, slightly translucently striate towards margin, then sulcate when old, margin entire, then undulating when maturity, dark brown (8F8) overall when very young, gradually changing to paler with age, finally brownish grey (6C2) overall, darker at disc and sulci. Lamellae: subdistant, adnate, L = 9–13, l = 1–2, reddish grey (7B2) when young, becoming reddish brown (8D4) when old. Stipe: 12.9–15.2 mm long, 0.45–0.6 mm thick at the middle, central and instituted, cylindrical, sometimes compressed at the apex, dry, glabrous, white to whitish at upper part, pastel yellow (1A4) at lower part when young, then almost blonde (4C4) overall, finally becoming cinnamon (6D7) to brown (6E8), more or less paler or darker somewhere. Rhizomorphs: present, whitish to yellowish white (1A2), shiny, wiry, simple, repent. Odour: negligible.

Basidiospores: [n = 60] 7–9 × (3.5–)4–4.5(–5.5) µm (average = 7.8 × 4.3 µm, E = (1.51)1.63–2.05(–2.27), Q = 1.85), ellipsoid to oblong, hyaline, thin-walled. Basidia [n = 20] 19.5–32 × 6–8 µm, clavate, 4-spored. Basidioles: [n = 20] 20.5–28 × 4.5–8 µm, clavate. Cheilocystidia [n = 22] 12–40.5 × 5–15 µm, narrowly clavate to broadly clavate, often with more or less finger-like apical projections, sometimes lobed or forming Siccus-type broom cells, thin-walled, hyaline. Pleurocystidia absent. Pileipellis: an entangled, repent cutis of cylindrical, thin-walled, sometimes coarsely incrusted, otherwise smooth hyphae, terminal cells, diverticulate, lobed to irregularly branched, almost coralloid, mixed with some subglobose cells, slightly brownish in KOH. Stipitipellis: a cutis composed of cylindrical hyphae, parallelly arranged, often smooth, sometimes with scattered diverticula, sometimes dextrinoid, otherwise inamyloid, slightly thick-walled, hyaline. Caulocystidia: absent. Clamp connections: absent.

Additional specimen examined: China, Chongqing City, Gold Buddha Mountain National Scenic Area, 29°1’43” N, 107°11’1” E, elev. 2098 m, on dead broadleaves, 11 August 2020, J.P. Li, Z.Z. Cen, Q.Y. Lin, M. Wang, HGASMF01-11995.

Notes: Morphologically, the pale-coloured stipe and rhizomorphs of G. efibulatus is strongly reminiscent of G. pallipes J.P. Li and Chun Y. Deng and G. cremeostipitatus Antonín, Ryoo and Ka in the field. However, both G. pallipes from China and G. cremeostipitatus from South Korea, with smaller basidiospores (6.06 × 3.24 µm, 7.1 × 3 µm resp.) and the latter one with a pubescent stipe and scattered-to-frequent caulocystidia helps distinguish them from the new species [11,17]. Additionally, the absence of clamp connections, which is not quite common in the genus, strongly supports that they are not conspecific [11,17]. What is noteworthy is a description of Marasmius aurantiobasalis Desjardins and E. Horak, a member of Marasmius sect. Androsacei Kühner (≡ Gymnopus sect. Androsacei), based on individuals from Indonesia shares indistinguishable morphological features with the new species [49]. After checking the original description, Ma. aurantiobasalis from New Zealand differs by having smaller basidiospores (6.75 × 3–3.5 µm) and a pileipellis of subhymeniform that is made up of clavate to irregular, sometimes lobed, cells with dense diverticula [50].

Phylogenetically, the new species is closely related to G. cremeostipitatus, G. irresolutus Desjardin and B.A. Perry, G. neobrevipes R.H. Petersen and G. portoricensis R.H. Petersen. For the comparison with G. cremeostipitatus, see the above paragraph. Additionally, G. irresolutus from São Tomé and Príncipe is characterized by a greyish brown to black stipe with minute pruina and the presence of caulocystidia [22]; G. neobrevipes from the USA is characterized by the black rhizomorphs and smaller cheilocystidia (2.5–3.5 µm) [8]; G. portoricensis from the USA is characterized by the brown to nearly black rhizomorphs, smaller basidiospores [(5–)6–7 × (2.5–)3–4 µm] and the clamped structures [8].
**Figure 2.** Basidiomata of *Gymnopus*. (A,B) *G. efibulatus* (A) HGASMF01-7052 holotype! (B) HGASMF01-11995; (C,D) *G. iodes* (C) HMJAU 60388; (D) HGASMF01-10068 holotype!

**Gymnopus iodes** J.P. Li, Chang-Tian Li, Chun Y. Deng and Y. Li, sp. nov. (Figures 2C,D and 4).

MycoBank number: MB843240
Etymology: The specific name ‘iodes’ is derived from the ancient Greek, referring to the violet coloured pileus.

Type: China, Guizhou Province, Qiandongnan Miao and Dong Autonomous Prefecture, Liping Country, Deshun village, 26°13′59″ N, 109°22′20″ E, elev. 863 m, on dead twigs or broadleaves, 28 August 2020, J.P. Li, D.F. Wei, M. Wang, HGASMF01-10068 (holotype).

Diagnosis: This species is characterized by its garlicky basidiomata, violet-like pileus and oblong basidiospores 5.5–7.5(–8.5) × 3–4(–4.5) μm in size.

Description: Basidiomata solitary. Pileus 9.4–21.1 mm in diam., convex to planoconvex, with central papilla or umbo, sometimes with umbilicate centre, when moist radially striate to sulcate-striate except at the centre, then rugulose when drying, crenate margin, when moist greyish red (11D4) to violet brown (11F6) at disc, darker at umbo, fading towards margin to whitish, greyish red (11D5) at sulci, becoming almost pale violet (15A3) overall when drying, darker at sulci. Lamellae subdistant, L = 21–27, l = 2–4, emarginate and attached with a very small tooth, adnate when old, rugulose-intervenose at the base, purple grey (13B2), finally becoming greyish magenta (13C3), margin whitish. Stipe 16.8–54.2 mm long, 1–1.7 mm thick at the middle, central, cylindrical or laterally compressed, slightly broadened at the apex, entirely whitish tomentose, when young whitish at the upper part, greyish red (10D5) to violet brown (10E5) at the lower part, darker towards the base, almost reddish lilac (11B3) overall when old, with white basal mycelium, dense when old. Odour: distinct, garlic-like.

Basidiospores [n = 60] 5.5–7.5(–8.5) × 3–4(–4.5) μm (average = 6.5 × 3.3 μm, E = (1.67–) 1.73–2.30(–2.36), Q = 1.99), oblong, hyaline, thin-walled. Basidia [n = 20] 18.5–29 × 4.5–6 μm, clavate, 4-spored, hyaline, thin-walled. Basidioles [n = 20] 21–28 × 5–7.5 μm, hyaline, thin-walled. Cheilocystidia [n = 30] 13.5–35.5 × 3–6.5 μm, cylindrical or narrowly clavate, irregular, sometimes with forked, rostrate or one irregular filiform apical projection(s), thin-walled. Pleurocystidia absent. Pileocystidia a cutis consisting of interwoven arranged, cylindrical, sometimes slightly incrusted, otherwise smooth hyphae, terminal cells cylindrical to subclavate, irregular to lobate, sometimes with lateral diverticula or projections, turn green in KOH. Stipitipellis a cutis composed of cylindrical hyphae, parallelly arranged, hyaline, thin-walled. Caulocystidia [n = 20] 25.5–75 × 5–9 μm, cylindrical, sometimes with scattered irregular lobate, obtuse apical projections. Clamp connections present.

Additional specimens examined: China, Guizhou Province, Qiandongnan Miao and Dong Autonomous Prefecture, Liping Country, Deshun village, 26°13′36″ N, 109°19′44″ E, elev. 842.4 m, on dead broadleaves, 28 August 2020, J.P. Li, D.F. Wei, M. Wang, HGASMF1-10069; Hunan Province, Xiangxi Tujia and Miao Autonomous Prefecture, Yongshun County, Xiaoxi Town, Xiaoxi Village, 28°48′20″ N, 110°15′27″ E, elev. 512 m, on dead broadleaves, 22 July 2021, L.N. Liu, HMJAU 60388.

Notes: Morphologically, G. iodes resembles G. iocephalus (Berk. and M.A. Curtis) Halling, G. similis Antonin, R. Ryoo and K.H. Ka and G. varicolor Antonin, Ryoo, Ka and Tomšovský by having a striate pileus, an unpleasant odour and similar-sized basidiospores, which agree to their phylogenetic relationship. However, G. iocephalus from the USA, differs by the pilepellis hyphae turning blue in KOH and the hymenium lacking cheilocystidia [6]. Furthermore, G. similis from South Korea can be distinguished by the darker (reddish) brown stipe and larger cheilocystidia (20–65 × 5–9 μm) [12], and G. varicolor from South Korea, differs by having more brownish pileus, greyish brown or greyish red that becoming pale brownish orange lamellae and larger cheilocystidia (16–40 × 5–9 μm) [12].
**Gymnopus sinopolyphyllus** J.P. Li, Chang-Tian Li and Y. Li, sp. nov. (Figures 5A,B and 6).

MycoBank number: MB843241

Etymology: The specific name ‘sinopolyphyllus’ (Latin), referring to the species described from China and similar to *G. polyphyllus*.

Type: China, Jilin Province, Dunhua City, Xinxing Forest Farm, 43°5′18″ E, elev. 725 m, on dead broadleaves, 16 April 2021, J.P. Li, N.G. Pan, X. Wang, HMJAU 60386 (holotype).

Diagnosis: This species is characterized by its garlicky basidiomata, reddish-orange to yellowish-grey pileus disc, white powdery-tomentose stipe with basal mycelium, ellipsoid to oblong basidiospores (4.5–)5–7 × (2.5–)3–4 μm in size and pileipellis lacking incrusted hyphae.

Description: *Basidiomata*: solitary to cespitose. **Pileus**: 15–35.5 mm in diam., convex to plano-convex, rounded at disc when young, then expanding to plane, slightly and broadly umbонate at disc, margin entire to slightly uneven, hygrophanous at margin, smooth, glabrous, almost reddish orange (7A6) at disc, gradually fading to orange white (6A2) towards margin, occasionally with dark brown (8F8) tinge on the surface somewhere, finally yellowish grey (3B2) at disc, otherwise whitish. **Lamellae**: very close, free to adnate, very narrow, L = 53–70, l = 4–5, whitish. **Stipe**: 28–58 mm long, 2.5–5 mm thick at the apex, 2.5–5.5 mm thick at the base, cylindrical, slightly broadened at the apex and sometimes also the base, white powdery-tomentose overall, smooth, hollow, whitish to orange white (6A2) tinted with orange red (8B7), darker to garnet brown (9D8) at the apex, sometimes with brownish red (8C8) to reddish brown (8D8) tinge somewhere, with white basal mycelium at the base. **Odour**: distinct, garlic-like.

**Basidiospores**: [n = 40] (4.5–)5–7 × (2.5–)3–4 μm (average = 5.9 × 3.2 μm, E = (1.47–)1.58–2.13(–2.3), Q = 1.85), ellipsoid to oblong, hyaline, thin-walled. **Basidia**: [n = 30] 20–29.5 × 5–7.5 μm, clavate, 4-spored. **Basidioles**: [n = 20] 18.5–28 × 5.5–7 μm, clavate.

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**Figure 4.** Microscopic features of *G. iodes* (HGASMF01-10068, holotype!). (A) Cheilocystidia; (B) Caulocystidia; (C) Basidiospores; (D) Terminal elements of the pileipellis. Drawing by J.P. Li. Scale bars: 10 μm (A, B, D), 5 μm (C).
Cheilocystidia: \( [n = 30] 13-43 \times 2.5-8.5 \, \mu m \), narrowly to irregular clavate, smooth, or with one or more projections or irregular and branched outgrowth at the apex, hyaline, thin-walled. Pleurocystidia: absent. Pileipellis: a cutis consisting of interwoven, cylindrical hyphae, branched, smooth, often with oily contents, sometimes with scattered diverticula, terminal cells cylindrical, sometimes irregularly branched, coralloid at the apex. Stipitipellis: a cutis consisting of interwoven, cylindrical hyphae, smooth or with scattered diverticula, thin-walled. Caulocystidia: \( [n = 21] 24-62.5 \times 3-5.5 \, \mu m \), cylindrical, often tapering towards the apex. Clamp connections: present.

Additional specimens examined: China, Jilin Province, Baishan City, Linjiang City, near Tieshigou Ravine, 41°56′49″ N, 126°44′40″ E, elev. 966 m, on dead broadleaves, 20 July 2021, J.P. Li, N.G. Pan, X. Wang, HMJAU 60387.

Notes: Compared with the species with odorous basidiomata and close to crowded lamellae, G. atlanticus V. Coimbra and Wartchow, G. densilamellatus Antonín, Ryoo and Ka, G. hariolorum (Bull.) Antonín, Halling and Noordel., G. polyphyllus (Peck) Halling, and G. virescens A.W. Wilson, Desjardin and E. Horak are similar to the new species. However, G. atlanticus from Brazil, differs by having a sulcate pileus margin, less lamellulae tiers \((l = 3)\) and smaller basidiospores \((7.5 \times 3.6 \, \mu m)\) [21]; G. densilamellatus from South Korea and G. polyphyllus from the USA differ by having incrusted hyphae in pileipellis [6,12]; G. hariolorum from Switzerland differs by a more brownish pileus disc and a slightly longitudinally grooved stipe [2]; and G. virescens from Indonesia differs by having an entirely dark-brown to dark-reddish-brown stipe, larger basidiospores \((7.88 \times 3.53 \, \mu m)\) and a pileipellis with brown-incrusted hyphae that turn oliveaceous in alkali [15].

Phylogenetic analyses suggest that G. sinopolyphyllus is closely affinities with G. densilamellatus and G. polyphyllus, consistent with the morphological study.

Figure 5. Basidiomata of Gymnopus. (A,B) G. sinopolyphyllus (A) HMJAU 60387; (B) HMJAU 60386 holotype! (C–E) G. strigosipes (C,D) HMAS 295796 holotype! (E) HMAS 295797.
Figure 6. Microscopic features of G. sinopolyphyllus (HMJAU 60386, holotype!). (A) Cheilocystidia; (B) Caulocystidia; (C) Basidiospores; (D) Terminal elements of the pileipellis. Drawing by J.P. Li. Scale bars: 10 µm (A,B,D), 5 µm (C).

Gymnopus strigosipes J.P. Li, Chang-Tian Li, Yi. Li and Y. Li, sp. nov. (Figures 5C–E and 7).

MycoBank number: MB843242

Etymology: The specific name ‘strigosipes’ (Latin), referring to the strigose stipe base.

Type: China, Guizhou Province, Tongren City, Yanhe County, Huangtu town, Huaxi village, Shengjiling Ridge, 28°42′45″ N, 108°16′27″ E, elev. 765 m, on dead broadleaves, 27 October 2020, A. Xu, HMAS 295796 (holotype).

Diagnosis: This species is characterized by its reddish-brown to dark-brown pileus, strigose stipe, oblong basidiospores (5.5–)6–7(–7.5) × 3–3.5(–4) µm in size and the presence of caulocystidia.

Description: Basidiomata: cespite. Pileus: 17.5–25 mm in diam., convex to planoconvex when young, then applanate, with rounded to shallowly depressed centre, rugulose at disc when maturity, radially sulcate towards margin, with deflexed to reflexed, finally more or less undulate margin, glabrous, dry, rust brown (6E8) to agate (7E8) at disc when young, gradually becoming reddish brown (8E8) to dark brown (8F8) with age, paler towards margin (nearly orange white (5A2) at margin), but slightly darker at sulci. Lamellae: subdistant, adnate, sometimes with a slightly decurrent tooth, arcuate to ventricose, L = 17–21, l = 4–5, orange grey (6B2) to flesh (6B3), whitish at edge. Stipe 25–41 mm long, 1.5–2 mm thick at the apex, 1.5–3.5 mm thick at the base, centrally attached, compressed, fibrous, hollow, smooth, tomentose at the lower part, mostly reddish brown overall, more or less paler somewhere, long strigose near the base, whitish to reddish white (7A2). Odour: not distinct.

Basidiospores: [n = 60] (5.5–)6–7(–7.5) × 3–3.5(–4) µm (average = 6.3 × 3.3 µm, E = (1.71–)1.72–2.16(–2.2), Q = 1.94), oblong, hyaline, thin-walled. Basidia [n = 20] 18–31 × 4.5–6.5 µm, clavate, 4-spored. Basidioles: [n = 20] 20–32 × 4.5–6.5 µm, clavate. Cheilocystidia: [n = 50] 13–38.5 × 3.5–13 µm, clavate to narrowly clavate, subfuscoid, irregular, lobed, sometimes with filiform apical projection, hyaline, thin-walled. Pleurocystidia: absent. Pileipellis: a cutis consisting of interwoven, cylindrical hyphae, smooth, terminal cells lobed, irregular branched, coralloid, forming a Dryophila-structure. Stipitipellis: a cutis composed of cylindrical hyphae, parallelly arranged, hyaline, slightly thick- to thick-walled. Caulocystidia: [n = 20] 14.5–41 × 3–6 µm, cylindrical, hyaline, thin-walled. Clamp connections present.
Additional specimen examined: China, Guizhou Province, Tongren City, Yanhe County, Huangtu town, Huaxi village, Shengjiling Ridge, 28°42′45″ N, 108°16′27″ E, elev. 765 m, on dead broadleaves, 27 October 2020, A. Xu, HMAS 295797.

Notes: Amongst the known species within G. sect. Levipedes (Quél.) Halling with brownish-coloured pileus and similar lamellae spacing, G. agricola Murrill, G. hybridus (Kühner and Romagn.) Antonín and Noordel., G. loiseleurietorum (M.M. Moser, Gerhold and Tobies) Antonín and Noordel., G. sepiiconicus (Corner) A.W. Wilson, Desjardin and E. Horak, G. spongiosus (Berk. and M.A. Curtis) Halling and G. vitellinipes A.W. Wilson, Desjardin and E. Horak are close to the new species. However, G. agricola, from the USA, can be distinguished by its estriate pileus margin, a cartilaginous and non-strigose stipe [5]; G. hybridus, from France, and G. sepiiconicus, from South Solomons, are characterized by the non-strigose stipe and the absence of caulocystidia [2,14]; G. vitellinipes, from Indonesia, has larger basidiospores (8.3–9.3 × 4–4.4 μm) and a poorly developed Dryophila-structure in the pileipellis [15]; G. loiseleurietorum, from Austria, differs by the absence of true cheilocystidia and hyphae turn green in KOH [2]; G. spongiosus, from the USA, has smaller basidiospores (8.4 × 3.6 μm) that often turn olive green in alkali [20].

Phylogenetic analyses agree with the morphological study, which showed the new species is close to G. spongiosus.

**Figure 7.** Microscopic features of G. strigosipes (HMAS 295796, holotype). (A) Cheilocystidia; (B) Caulocystidia; (C) Basidiospores; (D) Terminal elements of the pileipellis. Drawing by J.P. Li. Scale bars: 10 μm (A,B,D), 5 μm (C).

**Key to species within Gymnopus s. str. with morpho-molecular evidence in China**

1. Terminal cells of pileipellis broad, mostly inflated, mixed with irregularly branched elements and some resembling Dryophila-type structures ........................................ 2.
   - Terminal cells of pileipellis coralloid, more or less diverticulate, lobed to irregularly branched, or with Dryophila-type structures ....................................................... 3.
2. Pileus generally deeply umbilicate; lamellae ventricose ...................... G. omphalinoides
   - Pileus more or less depressed; lamellae linear to arcuate .................... G. schizophyllus
3. Rhizomorphs present, cheilocystidia consist of *Siccus*-type broom cells, stipitipellis with dextrinoid hyphae ........................................ 4.
   – Rhizomorphs absent, cheilocystidia never a *Siccus*-type broom cell, stipitipellis without dextrinoid hyphae ........................................ 5.

4. Clamp connections present ................................................. *G. pallipes*
   – Clamp connections absent .............................................. *G. efibulatus*

5. Basidiomata with unpleasant odour ........................................ 6.
   – Basidiomata with negligible odour ..................................... 10.

6. Lamellae not close or crowded ............................................. 7.
   – Lamellae close or crowded ................................................ 9.

7. Pileus general white overall ................................................. *G. alliifoetidissimus*
   – Pileus not white ............................................................... 8.

8. Pileus light brown, orange white to greyish orange when old ........ *G. similis*
   – Pileus almost reddish lilac overall when drying ..................... *G. iodes*

9. Pileipellis consist of incrusted hyphae ................................. *G. densilamellatus*
   – Pileipellis without incrusted hyphae .................................. *G. sinopolyphyllus*

10. Caulocystidia present ......................................................... *G. strigosipes*
    – Caulocystidia not recorded ................................................ 11.

11. Stipe smooth or tomentose .................................................. 12.
    – Stipe with hairs .............................................................. 15.

12. Pileipellis made up of smooth hyphae ..................................... 13.
    – Pileipellis with incrusted hyphae ....................................... 14.

13. Basidia sterigmata extremely long, up to 32 µm ..................... *G. macrosporus*
    – Basidia sterigmata normally long ........................................ *G. tiliicola*

14. Basidia sterigmata extremely long, up to 33 µm ..................... *G. longus*
    – Basidia sterigmata normally long ........................................ *G. globulosus*

15. Pileus tomentose or pileipellis with incrusted hyphae ................... 16.
    – Pileus without tomenta and pileipellis made up of smooth hyphae ........ 17.

16. Pileus tomentose, pileipellis made up of smooth hyphae ............ *G. tomentosus*
    – Pileus without tomenta, pileipellis with incrusted hyphae ........ *G. longisterigmaticus*

17. Pileus estriate ............................................................... *G. erythropus*
    – Pileus striate ................................................................. *G. striatus*

5. Discussion

A total of 28 known species of *Gymnopus* s. str. have been reported in China as yet, of which 15 taxa were reported based on morpho-molecular evidence [16–18,33]. This study provides descriptions of four new *Gymnopus* species and DNA barcodes. The newly proposed species, except *G. efibulatus*, a member of *G. sect. Androsacei*, embrace the current sectional concept well. Four odorous fungi, namely, *G. iocphalus*, *G. iodes*, *G. similis* and *G. variicolor* formed an independent clade implying their close affinities phylogenetically.
When revisiting these four gymnopoid fungi in morphology, it is not hard to find that they share the striate pileus and the distant to subdistant lamellae \([6,12]\). Similarly, \textit{G. densilamellatus}, \textit{G. polyphyllus} and \textit{G. sinopolyphyllus}, forming an independent clade, share the very close to crowded lamellae \([6,12]\). Besides, \textit{G. sect. Androsacei} is still an unsolved clade thus far, phylogenetically. Formally, Li et al. discussed the sectional circumscription and noted the broom cells were absent or weakly present in the pilepellis of several taxa \([17]\). Furthermore, the pilepellis of \textit{G. ephibulatus} also lack the bloom cells but subglobose cells were observed. Accordingly, this section is worthy of further exploration in the future based on morphology inferred from more materials and multilocus phylogenetic analyses.

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