1. Introduction

*Mycena* (Pers.) Roussel is a large genus in Agaricales with up to 600 species worldwide [1]. Persoon was the first mycologist who used the name *Mycena* as a section in *Agaricus* L. [2], and this section is characterized by pileus membranous and convex, with sulcate margin and stipe glabrescent. Roussel later raised sect. *Mycena* to generic rank [3]. It has been widely accepted now and many species in *Mycena* are found and several monographs have been published [4–8].

The orchid *Gastrodia elata* Blume, known as “Tianma” in traditional Chinese medicine, has been used in Asia for centuries to treat many human diseases, such as headache, vertigo, blackout, hemiplegia, and epileptic convulsions [9,10]. This species also has strong potential for treating Alzheimer’s and Parkinson’s diseases [11]. The seeds of *G. elata* are minute, and most contain an undifferentiated embryo that lacks a well-defined endosperm [12]. The few-celled embryo contains small amounts of proteins and lipids and very little sugar [13,14]. Because of this absence of nutritional reserves, the seed germination of *G. elata* in nature completely depends on mycorrhizal fungi [15,16].

Extensive research has shown that several *Mycena* species are essential for stimulating germination and the early stages of protocorm development in *G. elata* [17–23]. In the cited studies, most mycorrhizal *Mycena* were isolated from various Orchidaceae members or protocorms of *G. elata*. Species in *Mycena* with tiny basidiomata are abundant, which complicates the identification without basidiomata solely based on the few reliable DNA sequences in GenBank. Many researchers have focused on the mycorrhizal *Mycena* of *G. elata* and they intended to culture and identify them in the lab, however, only four species (M. osmundicola J.E. Lange, M. orchidicola Fan et Guo, M. dendrobii Fan et Guo, and M. anoectochila Fan et Guo) are able to form basidiomata in cultivation and have thus been successfully identified [17,19,20,24].

During field investigations in subtropical areas of China, we discovered a species of *Mycena* in Hunan Province and successfully obtained this strain by tissue isolation. According to our morphological observations, phylogenetic analyses based on nuclear ribosomal DNA internal transcribed spacer (ITS) and large subunit (LSU) sequences, and germination experiments, the isolated taxon is new to science and can strongly improve the germination rates of *G. elata* seeds.

2. Materials and methods

2.1. Sampling and morphological observations

Two specimens (HUIF50007 and HUIF50036) collected from Hunan Province, China, were dried in silica gel and preserved at the herbarium of Hunan Institute of Forestry (HUIF). The strain of the new taxon was isolated from basidiomata of the type specimen (HUIF50007). Macroscopic characteristics of...
fresh specimens were recorded with colors described according to Kornerup and Wanscher [25]. To obtain microscopic characteristics, dried specimens were examined by light microscopy (Olympus BX51, Olympus Cooperation, Tokyo, Japan). Microscopic characterization and examination of chemical reactions were carried out in 5% KOH or 1% Congo Red solution (in distilled water). Basidiospores, cheilocystidia, pileipellis, stipitipellis, and tramas were tested for their chemical reaction to Melzer’s reagent [26]. The spore quotient ($Q = \frac{\text{length (L)}}{\text{breadth (B)}}$) was calculated from measurements of 30 basidiospores per collection. And more than 20 individuals for other structures were also measured in each collection.

2.2. DNA extraction, PCR amplification, and sequencing

Total genomic DNAs from the two dried specimens and related strains (8103, TMMFJ, MF2XG, and SHXG from the Institute of Applied Mycology of Huazhong Agricultural University and MFJ from the professional cooperative of lv-zhou Gastrodia elata in Sui-ning county which are widely used in China) were extracted using a NuClean Plant Genomic DNA kit (CWBIO, Norcross, GA). ITS and LSU regions of the extracted DNA were, respectively, amplified using primer pairs ITS4/ITS5 and LROR/LR7 [27] according to the PCR cycling conditions described in Liu and Bau [28]. The resulting products were sequenced by the Tsingke Biotechnology Company (Changsha, Hunan, China).

2.3. Data analyses

A total of 88 ITS and LSU sequences of Mycena, including four sequences from the new taxon, were subjected to molecular phylogenetic analyses. The analyzed sequences included those selected according to the results of a GenBank BLAST search as well as previously reported sequences of unidentified symbiotic Mycena of Gastrodia spp. or Dendrobium sp. [22,23,29,30]. Xeromphalina campanella (Batsch) Kühner & Maire was used as an outgroup. Detailed information on the sequences analyzed is provided in Table 1. Sequences were aligned using MUSCLE version 3.8.31 (Mill Valley, CA) [31]. After selection of the optimal evolutionary model in MrModeltest version 2.3 Uppsala (Sweden) [32], the aligned data set was analyzed by Bayesian inference (BI) and maximum likelihood (ML). The BI analysis was performed with MrBayes version 3.2.6 (Uppsala, Sweden) [33]. The ML analysis was performed in RAxMLGUI version 1.5b1 (Heidelberg, Germany) [34] using a rapid bootstrapping algorithm and 1000 replicates, followed by a ML tree search. The resulting tree was visualized in Figtree version 1.4.3 (Edinburgh, UK) [35].

2.4. Cultivation

The isolated tissues were cultured on potato dextrose agar (PDA) plates containing 50 ppm ampicillin. The plates were incubated in the dark at 25°C until hyphae were visible. Hyphal tips were transferred to fresh PDA and then serially transferred until pure cultures were obtained. Decayed leaves of Castanea molliissima Blume or Pinus massoniana Lamb. were then added to PDA to optimize the medium.

2.5. Symbiotic seed germination and protocorm development of G. elata

Mycena citrinomarginata Gillet strains 8103, TMMFJ, MF2XG, and SHXG from the Institute of Applied Mycology of Huazhong Agricultural University and MFJ from the professional cooperative of lv-zhou Gastrodia elata in Sui-ning county were also selected for use in comparisons. Mature un-dehisced fruits of G. elata were collected from the professional cooperative of lv-zhou Gastrodia elata in Sui-ning county. After collection, fruits were sterilized using 75% ethanol, washed three times using distilled water, and dried on sterile filter paper. Mycena strains were placed on water agar medium (0.1% agar), and G. elata seeds were then scattered around the mycelium. The MFJ strain, which is widely used for seed germination of G. elata in Hunan, was selected as a positive control. After incubation of seeds at 25°C in the dark for 20 d, the number of seeds was determined under a dissecting stereomicroscope every 5 d for 60 d. Six replicates of each plate were counted. And we did this experiment three times.

3. Results

3.1. Phylogenetic analyses

BI and ML phylogenetic trees based on ITS and LSU sequences had similar topologies. As shown in the BI tree in Figure 1, the analyzed taxa were divided into two distinct groups. The two accessions of the new taxon and its isolated strain grouped together (Bayesian posterior probability = 1.00/ML bootstrap = 100%) in Clade 3. The new taxon is thus clearly separate from allied Mycena species.

3.2. Taxonomy

Mycena subpiligera L.N. Liu, sp. nov.

Mycobank: MB842467
### Table 1. Sequences of basidiomata and strains for phylogenetic analyses used in this study.

| Species                  | Voucher                  | GenBank Accession no. | Basidiomata/Strain | Country        |
|--------------------------|--------------------------|-----------------------|--------------------|----------------|
| Mycena abramsii          | HMJAU43606               | MH9629               | Basidiomata       | China          |
| M. abramsii              | HUIFS50004               | OM228756             | Basidiomata       | China          |
| M. abramsii              | HMJAU43282               | MH629348             | Basidiomata       | China          |
| M. abramsii              | HMJAU43523               | MH629350             | Basidiomata       | China          |
| M. adena                 | HMJAU43533               | MH629350             | Basidiomata       | China          |
| M. adena                 | HMJAU43691               | MK73239              | Basidiomata       | China          |
| M. albiceps              | F2762                    | MZ303026             | –                  | Basidiomata    |
| M. albiceps              | RA705-6                  | MK34177              | –                  | Basidiomata    |
| M. alpeniensis           | HMJAU43798               | MK732299             | –                  | Basidiomata    |
| M. arcangeliana          | 252b                     | JF908401             | –                  | Basidiomata    |
| M. arcangeliana          | 252f                     | JF908402             | –                  | Basidiomata    |
| M. cf. cinerella         | 173                      | MF926553             | –                  | Basidiomata    |
| M. cinerella             | Arasen050104             | KT900146             | –                  | Basidiomata    |
| M. citrinomarginata      | SHXG                     | OM228755             | Strain            | China          |
| M. citrinomarginata      | MFJ                      | OM228754             | Strain            | China          |
| M. citrinomarginata      | 8103                     | OM228752             | Strain            | China          |
| M. citrinomarginata      | MFXG                     | OM228753             | Strain            | China          |
| M. citrinomarginata      | TMJMJ                    | OM228751             | Strain            | China          |
| M. citrinomarginata      | HMJAU43563               | MG654739             | Basidiomata       | China          |
| M. deeptha               | DM334q (KMS178333)       | JX481737             | –                  | Basidiomata    |
| M. entolomoides          | HMJAU43126               | MG654738             | Basidiomata       | China          |
| M. galericulata          | TENN-F-014675h1          | MN088380             | –                  | Basidiomata    |
| M. galericulata          | TENN-F-069080s51         | MN088383             | –                  | Basidiomata    |
| M. galericulata          | TENN-F-069380           | MN088382             | –                  | Basidiomata    |
| M. haematopus            | HMJAU43494               | MK732296             | Basidiomata       | China          |
| M. hyalinostipitata       | HMJAU43693               | MH136828             | Basidiomata       | China          |
| M. inclinata             | S.D.Russell MycoMap 4978 | MK32829              | Basidiomata       | America        |
| M. inclinata             | iNat3919741              | MH64198              | Basidiomata       | America        |
| M. laevigata             | 4747                     | MH930175             | –                  | Basidiomata    |
| M. laevigata             | HMJAU43187               | MK73302              | –                  | Basidiomata    |
| M. laevigata             | HMJAU43604               | MK73303              | –                  | Basidiomata    |
| M. laevigata             | HMJAU43618               | MK73304              | –                  | Basidiomata    |
| M. meligera              | 39d                      | JF908429             | –                  | Basidiomata    |
| M. meligera              | 39                      | JF908423             | –                  | Basidiomata    |
| M. metata                | HMJAU43625               | MH96636              | –                  | Basidiomata    |
| M. pearsoniana           | HMJAU43826               | MK73305              | Basidiomata       | China          |
| M. pura                  | TENN-F-065043            | MN182202             | Basidiomata       | America        |
| M. purpureofooceus       | HMJAU43624               | MG654740             | Basidiomata       | China          |
| M. rosea                 | Champ-21                 | KX449424             | –                  | Basidiomata    |
| M. seminau               | KLUM 1223                | KF352720             | Basidiomata       | Malaysia       |
| M. seminau               | KLUM 1122                | KF352722             | Basidiomata       | Malaysia       |
| M. seministipes          | HMJAU43825               | MK733208             | Basidiomata       | China          |
| Mycena sp.               | F69                      | LC314115             | –                  | Strain         |
| Mycena sp.               | taxon:1916079            | LC314114             | –                  | Strain         |
| Mycena sp.               | NIFOS101                 | KY44928              | –                  | Strain         |
| Mycena sp.               | taxon:669029             | FJ544251             | –                  | Strain         |
| Mycena sp.               | KFRI1212                 | HQ662845             | –                  | Strain         |
| Mycena sp.               | KFRI2121                 | HQ662846             | –                  | Strain         |
| M. subgilgera            | HUIFS50007               | OM228757             | Basidiomata       | China          |
| M. subgilgera            | HUIFS50007               | OM228758             | Basidiomata       | China          |
| M. subgilgera            | HUIFS50007               | OM228759             | Basidiomata       | China          |
| M. subtilobates          | HMJAU43418               | MH216189             | –                  | Basidiomata    |
| M. supina                | 128a                     | JF908388             | –                  | Basidiomata    |
| M. tenax                 | OSC 113728               | EU669222             | Basidiomata       | America        |
| M. tenax                 | OSC 113746               | EU86252              | Basidiomata       | America        |
| M. tenuerrima            | HMJAU43816               | MK309796             | Basidiomata       | China          |
| M. vulgaris              | 447h                     | JF908435             | –                  | Basidiomata    |
| M. vulgaris              | 3781                     | KJ705177             | –                  | Basidiomata    |
| Xeromphalina campanella  | TENN-F-053583A           | KM204575             | Basidiomata       | Sweden         |
| K. campanella            | TENN-F-069178            | KP356578             | –                  | Basidiomata    |

**Diagnosis.** Pileus convex, with umbilicate or depressed center. Lamellae short decurrent to decurrent, often stained with yellow-brown to orange-brown spots (Figures 2 and 3). Cheilocystidia fusoid or cylindrical, thick walled. Pileipellis branched, anastomosing, smooth with scattered, cylindrical excrescences. Caulocystidia piliform.

**Etymology.** Referring to its piliform caulocystidia and it also be closed to *M. piligera* in morphology.

**Type.** CHINA. Hunan Province, Shaoyang city, Sui-ning County, Hunan Huangsan National Nature Reserve, April 26 2021, Lina Liu, HUIFS50007 (Holotype!).

Pileus 0.5–1.9 cm diameter, convex, somewhat flattened, umbilicate or depressed centrally, translucently striate, pale brown (6D7) to brown (6F7) when young, pale yellow-brown (6G6) to brownish-white (6A3) with age, whitish (6A2–6A1) in the peripheral regions, often stained with yellow-brown (6A7) to orange-brown.
Figure 1. Bayesian tree inferred from partial ITS and LSU sequences showing phylogenetic relationships of *Mycena subpiligera*. Bayesian posterior probability (≥0.95) and maximum likelihood support values (≥75) are shown (BPP/ML). New species is marked by ♦.

Figure 2. Basidiomata and mycelium of *Mycena subpiligera*. a. Basidiomata of *M. subpiligera* in the field (HUIF50007); b. Mycelium of *M. subpiligera* cultured on the media mixed with leaves of *Castanea mollissima*; c–e. *M. subpiligera* cultured on the media mixed with leaves of *Pinus massonina*. 
Lamellae short decurrent to decurrent, white, edges concolourous, often stained with yellow-brown (6A7) to orange-brown (6C8) spots. Stipe 2.1 – 6.5 × 0.2 – 0.4 cm, cylindrical, strait to somewhat flexuous, hollow, pruinose at apex, dense white-pubescent at base, white to brownish-white (6A3). Odorless and with a mild taste.

Basidiospores 6.2 – 7.4 × 3.1 – 3.8 μm, Q = 1.8 – 2.0, oblong to subcylindrical, hyaline, guttulate, thin walled, amyloid. Basidia 15 – 19 × 5 – 7 μm, four-spored, clavate. Cheilocystidia 15 – 32 × 3 – 6 μm, fusoid or lageniform, thick-walled, and hyaline. Pleurocystidia absent. Lamellar trama dextrinoid. Hyphae of the Pileipellis glutinosus, 2 – 4 μm wide, branched, anastomosing, smooth seldomly with scattered, and cylindrical excrescences. Hyphae of the stipitpellis 2 – 6 μm wide, smooth. Caulocystidia 84 – 215 × 4 – 7 μm, piliform, long fusoid or cylindrical, smooth, and thin to slightly thick-walled. Clamp-connections present in all tissues.

Habitat. Fasciculate or solitary on vegetable debris under forests which mainly composed by P. massoniana and Fagus sp.

Known distribution. Hunan Province, China.

Additional material examined. CHINA. Hunan Province, Xiangxi Tujia-Miao Autonomous Prefecture, Longshan County, the institute of crop sciences of Longshan, May 27 2021, Lina Liu, HUIF50036.

Figure 3. Features of Mycena subpiligera. a. Basidiomata; b. Basidia; c. Basidiospores; d. Cheilocystidia; e. Hyphae of Pileipellis; f. Caulocystidia. Scar Bars a = 1 cm; c = 5 μm; b, d, e, f = 10 μm. All drawings from holotype by Lina Liu.
3.3. Cultivation

We found that basidiomata only formed when tissues were cultivated on PDA mixed with decayed leaves of *P. massoniana* for 80–86 d.

3.4. Symbiotic seed germination and protocorm development of *G. elata*

Both strains (HUIFS50007 and MFJ) were able to stimulate seeds sprouting of *G. elata* (Figure 4), but the germination rate in the presence of HUIFS50007 (81%) was slightly higher than that of MFJ (74%). In addition, *G. elata* protocorms seem to develop faster with HUIFS50007 than with MFJ mycelium.

4. Discussion

*Mycena subpiligera* is characterized by the presence of a brown pileus, white lamellae, amyloid spores, fusoid or lageniform cheilocystidia, a smooth pileipellis, and piliform caulocystidia. The new species can be assigned to sect. *Fragilipedes* (Fr.) Qué. on the basis of its white lamellae, amyloid spores, fusoid or lageniform cheilocystidia, and smooth pileipellis [36,37]. Five other species in this section, namely, *M. piligera* Robich, *M. pilosella* Maas Geest., *M. scirpicola* M. Villarreal, Heykoop, Esteve-Rav. & Maas Geest., *M. pruinatipes* Robich, and *M. villicaulis* Maas Geest., superficially resemble the new species in having piliform caulocystidia. Our new taxon can be easily confused with *M. piligera* on account of its similar macroscopic characters and piliform caulocystidia, but *M. piligera* has larger, differently shaped basidiospores (7.5–10 × 4.5–6 μm), thin-walled cheilocystidia, and a diverticulate pileipellis [5]. Although some variation exists within *M. pilosella*, this species complex can be distinguished from *M. subpiligera* by the presence of a conical or hemispheric cap without a depressed center, a diverticulate pileipellis not embedded in gelatinous matter, and a diverticulate stipitipellis [4,36]. Compared with *M. scirpicola*, it has a conical to conical-campanulate cap, adnate lamellae, and a different pileipellis and stipitipellis [7]. *Mycena pruinatipes* differs from our new taxon in possessing a smaller conical cap, pleurocystidia, and a diverticulate pileipellis and stipitipellis [5]. The fact that basidiomata of our newly described taxon only formed on the medium mixed with *P. massoniana* is clearly reminiscent of *M. villicaulis* with a similar habitat, but *M. villicaulis* differs in having a differently shaped cap, a diverticulate pileipellis, a diverticulate stipitipellis, and obvious thick-walled caulocystidia [4].

In our BI and ML phylogenetic trees based on ITS and LSU sequences, the two collected accessions grouped together with high support with one strain of *M. subpiligera* in Clade 3, which in turn was sister to an unidentified *Mycena* (voucher no. TENN054423). This latter voucher was selected for analysis because this sample was the most similar *Mycena* according to the results of a GenBank BLAST search. Although we do not know the morphological characteristics of the unidentified *Mycena*, which was collected in Argentina, it can clearly be distinguished phylogenetically.

To better understand the diversity of *Mycena* species able to enhance the germination efficiency of *G. elata* seeds, we sequenced six *Mycena* strains (including an unpublished one, HUIFS50004)
symbiotic on *G. elata* seeds in China as well as six unidentified symbiotic *Mycena* of *Gastrodia* spp. or *Dendrobium* sp. reported from various studies [22,23,29,30]. Ten strains were successfully identified on the basis of their ITS and LSU sequences. Interestingly, *M. abramsii* (Murrill) Murrill (HUIFS50004), *M. adenexa* T. Bau & Q. Na (taxon 1916079), and *M. citrinomarginata* (TMMFJ), 8103, MFXG, MFJ, SHXG, NIFOS101, and taxon 660929) together with our new taxon can all be assigned to sect. *Fragilipes* [36]. In contrast, *M. deeptha* Aravind. & Manim. (KFR11212) is a bioluminescent fungus in sect. *Exornatae* Maas Geest. [38], whereas symbiotic *Mycena* identified in previous studies (i.e., *M. osmundicola*, *M. orchidicola*, *M. dendrobii*, and *M. anoctochila*) are all in sect. *Sacchariferae* Kühn ex Singer [17,19,20,24]. In this study, all analyzed strains of *Mycena* spp. were able to stimulate the germination of *G. elata* seeds to some extent. Determining which members of *Mycena* and related genera can stimulate the germination of *G. elata* or other orchids is an interesting research problem that we plan to address in future work.

**Acknowledgments**

The authors sincerely thank Dr. Xin Chen in Huazhong Agricultural University, Dr. Liang-bin Zeng in Chinese Academy of Agricultural Sciences, Mrs Kai-lin Tan, Mr shu-yuan Tang in the professional cooperative of lv-zhou *Gastrodia elata* in Sui-ning county, and Mr Zu-heng Xiang, Mr. Peng Zhang in Forestry Bureau of Long-shan County for the help in the experimental process. We also thank the kind editors and two anonymous reviewers for their corrections and suggestions to improve our work.

**Disclosure statement**

No potential conflict of interest was reported by the author(s).

**Funding**

This work was supported by two projects from the Forestry Department of Hunan Province which named “Study on key techniques of reintroduction of rare orchids” and “Comparative evaluation and cultivation demonstration of different genotypes of rare orchids”.

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**Data availability statement**

This data can be opened available from GenBank.

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