New insights into the genus Gyroporus (Gyroporaceae, Boletales), with establishment of four new sections and description of five new species from China

Ming Zhang, De-Chun Xie, Chao-Qun Wang, Wang Qiu Deng and Tai-Hui Li

*State Key Laboratory of Applied Microbiology Southern China, Guangdong Provincial Key Laboratory of Microbial Culture Collection and Application, Institute of Microbiology, Guangdong Academy of Sciences, Guangzhou, Guangdong Province, China; \(^4\)Department of Public Health Laboratory Sciences, School of Public Health, Hengyang Medical School, University of South China, Hengyang, Hunan, China

**ABSTRACT**

Species of *Gyroporus* from southern China were studied in this study. Based on morphology and molecular phylogenetic analyses of DNA sequences from the nuclear ribosomal internal transcribed spacer (ITS), the nuclear ribosomal large subunit (nLSU), and the mitochondrial adenosine triphosphate ATP synthase subunit 6 (*atp6*), *Gyroporus* was divided into four main branches in the phylogenetic tree, and four sections were firstly proposed i.e. *Gyroporus* sect. Castaneus, G. sect. Cyanescens, G. sect. Longicy Sti diatus and G. sect. Pallidus. Five new species, i.e. G. alboluteus, G. atrocyanescens, G. pseudolongicystidiatus, G. pallidus and G. subcaeruleus, were revealed from China, and their phylogenetic positions were also analysed. Among them, G. alboluteus and G. pallidus were nested into the sect. Pallidus, although morphologically similar to G. castaneus; G. atrocyanescens and G. subcaeruleus, with obvious cyanescent oxidation reactions, were nested into the sect. Cyanescens; and G. pseudolongicystidiatus characterised by its long cystidia and was nested into the sect. Longicy Sti diatus. The new species were formally described and illustrated in the present study, and a key to the sections and species of *Gyroporus* in China was provided.

**Introduction**

*Gyroporus* Quél., typified by *G. cyanescens* (Bull.) Quél., is a small but poorly understood bolete genus in the family Gyroporaceae of Boletales. Members of *Gyroporus* are widely scattered throughout temperate, subtropical and tropical regions of the world, and strongly implicated as symbionts with an array of ectotrophic plants, such as Fabaceae, Fagaceae, Myrtaceae, Pinaceae, Phyllanthaceae, etc. (Singer et al. 1983; Agerer 1999; Raidl et al. 2006; Watling 2006, 2008; Wilson et al. 2012). Species in *Gyroporus* can be easily identified by the brittle and hollow stipe, the white to yellowish white hymenophore unchanging or changing to blue when bruised, white spore print, ellipsoid basidiomycetes and the presence of clamp connections (Singer 1986; Watling 2008; Das et al. 2017; Magnago et al. 2018; Huang et al. 2021; Xie et al. 2022). However, it is extremely complicated to determine their taxonomic positions at the species level owing to the overlap of phenotypic variation among species. Recently, molecular phylogenetic studies have provided more effective and accurate evidences for species identification of *Gyroporus*, and some new species have been reported (Das et al. 2017; Magnago et al. 2018; Huang et al. 2021; Xie et al. 2022), while the gene of mitochondrial adenosine triphosphate ATP synthase subunit 6 (*atp6*) has been identified as a utility DNA barcoding marker to determine the infraspecific relationships of *Gyroporus* (Davoodian et al. 2018; Huang et al. 2021).

In China, sixteen species have been recorded, including eight species originally reported from China, i.e. *G. alpinus* Yan C. Li, C. Huang & Zhu L. Yang, *G. brunneoflaccosus* T.H. Li, W.Q. Deng & B. Song, *G. flavocyanescens* Yan C. Li, C. Huang & Zhu L. Yang, *G. memnonius* N.K. Zeng, H.J. Xie & M.S. Su, *G. porphyreus* N.K. Zeng, H.J. Xie & Zhi Q. Liang, *G. pseudomicrosporus* M. Zang, *G. subglobosus* N.K. Zeng, H.J. Xie, L.P. Tang & M. Mu, and...
describes basidiospore dimensions, where the range b−c represented 90% or more of the measured values and “a” and “d” were the extreme values; Q referred to the length/width ratio of an individual basidiospore and Qm referred to the average Q value of all basidiospores ± sample standard deviation. All line-drawings of microstructures were made based on rehydrated materials.

**DNA extraction, PCR amplification and sequencing**

Genomic DNA was extracted from the voucher specimens using the Sangon Fungus Genomic DNA Extraction kit (Sangon Biotech Co. Ltd., Shanghai, China), according to the manufacturer’s instructions. Primer pairs ITS5/ITS4 (White et al. 1990), LROR/LR5 (Vilgalys and Hester 1990), and atp6-2/atp6-3 (Kretzer and Bruns 1999) were used for amplifying ITS, nrLSU and atp6, respectively. PCR reactions were performed in a total volume of 25 μl containing 0.5 μl template DNA, 11 μl distilled water, 0.5 μl of each primer and 12.5 μl 2 × PCR mix (DreamTaq™ Green PCR Master Mix, Fermentas). Amplification reactions were performed in a Tprofessional Standard Thermocycler (Biometra, Göttingen, Germany) under the following conditions: 95°C for 4 min; then 35 cycles of denaturation at 94°C for 60s, annealing at 53°C for 60s, and extension at 72°C for 60s; with a final extension at 72°C for 8 min. The PCR products were electrophoresed on 1% agarose gels and sequencing was performed on an ABI Prism® 3730 Genetic Analyser (PE Applied Biosystems, Foster, CA, USA) at the Beijing Genomic Institute (BGI) using the same PCR primers. The raw sequences were assembled and checked with SeqMan implemented in Lasergene v7.1 (DNASTAR Inc., USA). The newly generated sequences in this study were submitted to GenBank.

**Materials and methods**

**Morphological studies**

Photographs of the fresh basidiomata were taken in the field. Specimens were dried and deposited in the Fungarium of Guangdong Institute of Microbiology (GDGM). Descriptions of macro-morphological characters and habitats were obtained from photographs and field notes. Colour codes followed Kornerup and Wanscher (1981). Microscopic observations were carried out on tissue sections stained with 5% KOH and 1% aqueous Congo red under a light microscope (Olympus BXS1, Tokyo) with magnification up to 1000 x. All measurements were made in 5% KOH. For basidiospore descriptions, the notation (a−b−c−d−) describes basidiospore dimensions, where the range b−c represented 90% or more of the measured values and “a” and “d” were the extreme values; Q referred to the length/width ratio of an individual basidiospore and Qm referred to the average Q value of all basidiospores ± sample standard deviation. All line-drawings of microstructures were made based on rehydrated materials.

**Phylogenetic analyses**

Sequences generated in this study and those downloaded from GenBank were combined and used for phylogenetic reconstruction. Detailed information of specimens included in this study was given in Table 1. Sequence matrix of ITS, nrLSU and atp6 were separately aligned with software MAFFT v7 using the E-INS-i strategy (Katoh and Standley 2013) and manually adjusted in MEGA 6 (Tamura et al. 2013).
Table 1. Information on specimen used in phylogenetic analyses. Sequences newly generated in this study are indicated in bold.

| Taxa                  | Voucher          | Locality         | GenBank accession number | References                  |
|-----------------------|------------------|------------------|--------------------------|-----------------------------|
| G. alboluteus         | GDGM25474-1      | -                | -                        | This study                  |
| G. alboluteus         | GDGM25474-2      | -                | -                        | This study                  |
| G. alboluteus         | GDGM86706        | -                | -                        | This study                  |
| G. allocyanescens     | REH9700A         | Queensland       | MF818179                 | Davoodian et al. 2018       |
| G. alpinus            | Li1478a          | China            | MW149438 MW151268 MW452609 | Huang et al. 2021           |
| G. alpinus            | Li1478b          | China            | MW149435 MW151269 MW452610 | Huang et al. 2021           |
| G. ammorphilus        | AH45814          | Spain            | KX869878 KX869892         | Crous et al. 2016           |
| G. ammorphilus        | AH45842          | Spain            | KX869876 KX869890         | Crous et al. 2016           |
| G. australiensis      | REH9312          | Queensland       | -                         | Davoodian et al. 2018       |
| G. australiensis      | REH9559          | Queensland       | -                         | Davoodian et al. 2018       |
| G. australiensis      | REH9422          | Queensland       | -                         | Davoodian et al. 2018       |
| G. australiensis      | REH9501          | Queensland       | -                         | Davoodian et al. 2018       |
| G. austrobrasiliensis | ICN 184400       | Brazil           | MF437000 MF437015         | Magnago et al. 2018         |
| G. austrobrasiliensis | ICN 184402       | Brazil           | MF437001 OM068915         | Magnago et al. 2018         |
| G. australiensis      | ICN 184399       | Brazil           | MF436999 MF437014         | Magnago et al. 2018         |
| G. australiensis      | REH9700          | Queensland       | MF818176                 | Davoodian et al. 2018       |
| G. brunneofoccatus    | GDGM74550        | China            | ONS02904 ONS02927 ON100612 | This study                  |
| G. brunneofoccatus    | GDGM77113        | China            | ONS02907 ONS02930 ON100615 | This study                  |
| G. brunneofoccatus    | GDGM77125        | China            | ONS02906 ONS02929 ON100614 | This study                  |
| G. brunneofoccatus    | GDGM74638        | China            | ONS02905 ONS02928 ON100613 | This study                  |
| G. brunneofoccatus    | GDGM78301        | China            | ONS02908 ONS02931 ON100616 | This study                  |
| G. brunneofoccatus    | Wu2644a          | China            | MW149436 MW151267 MW452611 | Huang et al. 2021           |
| G. brunneofoccatus    | HKA107735        | China            | MW149436                 | Davoodian et al. 2018       |
| G. brunneofoccatus    | OR1482           | -                | MF818146                 | Davoodian et al. 2018       |
| G. eff. castaneus      | CM061            | Algeria          | KP826761                 | Unpublished                 |
| G. eff. castaneus      | E843c            | -                | EU718170                 | Wilson et al. 2012          |
| G. cf. castaneus       | FHMJ3368         | China            | MW38086 MW352984         | Xie et al. 2022             |
| G. cf. castaneus       | HKAS56672        | China            | KF112478                 | Unpublished                 |
| G. eff. castaneus      | iNaturalist 31,940,211 | USA | MN498109                 | Unpublished                 |
| G. castaneus           | Arora 01.512     | USA              | FJ710209                 | Unpublished                 |
| G. castaneus           | FLAS F 61255     | USA              | MH211836                 | -                           |
| G. castaneus           | SD Russell MycoMap 6269 | USA | MK332856                 | -                           |
| G. castaneus           | JMP0028          | USA              | EU819468                 | -                           |
| G. castaneus           | F-PRLS664MAN     | USA              | GQ166887                 | Unpublished                 |
| G. castaneus           | F-PRLS872MAN     | USA              | GQ166884                 | Unpublished                 |
| G. castaneus           | F-PRLS948MAN     | USA              | GQ166885                 | Unpublished                 |
| G. castaneus           | FLAS F 61844s    | USA              | MH212108                 | Unpublished                 |
| G. castaneus           | FLAS F 61497     | USA              | MH211929                 | Unpublished                 |
| G. castaneus           | ND31             | USA              | -                         | MF818163                   | Davoodian et al. 2018       |
| G. castaneus           | REH7761          | Costa Rica       | -                         | MF816162                   | Davoodian et al. 2018       |
| G. castaneus           | CS1              | USA              | -                         | MF818169                   | Davoodian et al. 2018       |
| G. castaneus           | MG531            | Italy            | -                         | MF818167                   | Davoodian et al. 2018       |
| G. castaneus           | VDK0979         | Belgium          | -                         | MF818168                   | Davoodian et al. 2018       |
| G. castaneus           | MG591            | Italy            | -                         | MF818189                   | Davoodian et al. 2018       |
| G. castaneus           | SW7              | Pakistan         | -                         | MF818184                   | Davoodian et al. 2018       |
| G. castaneus           | SW3              | Pakistan         | -                         | MF818164                   | Davoodian et al. 2018       |
| G. castaneus           | JFA13725         | USA              | -                         | MF818193                   | Davoodian et al. 2018       |
| G. castaneus           | NJ139358         | USA              | -                         | MF818187                   | Davoodian et al. 2018       |
| G. castaneus           | NS94WS          | USA              | -                         | MF818161                   | Davoodian et al. 2018       |
| G. castaneus           | NS58WS          | USA              | -                         | MF818160                   | Davoodian et al. 2018       |
| G. castaneus           | JPN12 770        | Japan            | -                         | MF818190                   | Davoodian et al. 2018       |
| G. castaneus           | TBG12 712        | Japan            | -                         | MF818188                   | Davoodian et al. 2018       |
| G. castaneus           | NY1782655        | Italy            | -                         | MF818186                   | Davoodian et al. 2018       |
| G. aff. cyanescens     | OMK23719         | -                | EU718104 EU718140         | Unpublished                 |
| G. aff. cyanescens     | REH8819          | -                | EU718172                 | Wilson et al. 2012          |
| G. aff. cyanescens     | E486             | -                | EU718173                 | Wilson et al. 2012          |
| G. aff. cyanescens     | ES685            | -                | EU718174                 | Wilson et al. 2012          |
| G. cyanescens          | 0733             | Japan            | -                         | MF818191                   | Davoodian et al. 2018       |
| G. cyanescens          | AH46009          | Spain            | KY367810 KY367811         | Unpublished                 |
| G. cyanescens          | MCE28580         | Italy            | KT363684 KT363685         | Vizzini et al. 2015         |
| G. cyanescens          | 17.184           | Italy            | JP907875                 | Osmondson et al. 2013       |
| G. cyanescens          | 2837             | -                | KM248948                 | Unpublished                 |
| G. cyanescens          | FLAS F 60581     | USA              | MH016792                 | -                           |
| G. cyanescens          | FLAS F 61545     | USA              | MH211963                 | -                           |
| G. cyanescens          | FLAS F 61592     | USA              | MH211964                 | -                           |
| G. cyanescens          | FLAS F 61205     | USA              | MH211810                 | -                           |
| G. cyanescens          | MBO5-04          | -                | EU710512                 | Unpublished                 |
| G. cyanescens          | NY1782681        | Italy            | -                         | MF818185                   | Davoodian et al. 2018       |
| G. cyanescens          | CNV67            | USA              | MT345244                 | Unpublished                 |

(Continued)
| Taxa                        | Voucher | Locality | GenBank accession number | References          |
|----------------------------|---------|----------|--------------------------|---------------------|
| G. cyaneus                 | 0745    | Japan    | -                        | M8F8192             |
| G. cyaneus                 | ND11    | USA      | -                        | M8F8173             |
| G. cyaneus                 | REH970  | USA      | -                        | M8F8174             |
| G. cyaneus                 | REH8758 | -        | EU718171                 | M8F8177             |
| G. cyaneus                 | MG639a  | Italy    | -                        | M8F8172             |
| G. cyaneus var. cyaneus    | NAM190  | USA      | EU819495                 | M8F8172             |
| G. flavoyanecens           | WXL118  | China    | MW44050, MW442950, MW452613 | Huang et al. 2021 |
| G. flavoyanecens           | WXL1187 | China    | MW44051, MW442951         | Huang et al. 2021  |
| G. flavoyanecens           | GDGM86062| China   | ONS05949, ONS087646       | This study          |
| G. furvescens              | REH9673 | Queensland | -                       | M8F8175             |
| G. lacteus                 | MCVE2858 | Italy   | KT363682, KT363683       | Vizzini et al. 2015 |
| G. atrocyaneus             | GDGM75894 | China   | ONS02909, ONS02932       | This study          |
| G. atrocyaneus             | GDGM88584 | China   | -                        | ONS02934             |
| G. atrocyaneus             | GDGM83673 | China   | -                        | ONS02933             |
| G. atrocyaneus             | GDGM76540 | China   | -                        | ONS02910             |
| G. longicystidatus         | GDGM25857 | China   | -                        | ONS087649             |
| G. longicystidatus         | OR74    | Thailand | -                        | M8F8152             |
| G. longicystidatus         | OR394   | Thailand | -                        | M8F8153             |
| G. longicystidatus         | GDGM46175 | China   | ONS02912, ONS02936       | This study          |
| G. longicystidatus         | GDGM42941 | China   | ONS02911, ONS02935       | This study          |
| G. longicystidatus         | GDGM52128 | China   | ONS02913, ONS02937       | This study          |
| G. longicystidatus         | EN99-67 | Japan    | -                        | M8F8151             |
| G. longicystidatus         | OR235   | China    | -                        | M8F8152             |
| G. longicystidatus         | OR238   | China    | -                        | M8F8153             |
| G. longicystidatus         | FHMU1997 | China    | MW380860, MW352983       | Xie et al. 2022    |
| G. longicystidatus         | FHMU2234 | China    | -                        | MW352966             |
| G. longicystidatus         | FHMU3367 | China    | -                        | MW352970             |
| G. longicystidatus         | FHMU1935 | China    | MW380859, MW352982       | Xie et al. 2022    |
| G. longicystidatus         | FHMU9000 | China    | MW380852, MW352975       | Xie et al. 2022    |
| G. longicystidatus         | FHMU954  | China    | MW380857, MW352980       | Xie et al. 2022    |
| G. longicystidatus         | FHMU1582 | China    | MW380845, MW352965       | Xie et al. 2022    |
| G. longicystidatus         | FHMU3366 | China    | MW380849, MW352971       | Xie et al. 2022    |
| G. longicystidatus         | REH7899 | Thailand | EU718142, EU718106       | M8F8147             |
| G. mcnabbii                | EB155   | USA      | -                        | EF561627             |
| G. mcnabbii                | REH9808 | Queensland | -                       | M8F8197             |
| G. mcnabbii                | REH8955 | Queensland | -                       | M8F8198             |
| G. mcnabbii                | REH8955 | Queensland | -                       | M8F8198             |
| G. memnonius               | GDGM44779 | China   | ONS02914, ONS02938       | ONS087653           |
| G. memnonius               | GDGM78781 | China   | ONS02915, ONS02939       | ONS087654           |
| G. memnonius               | FHMU3369 | China    | MW380858, MW352981       | Xie et al. 2022    |
| G. memnonius               | FHMU929  | China    | MW380856, MW352979       | Xie et al. 2022    |
| G. narangus                | REH9020 | Queensland | -                       | M8F8158             |
| G. narangus                | REH9411 | Queensland | -                       | M8F8157             |
| G. occidentalis            | EB164   | USA      | -                        | M8F8194             |
| G. occidentalis            | REH8821 | Australia | EU718130, EU718139      | M8F8177             |
| G. pallidus                | GDGM46275 | China   | ONS02918, ONS02942       | ONS087657           |
| G. pallidus                | GDGM46401 | China   | ONS02920                | ONS087659           |
| G. pallidus                | GDGM46405 | China   | ONS02921, ONS02944       | ONS087660           |
| G. pallidus                | GDGM46509 | China   | ONS02922, ONS02945       | ONS087663           |
| G. pallidus                | GDGM46387 | China   | ONS02919, ONS02943       | ONS087658           |
| G. pallidus                | GDGM46419 | China   | ONS02922, ONS02945       | ONS087661           |
| G. pallidus                | GDGM46433 | China   | ONS02923, ONS02946       | ONS087662           |
| G. paralongicystidatus     | NY48429 | Colombia | -                        | M8F81848             |
| G. paralongicystidatus     | REH8274 | Costa Rica | -                      | M8F81850             |
| G. paralongicystidatus     | REH7725 | Costa Rica | -                      | M8F81849             |
| G. paramajitii             | FHMU2243 | China    | MW380847, MW352968       | Xie et al. 2022    |
| G. paramajitii             | FHMU2240 | China    | MW380846, MW352967       | Xie et al. 2022    |
| G. paramajitii             | GDGM52188 | China   | ONS02917, ONS02941       | This study          |
| G. paramajitii             | CAL KD 162-002 | India | MF120824, MF120825      | Das et al. 2017    |
| G. paramajitii             | HKA563505 | China   | -                        | KF112476             |
| G. phaeocyaneus            | ARB1309 | USA      | -                        | M8F81844             |
| G. porphyreus              | FHMU917  | China    | MW380854, MW352977       | Xie et al. 2022    |
| G. porphyreus              | FHMU926  | China    | MW380853, MW352978       | Xie et al. 2022    |
| G. porphyreus              | FHMU888  | China    | MW380850, MW352973       | Xie et al. 2022    |
| G. porphyreus              | FHMU2273 | China    | MW380848, MW352969       | Xie et al. 2022    |
| G. porphyreus              | FHMU905  | China    | MW380853, MW352976       | Xie et al. 2022    |
| G. pseudooyanecens         | AH55729 | Spain    | KYS67808, KYS67806       | Unpublished        |
| G. pseudooyanecens         | AH5840  | Spain    | KYS67808, KYS67807       | Unpublished        |
| G. pseudooyanecens         | ECC17070501 | Spain | WM366657                | Unpublished        |
| G. pseudolongicystidatus   | GDGM42787 | China   | ONS02916, ONS02940       | ONS087655           |

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Phylogenetic analyses were performed in the software of PhyloSuite (Zhang et al. 2020). Maximum likelihood phylogenies were inferred using IQ-TREE (Nguyen et al. 2015) under the TPM2u+R3 + F model for 5000 ultrafast bootstraps, as well as the Shimodaira-Hasegawa-like approximate likelihood-ratio test. Bayesian Inference (BI) phylogenies were inferred using MrBayes 3.2.6 (Ronquist et al. 2012), the best models for the combined datasets ITS-nrLSU were searched via PartitionFinder 2 (Lanfear et al. 2017), and for atp6 region was searched via ModelFinder (Kalyaanamoorthy et al. 2017). BI analysis using 4 chains were conducted by setting generations to 20 million and stopprul command with the value of stopval set to 0.01, trees were sampled every 1000 generations, the first 25% generations were discarded as burn-ins and posterior probabilities (PP) were then calculated from the posterior distribution of the retained Bayesian trees. The phylogenetic trees were visualised using FigTree v1.4.23.

Results

**Molecular phylogeny**

In the concatenated (nrLSU + ITS) dataset, 188 sequences (95 for nrLSU and 88 for ITS) from 121 fungal collections were included, including 39 sequences newly generated in this study. The alignment length was 1816 characters including gaps (888 characters for ITS, and 928 characters for nrLSU), TVM + I + G and TIM + I + G were selected for ITS and nrLSU respectively for the BI analysis. In the atp6 dataset, 89 sequences were included, including 23 sequences newly generated in this study. The alignment length was 616 characters. GTR + F + I + G4 was selected as the best models for Bayesian inference. *Phlebopus spongiosus* Pham & Har. Takah. was selected as outgroup based on recently studies (Davoodian et al. 2018; Xie et al. 2022). The tree topologies obtained by ML and Bayesian analyses were similar; thus, only the ML topology was shown in Figures 1 and 2. Phylogenetic analyses showed that *Gyroporus* was supported as a monophyletic group, and five new

| Taxa | Voucher | Locality | GenBank accession number | References |
|------|---------|----------|--------------------------|------------|
| G. pseudolongicystidiatus | GDGM42986 | China | - | ON505946 ON087656 | This study |
| G. pseudolacteus | AH54850 | Spain | KX869871 KX869885 | Crous et al. 2016 |
| G. pseudolacteus | AH54849 | Spain | KX869868 KX869882 | Crous et al. 2016 |
| G. pseudolacteus | AH39964 | Spain | KX869866 KX869880 | Crous et al. 2016 |
| G. pseudolacteus | AH44522 | Spain | KX869873 KX869887 | Crous et al. 2016 |
| G. pseudolacteus | AH54812 | Spain | KX869870 KX869884 | Crous et al. 2016 |
| G. pseudolacteus | AH54848 | Spain | KX869867 KX869881 | Crous et al. 2016 |
| G. pseudolacteus | AH37878 | Spain | KX869872 KX869886 | Crous et al. 2016 |
| G. pseudolacteus | AH54811 | Spain | KX869869 KX869883 | Crous et al. 2016 |
| G. pseudolacteus | Hal BP16 | Spain | MT594507 | - | Leonardo et al. 2020 |
| G. purpurinus | Chpn776 | USA | KX389110 | - | Unpublished |
| G. purpurinus | PRL3737 | - | EU718105 EU718141 | Wilson et al. 2012 |
| G. robinsonii | ND13 | USA | - | - | M8F81878 Davoodian et al. 2018 |
| G. smithii | REH4511 | USA | - | - | M8F81859 Davoodian et al. 2018 |
| G. smithii | ND57 | USA | - | - | M8F81865 Davoodian et al. 2018 |
| G. smithii | MIC232867 | USA | - | - | M8F818166 Davoodian et al. 2018 |
| G. sp. | OR182 | Thailand | - | - | M8F81856 Davoodian et al. 2018 |
| G. sp. | BO5472 | BLZ | - | - | M8F81896 Davoodian et al. 2018 |
| G. sp. | TH9913 | CMRN | - | - | M8F81870 Davoodian et al. 2018 |
| G. sp. | Thoem7634 | SEN | - | - | M8F8171 Davoodian et al. 2018 |
| G. sp. | Arora00 429 | - | EU718107 EU718143 | Wilson et al. 2012 |
| G. sp. | Arora14800 | USA | MW343686 | - | Unpublished |
| G. sp. | E4879c | - | FJ710208 | Wilson et al. 2012 |
| G. sp. | JLF8835 | USA | MW343688 | - | Unpublished |
| G. sp. | JLF8747 | USA | MW343687 MW341339 | - | Unpublished |
| G. subglobulatus | OKM24077 | USA | EU718108 EU718144 | Wilson et al. 2012 |
| G. aff. subglobulatus | HONDURAS19 | USA | MT571529 | - | Haelewaters et al. 2021 |
| G. subglobulatus | GDGM60494-1 | China | ONS02924 ONS02947 ON087665 | This study |
| G. subglobulatus | GDGM60494-2 | China | - | - | ONS087664 This study |
| G. subglobulosus | FHU3364 | China | - | - | MW352985 Xie et al. 2022 |
| G. subglobulosus | FHU3359 | China | MW380851 MW352974 | - | Xie et al. 2022 |
| G. umbilicosus | BUF-Both3525 | USA | - | - | M8F81145 Davoodian et al. 2018 |
| Phlebopus spongiosus | CMUB93624 | Thailand | KX575660 KX575655 | - | Thongkantha et al. 2021 |
| Ph. spongiosus | BC0166 | Thailand | - | - | MT575956 MT755374 Unpublished |
lineages were discovered in present study (Figures 1 and 2). Species of Gyroporus formed four main branches, and four new sections were firstly proposed herein, i.e. “G. sect. Castaneus”, “G. sect. Cyanescens”, “G. sect. Longicystidatus” and “G. sect. Pallidus”. Gyroporus sect. Castaneus was well-supported as a monophyletic group, and located at the base of the phylogenetic trees. Gyroporus sect. Cyanescens formed an independent branch, but with moderate support in the atp6 tree, and weak support in the ITS-nrLSU tree. Two new species G. atrocyanescens and G. subcaerulescens nested into the sect. Cyanescens. Gyroporus atrocyanescens was well-supported as an
independent clade in the phylogenetic trees (Figures 1 and 2), and formed sister relationship with G. flavocyanescens. Gyroporus subcaerulescens formed an independent clade in Figure 1, while clustered together with G. atracyonanesces and G. flavocyanescens in Figure 2. The sect. Longicystidiatus was well-supported in the phylogenetic trees, and three species were included, containing a new species discovered in present study. The sect. Pallidus was well-supported as an independent branch in the trees (Figures 1 and 2), and different from the sect. Castaneus. Two new species G. alboluteus and G. pallidus nested into the branch, and close to “G. cf. castaneus” and G. memnonius.

**Taxonomy**

Gyroporus section Castaneus Ming Zhang & T.H. Li sect. nov.

Fungal Name: FN570996

Type species: Gyroporus castaneus (Bull.) Quél., Enchir. fung. (Paris): 161 (1886)

Etymology: “castaneus” refers to the species in this section similar to G. castaneus.

Basidiomata small to medium-sized. Pileus hemispherical to convex, dry, greyish yellow, greyish orange, brown or red-brown, covered with floccose-scaly to coarsely tomentose squamules; context white, becoming bluish, greenish blue or dark blue or deep blue when bruised. Hymenophore poroid, white, yellowish, to greenish-yellow, becoming bluish, greenish blue or dark blue when bruised. Stipe central, dry, covered with tomentose to fibrillose squamules, unchanging or changing to blue when handled; basal mycelium white; annulus indistinct to as a weak annular zone. Basidiospores ellipsoid to broadly ellipsoid, smooth, yellowish in 5% KOH. Basidia clavate, 4-spored, hyaline in 5% KOH. Cheilocystidia clavate to subfusiform, thin-walled, yellowish to hyaline in 5% KOH. Pleurocystidia absent or present. Pileipellis a trichodermium, composed of elongated or somewhat clumped, parallel to slightly interwoven, thin to thick-walled hyphae, colourless or yellowish in 5% KOH. Stipitipellis composed of thin- to thick-walled hyphae, colourless to yellowish. Clamp connections frequently present in all tissues.

Notes: Gyroporus sect. Castaneus as a monophyletic branch is strongly supported in our phylogenetic analyses (Figures 1 and 2, BS/BPP = 96%/0.98; BS/ BPP = 100%/1). Species in this section are mainly characterised by their brown to yellowish brown pileus, usually with red or purple tinge, white context unchanging when bruised, oval to elliptical basidiospores, and a trichoderm pileipellis composed of clavate to subcylindrical hyphae. Seven species, G. castaneus, G. mcnabbii Davoodian, Bougher & Halling, G. naranjus Davoodian, Bougher, Fechner & Halling, G. paramjittii, G. porphyreus, G. purpurinus of Davoodian & Halling, and G. subglobosus have been proved to belong to this section based on the morphological features and phylogenetic analyses.

Gyroporus section Cyanescens Ming Zhang & T.H. Li sect. nov.

Fungal Name: FN570997

Type species: Gyroporus cyanescens (Bull.) Quél., Enchir. fung. (Paris): 161 (1886)

Etymology: “cyanescens” refers to the species in this section usually with cyanescent oxidation reactions similar to that of G. cyanescens.

Basidiomata medium to large-sized. Pileus hemispherical to convex, dry, greyish yellow, greyish orange, brown or red-brown, covered with floccose-scaly to coarsely tomentose squamules; context white, becoming bluish, greenish blue or dark blue or deep blue when bruised. Hymenophore poroid, white, yellowish, to greenish-yellow, becoming bluish, greenish blue or dark blue when bruised. Stipe central, dry, covered with tomentose to fibrillose squamules, unchanging or changing to blue when handled; basal mycelium white; annulus indistinct to as a weak annular zone. Basidiospores ellipsoid to broadly ellipsoid, smooth, yellowish in 5% KOH. Basidia clavate, 4-spored, hyaline in 5% KOH. Cheilocystidia clavate to subfusiform, thin-walled, yellowish to hyaline in 5% KOH. Pleurocystidia absent or present. Pileipellis a trichodermium, composed of elongated or somewhat clumped, parallel to slightly interwoven, thin to thick-walled hyphae, colourless or yellowish in 5% KOH. Stipitipellis composed of thin- to thick-walled hyphae, colourless to yellowish. Clamp connections frequently present in all tissues.

Notes: Gyroporus sect. cyanescens formed an independent branch in the phylogenetic trees (Figures 1 and 2), but with moderate support at atp6 tree and weak supported at ITS-nrLSU tree. Morphologically, species in this section all can produce cyanescent oxidation reactions, and pileus surface always covered with elongated and somewhat clumped tomentum. Fourteen species were proved to belong to this section, including two new species G. atracyonanesces and G. subcaerulescens discovered in present study.
Gyroporus atrocyaneascens Ming Zhang & T.H. Li sp. nov. Figures 3a–f

Fungal Name: FN570980
Etymology: “atro-” means black, “cyanescens” means becoming blue, “atrocyaneascens” refers to the basidiomata instantly changing to blackish blue when bruised.

Diagnosis: This species is characterised by its white to greyish yellow pileus densely covered with greyish yellow floccose squamules, white to yellowish white hymenophore, broadly elliptical basidiospores (7.5–10 × 4.8–6 μm), and the whole basidiomata immediately staining dull blue, deep blue to dark blue when bruised.

Holotype: CHINA. Guangdong Province, Shaoguan City, Renhua County, Danxiashan National Natural Reserve, alt. 300 m, 27 September 2018, Xiang-Rong Zhong (GDGM75894).

Basidiomata medium sized. Pileus 4–6 cm broad, sub-hemispherical to convex when young, broadly convex to nearly applanate at maturity, dry, white to
yellowish white when young, dull yellow, olive yellow to greyish yellow (3B3–4B3, 3B4–4B4, 3C6) when mature; densely covered with greyish yellow (4B3) appressed scales to floccose squamules; margin incurved and slightly extended, usually cracked at maturity. Context white (1A1), 8–15 mm thick at pileus centre, immediately and intensely staining deep blue (19D8–21D8), blackish blue to dark blue (19F8–21F8) when bruised. Hymenophore adnate to slightly depressed around stipe when mature, 3–5 mm long, white (1A1) when young, yellowish white (3A2) when mature, staining deep blue (19D8–21D8), blackish blue to dark blue (19F8–21F8) when bruised; pores angular to roundish, 3–4 per mm, staining deep blue to dark blue when bruised. Stipe 5–7 × 1.5–2.5 cm, central, sub-cylindrical to clavate, white (2A1) when young, yellowish-white (2A2–4A2) when mature; surface rough, staining dull blue to greyish blue when bruised (22D5–23D5); context white to yellowish white, spongy when young and then hollow in age, staining deep blue to dark blue when bruised. Odour none. Taste mild.

Basidiospores (7.5)8–10(10.5) × (4.5)4.8–6.5(7) µm, [Q = (1.5)1.54–1.7(1.8), Qm = 1.65 ± 0.09], smooth, ellipsoid to somewhat broadly ellipsoid, yellowish in 5% KOH. Basidia 24–35 × 8–10 µm, clavate, 4-spored, hyaline in 5% KOH. Cheilocystidia 28–40 × 8–12 µm, clavate to subfusiform, thin-walled, vivid yellow in 5% KOH at first, then hyaline. Pleurocystidia not observed. Tube trama composed of 4–10 µm wide parallel hyphae, hyaline to yellowish in 5% KOH. Pileipellis a cutis, composed of 8–16 µm wide, repent to suberect, parallel to slightly interwoven hyphae, thin-walled, hyaline to yellowish in 5% KOH; terminal cells 60–130 × 8–14 µm, clavate to subcylindrical, obtuse at apex. Pileal trama made up of hyphae 6–18 µm broad, hyaline in 5% KOH. Stipitipellis composed of thin-walled hyphae, 5–15 µm wide, light yellow in 5% KOH. Stipe trama composed of cylindrical, light yellow in 5% KOH, thin-walled, interwoven hyphae 5–16 µm wide. Clamp connections frequently present in all tissues.

Additional specimens examined: CHINA. Guangdong Province, Shaoquan City, Renhua County, Danxiashan National Natural Reserve, alt. 300 m, 26 June 2021, Ming Zhang (GDGM85841); same location, alt. 350 m, 24 September 2021, Guo-Rui Zhong (GDGM83673); same location, alt. 330 m, 15 May 2019, Juan-Yan Xu (GDGM76540).

Habitat and distribution: Solitary or scattered on soil in subtropical broad-leaf forest dominated by Fagaceae trees. Currently known only from southern China.

Notes: Phylogenetic analyses showed that G. atrocyaneos was nested into the sect. Cyanescens, and closely related to G. flavocyaneos.
However, the latter species, recently reported from southwestern China, differs in its larger basidiomata, dull yellow to greyish-orange pileus, nearly glabrous or somewhat fibrillose to finely tomentose pileal surface, broader basidiospores (8–10 × 5.5–6.5 µm) and hyaline cheilocystidia in 5% KOH (Huang et al. 2021).

In morphology, *G. occidentalis* Davoodian, Bougher & Halling resembles *G. atrocyaneos* in the rapidly bluing oxidation reaction. However, *G. occidentalis*, reported from Western Australia, differs in its larger basidiomata, yellow-white to yellow buff to dirty yellow pileus, and smaller and narrower basidiospores 7.7–8.4(9.1) × 3.5–4.2 µm (Davoodian et al. 2018). The bluing species *G. alpinus*, *G. brunneofloccosus* and *G. cyanescens* are also similar to *G. atrocyaneos* in the discolouration. However, *G. alpinus* recently reported from southwestern China, differs in its ivory yellow to brownish-yellow pileus covered with concolourous appressed scaly to floccose squamules, broader basidiospores (5.5–8.5 µm broad), and distribution in alpine forests dominated by *Abies*, *Picea* and *Quercus* (Huang et al. 2021); *G. brunneofloccosus*,

**Figure 6.** Basidiomata of *Gyroporus* species. a–d. *Gyroporus pseudolongicystidiatus* (a–b from GDGM42787; c–b from GDGM42986); e–f. *Gyroporus alboluteus* (e from GDGM86706; f from GDGM25474); g–h. *Gyroporus pallidus* (g from GDGM46387; h from GDGM46275).
reported from subtropical regions of southern China, differs in its dark brown to light red brown pileus covered with concolorous floccose-scaly to coarsely tomentose squamules, yellowish to greenish-yellow hymenophore staining cerulean blue to greenish-blue when bruised, brownish to light red-brown stipe, and clavate to subfusiform cheilocystidia hyaline in 5% KOH (Li et al. 2003; Huang et al. 2021); while G. cyanescens, originally described from Europe, differs in its larger basidiomata, pale straw, buff to ivory pileus covered with obviously fibrillose tomentum, more robust stipe with a pseudo-annular zone and horizontal fissures at stipe apex, and distribution in forests dominated by Pinus sylvestris or Fagus sylvatica (Watling 1970; Vizzini et al. 2015).

Gyroporus subcaerulescens Ming Zhang & T.H. Li sp. nov. Figures 3g–h, 5

Fungal Name: FN570983

Etymology: “subcaerulescens” means “becoming pale blue or blueish”, refers to the context slightly changing to bluish when exposed.

Diagnosis: This species is characterised by its white to orange white pileus covered with orange white to reddish white coarsely tomentose squamules, white hymenophore and pileus context slowly changing to pastel blue when bruised, elliptical basidiospores (6.5) 8–10 × 5.5–6.5 (7.0) μm.

Holotype: CHINA. Hunan Province, Chenzhou City, Mangshan National Natural Reserve, alt. 1000 m, 30 July 2017, Hao Huang (GDGM70494).

Basidiomata small to medium sized. Pileus 3–5.8 cm broad, sub-hemispherical to convex when young, broadly convex to nearly planate at mature, surface dry, white to orange white (5A1, 5A2–6A2), densely covered with orange white to reddish white (5A2–8A2) floccose scales to coarsely tomentose squamules, paler towards margin, margin incurved and slightly extended, usually cracked at age; context white (1A1), slowly
staining pale blue to pastel blue (22A4–23A4) when bruised. Hymenophore adnate to slightly depressed around stipe when mature, 5–7 mm long, white (1A1) when young, yellowish white (1A2–2A2) when mature, unchanging when bruised; pores angular to roundish, 2–3 per mm, staining bluish white when bruised. Stipe 4–6 × 1–1.6 cm, sub-cylindrical to clavate, white (2A1) when young, yellowish-white (2A2) to concolourous with pileal surface when mature; surface roughened, unchanging when bruised; context white to cream or yellowish, spongy when young and then hollow in age, unchanging when bruised. Odour none. Taste mild.

Basidiospores (6.5) 8–10 × 5.5–6.5 (7.0) µm, Q = (1.28)1.35–1.64 (1.81), Qₘ = 1.48 ± 0.13, smooth, elliptical, oval, to somewhat oblong, yellowish in 5% KOH. Basidia 23–32 × 9–14 µm, clavate, 4-spored, hyaline in 5% KOH. Cheilocystidia 31–45 × 9–15 µm, clavate to subfusiform, thin-walled, hyaline to yellowish in 5% KOH; Pleurocystidia not observed. Tube trama composed of interwoven hyphae, 5–13 µm wide, hyaline to yellowish in 5% KOH. Pileipellis a trichoderm, composed of erect, parallel to somewhat clumped hyphae, 8–22 µm wide, hyaline to yellowish in 5% KOH; terminal cells 55–130 × 8–22 µm, clavate to subcylindrical, with obtuse apex. Pileal trama made up of hyphae 6–20 µm diam, colourless in 5% KOH. Stipitipellis composed of thin-walled hyphae, 5–10 µm wide, light yellow in 5% KOH. Stipe trama composed of cylindrical, light yellow in 5% KOH, thin-walled, interwoven hyphae 5–10 µm wide. Clamp connections frequently present in all tissues.

Habitat and distribution: Solitary or scattered on soil in subtropical mixed forest mainly dominated by Fagaceae trees, with a few pine trees (Cunninghamia sp.). Currently known from Hunan Province, China.

Notes: Phylogenetic analyses shown that G. subcaerulescens was well nested into the sect. Cyanescent, and closely related to G. alpinus, G. cyanescens, G. flavocyaneascens and G. atrocyaneascens. However, they can be separated from each other by the genetic distance. Additionally, G. alpinus, recently reported from alpine forests of China, differs in its ivory yellow to brownish-yellow pileus densely covered with concolourous appressed flocose squamules, and broader basidiospores (6.5) 7–10 × 5.5–7.5 (8.5) µm (Huang et al. 2021); G. cyanescens, originally reported from Europe, differs in its larger basidiomata can up to 12 cm broad, pale straw pileus, larger but narrow basidiospores (9–11 × 4.5–6 µm) (Watling 1970; Vizzini et al. 2015; Huang et al. 2021); G. flavocyaneascens, recently reported from tropical forests of China, differs in its larger basidiomata can up to 10 cm broad, nearly glabrous and flavus to greyish-orange pileus, white context staining strong dark blue when bruised, white to yellowish hymenophore staining cyanine blue to porcelain blue when bruised (Huang et al. 2021); G. atrocyaneascens, newly described in this study, can be easily distinguished by its strongly cyanescent oxidation reactions.

In morphology, G. subcaerulescens resembles G. robinsonii with the slowly and faintly bluing oxidation reaction. However, G. robinsonii reported from Western Australia, differs in its yellow-white to dirty buff pileus, large and narrow basidiospores (8.4)8.8–10.5(12) × 4.7–5.6(6) µm (Davoodian et al. 2019). Gyroporus brunneofloccosus, reported from southern China, is also similar to G. subcaerulescens in sharing with the pileus covered with floccose scales to coarsely tomentose squamules, but differs in its larger basidiomata can up to 9 cm broad, darker brown to reddish brown pileus, white context staining cerulean blue to dark blue when bruised, and greenish-yellow hymenophore staining cerulean blue to greenish-blue when bruised (Li et al. 2003; Huang et al. 2021).

Gyroporus section LongicystidiatuS Ming Zhang & T.H. Li sect. nov.

Fungal Name: FN570998
Type species: Gyroporus longicystidiatuS Nagas. & Hongo, in Nagasawa, Rep. Tottori Mycol. Inst. 39: 18 (2001)

Etymology: “longicystidiatus” refers to the longer cheiloc- or pleurocystidia.

Basidiomata medium-sized. Pileus hemispheric to convex, dry, subtomentose or glabrous, greyish orange, brownish orange, yellowish brown, dark brown; context white, unchanging when bruised. Hymenophore poroid, white, yellowish to greenish-yellow, unchanging when bruised. Stipe central, surface dry, glabrous to subtomentose unchanging when handled; basal mycelium white; annulus absent. Basidiospores elliptic, cylindrical to oblong,
smooth, thin-walled, yellowish in 5% KOH. Basidia clavate, 4-spored, hyaline in 5% KOH. Cheilocystidia narrowly fusoid to cylindrical, can up to 100 μm long, thin-walled. Pleurocystidia present or absent. Pileipellis a trichodermium, composed of elongated, interwoven, thin to thick-walled hyphae. Clamp connections frequently present in all tissues.

Notes: *Gyroporus* sect. *Longicystidiatus* was well-supported as a monophyletic clade in our phylogenetic analyses (Figures 1 and 2; BS/BPP = 99%/0.98; BS/BPP = 100%/1). Species in this section mainly characterised by their brownish orange to brownish yellow pileus, white context unchanging when bruised, longer cystidia can up to 100 μm, and trichoderm pileipellis. Three species were included in this section, containing a new species described as follow.

*Gyroporus pseudolongicystidiatus* Ming Zhang, D.C. Xie & T.H. Li sp. nov. Figures 6a–d, 7

**Fungal Name:** FN570981

**Etymology:** “pseudolongicystidiatus” refers to the species similar to *G. longicystidiatus*.

**Diagnosis:** This species is characterised by its brownish orange to brownish yellow pileus subglabrous when mature, white hymenophore and pileus context unchanging when bruised, and elliptical to cylindrical basidiospores (6.5) 8–10 × 5.5–6.5 (7.0) μm.

**Holotype:** CHINA. Hainan, Ledong County, Jianfengling National Forest Park, at 18°44’N, 108°52’E, alt. 940 m, 3 July 2013, Ming Zhang (GDGM42787).

Basidiomata small to medium. Pileus 5–10 cm broad, hemispheric, convex to plane, fleshy, surface dry, fibrillose, velvet-subtomentose when young and subglabrous in age, greyish orange (5B6), brownish orange to brownish yellow (5C4–5C8) at first, and gradually changing to light brown, yellowish brown to brown (5D5–5D8, 6D5–6D8) when mature. Context 8–10 mm thick at centre, white, unchanging when exposed to air. Tubes 4–6 mm deep, depressed or nearly free near the stipe in age, whitish, unchanging when cut. Pores 2–3 -per mm, circular, white at first, becoming pale yellow (3A3–4A3) in age, unchanging when bruised. Stipe 60–70 × 20–25 mm, central, equal or slightly swollen downwards, brittle, stuffed with a soft pith, becoming hollow or developing several cavities in age, surface dry, coarsely tomentose to floccose-scaly, not reticulate, concolourous with pileus or paler, unchanging when bruised; basal mycelium white; stipe context white, unchanging when exposed. Odour none and taste mild.

**Basidiospores** (6.5)7–9(9.5) × 3.5–4 μm, Q = (1.77)1.8–2.5(2.57), Qg = 2.01 ± 0.25, elliptic, cylindrical to somewhat oblong, smooth, thin-walled, yellowish to yellowish brown in 5% KOH and yellow brown to dark brown in Melzer’s reagent. Basidia 24–38 × 6–8 μm, 4-sterigmate, clamp, thin-wall, yellowish white to hyaline in 5% KOH. Pleurocystidia not observed. Cheilocystidia 37–100 × 6–10 μm, abundant and conspicuous, narrowly fusoid to cylindrical, smooth, thin-walled, hyaline. Hymenophoral trama subparallel, smooth or coarse, yellowish white to hyaline in 5% KOH, with hyphae 10–22 μm broad. Pileipellis a trichoderm, consisting of interwoven hyphae 7–10 μm in width, covered with yellowish brown to brown pigment on surface in 5% KOH, dark brown to rusty brown in Melzer’s reagent; terminal cells 30–95 × 7–10 μm, cylindrical or nearly clavate. Pileal trama subregular, composed of branched and interwoven hyphae up to 12–18 μm in width. Stipitipellis hyphae oriented in various directions, subparallel to repent, hyphae 6–15 μm broad, usually covered with yellowish brown to brown pigment in 5% KOH, end cells 30–90 × 6–15 μm, thin walled. Clamp connections present in all tissue.

**Additional specimens examined:** CHINA. Hainan Province, Ledong County, Jianfengling National Forest Park, at 18°44’N, 108°52’E, alt. 900 m, 4 July 2013, Ming Zhang (GDGM42986).

**Habitat and distribution:** Solitary or scattered on soil in mixed broadleaf-coniferous forests, mainly dominated by *Cyclabalanopsis* spp. and *Castanopsis* spp., alt. 900 m. Currently known from Hainan Province, China.

Notes: The combined morphological characters include the brownish orange to yellowish brown pileus covered with fibrillose or velvet-subtomentose when young and nearly smooth in age, the white context and tubes unchanging when bruised, the hollow and brittle stipe, elliptic to cylindrical basidiospores, and the longer cheilocystidia up to 100 μm; which allowed *G. pseudolongicystidiatus* to be easily separated from other species of the genus.

Phylogenetically, *G. pseudolongicystidiatus* is nested into the sect. *Longicystidiatus* and closely related to *G. longicystidiatus* and *G. paralongicystidiatus*. However, *G. longicystidiatus*, originally described from Japan, differs in the yellow-
brown pileus, the presence of the pleurocystidia (38–140 × 12–21 μm), and the broader basidiospores with a smaller \( Q_m \) value (1.56 ± 0.24) (Nagasawa 2001; Xie et al. 2022); \( G. \) paralongicystidiatus Davoodian, recently reported from Costa Rica, differs in its brown to pinkish brown pileus covered with tomentose to finely matted or fine squamules or furrfur, broader basidiospores (4.4)5.1–5.7(6.4) μm, and shorter cheilocystidia (17–55 × 6–13 μm)(Davoodian et al. 2018).

**Gyroporus** section **Pallidus** Ming Zhang & T.H. Li sect. nov.

Fungal Name: FN570999

Type species: **Gyroporus pallidus** Ming Zhang & T.H. Li

Etymology: “Pallidus” refers to the pale colour of basidiomata.

Basidiomata small to medium-sized. Pileus convex to applanate, dry, subtomentose, white, yellowish withe, yellowish brown, brownish orange to brown, without red or purple tinge; context white, unchanging when injured. Hymenophore poroid, white, unchanging when bruised. Stipe central, surface dry, glabrous or subtomentosus, concolourous with pileus or paler, unchanging when handled; basal mycelium white; annulus absent. Basidiospores ellipsoid to broadly ellipsoid, smooth, thin-walled, yellowish in 5% KOH. Basidia clavate, 4-spored, hyaline in 5% KOH. Cheilocystidia clavate to subfusiform, thin-walled, yellowish to hyaline in 5% KOH. Pleurocystidia not observed. Pileipellis a cutis or trichodermium, composed of interwoven, thin to thick-walled hyphae, colourless or yellowish in 5% KOH. Clamp connections present in all tissues.

Notes: The G. sect. Pallidus was well-supported as an independent branch in the phylogenetic trees (Figures 1 and 2), and four species, **G. alboluteus**, **G. memnonius**, **G. pallidus** and **G. subalbellus** were included. Of which, **G. alboluteus** and **G. pallidus** were newly discovered in the present study, **G. memnonius** was recently reported from southern China (Xie et al. 2022), and **G. subalbellus** originally reported in North America (Murrill 1910). In addition, two specimens named as “G. cf. castaneus”, and two unnamed sequences labelled as “OR182” and “BOS472” were also included in this section.

**Gyroporus alboluteus** Ming Zhang & T.H. Li sp. nov. 

**Figure 6e–f, 8**

Fungal Name: FN570979

Etymology: “alboluteus” refers to the yellowish white to pale yellow colour of the pileus.

Diagnosis: This species is characterised by its small basidiomata, pale yellow to pale orange pileus, white hymenophore and context unchanging when bruised, elliptical to cylindrical basidiospores (8)8.5–9.5(10) × 4.5–5 μm.

Holotype: CHINA. Guangdong Province, Shaoguan City, Shixing County, Chabaling National Natural Reserve, alt. 600 m, 15 July 2008, Tai-Hui Li (GDGM25474).

Basidiomata small. Pileus 2–3 cm broad, hemispheric, convex to plane, dry, fibrillose, velvet-subtomentose when young and nearly glabrous in age, white at first, pale yellow to pale orange at maturity, paler towards margin. Context 3–4 mm thick at centre, fleshy, white, unchanging when exposed. Tubes 3–4 mm deep, depressed or nearly free at stipe in age, white, unchanging when bruised. Pores 2–3 per mm, circular, white, unchanging when bruised. Stipe 30–50 × 6–10 mm, central, equal or slightly swollen downwards, brittle, stuffed with a soft pith, becoming hollow or developing several cavities in age, surface dry, glabrous or with white pruina, concolourous with pileus or paler, unchanging when handled, with white basal mycelium; stipe context white, unchanging when exposed. Odour none. Taste mild.

Basidiospores (8)8.5–9.5(10) × 4.5–5 μm, \( Q = (1.6)1.7–2(2.1) \), \( Q_m = 1.81 ± 0.13 \), elliptical, cylindrical to somewhat oblong, smooth, thin-walled, yellowish to yellowish brown in 5% KOH. Basidia 24–35 × 10–13 μm, 4-sterigmate, clavate, thin-wall, yellowish white to hyaline in 5% KOH. Pleurocystidia not observed. Cheilocystidia 28–40 × 8–15 μm, abundant and conspicuous, narrowly fusoid to cylindrical, smooth, thin-walled, hyaline. Hymenophoral trama subparallel, smooth or coarse, yellowish white to hyaline in 5% KOH, with hyphae 6–10 μm broad. Pileipellis a cutis, consisting of suberect to slightly interwoven hyphae 5–12 μm in width, covered with yellowish brown to brown pigment on surface in 5% KOH, terminal cells 30–95 × 7–10 μm, cylindrical or nearly clavate. Pileal trama subregular, composed of branch, parallel to slightly interwoven hyphae, 5–15 μm in width. Stipitipellis composed of thin-walled hyphae, 5–12 μm wide, light yellow in 5%
KOH. Stipe trama composed of cylindrical, light yellow in 5% KOH, thin-walled, interwoven hyphae 5–12 µm wide. Clamp connections frequently present in all tissues.

Additional specimens examined: CHINA, Guangdong Province, Shaoguan City, Shixing County, Chebaling National Natural Reserve, alt. 640 m, 22 June 2014, Ming Zhang (GDGM86706).

Habitat and distribution: Solitary or scattered on soil in mixed forest dominated by Fagaceae trees, and mixed with Pinus massoniana Lamb. Currently known from Guangdong Province, China.

Notes: The combined morphological features of the small basidiomata, the pale yellow to pale orange coloured pileus, the white hymenophore and context unchanging when bruised, and the elliptical to cylindrical basidiospores make G. alboluteus easily distinguished from other species of Gyroporus. Ecologically, G. alboluteus is distributed in subtropical mixed forests, which are dominated by Fagaceae trees and mixed with a small amount of Pinus massoniana.

Phylogenetically, G. alboluteus formed an independent clade in the sect. Pallidus, and was related to “G. cf. castaneus”, G. memnonius, G. pallidus and G. subalbellus Murrill, but they can be separated from each other by genetic distance. Besides, “G. cf. castaneus” distributed in northeastern China, differs in its larger basidiomata (pileus can up to 10 cm broad), yellow to yellow-brown pileus, yellow-brown to orange-brown stipe, broader basidiospores [(4–)4.5–6(–7) µm], and trichodermium pileipellis (Xie et al. 2022). Gyroporus memnonius, recently described from southern China, differs in its larger basidiomata up to 6 cm broad, dark brown pileus, yellowish brown stipe, and slightly thick-walled basidiospores up to 0.5 µm thick (Xie et al. 2022). Another new species to be described in present paper, G. pallidus, differs in its larger basidiomata, reddish brown to dark brown pileus, and broader basidiospores [8–10 × 5–6 µm, Q = (1.3)1.45–1.81 (1.9)]; additionally, G. pallidus was distributed in the southern margin of the temperate zone, and currently only known associated with Castanea mollissima BL. Gyroporus subalbellus, originally reported from North America, differs in its larger basidiomata (pileus up to 12 cm broad), apricot buff, pinkish buff to orange cinnamon pileus, and lager basidiospores measuring 8–14 × 4–6 µm (Murrill 1910; Bessette et al. 2000).

Gyroporus pallidus Ming Zhang & T.H. Li sp. nov.

Figure 6g–h, 9

Fungal Name: FNS70982

Etymology: “pallidus” refers to the paler basidiomata colour to compare with G. castaneus.

Diagnosis: This species is characterised by its small basidiomata, brownish orange to light brown pileus usually cracked into small scales on the surface, white to yellowish white context unchanging when bruised, and elliptical basidiospores 8–10 × 5–6 µm.

Holotype: CHINA. Henan Province, Xinyang City, alt. 400 m, 22 July 2016, Ming Zhang (GDGM46387).

Basidiomata small to medium-sized. Pileus 3–5 cm broad, convex when young, then planate with age; margin decurved at first, then slightly upward when old; surface dry, subtomentose, usually cracking into small scales when mature or in dry conditions, brownish orange, light brown to brown (5C4–5C6, 5D5–6D5); context 3–4 mm thick, white, unchanging in colour when injured. Hymenophore adnate to slightly depressed around stipe when mature, 3–5 mm long, white (1A1) when young, yellowish white (3A2) when mature, unchanging when bruised; pores angular to roundish, 2–3 per mm, white to yellowish white, unchanging when bruised. Stipe 4–6 × 0.6–1.2 cm, central, sub-cylindrical to clavate, concolourous with pileus, slightly paler to yellowish brown to yellowish downward the base; surface roughened, unchanging when bruised; context white to yellowish white, spongy when young and then hollow in age, unchanging when bruised. Odour none. Taste mild.

Basidiospores 8–10 × 5–6 µm, Q = (1.3)1.45–1.81 (1.9), Qm = 1.61 ± 0.15, smooth, elliptical, to somewhat broadly elliptical, yellowish in 5% KOH. Basidia 22–33 × 9–12 µm, clavate, 4-spored, hyaline in 5% KOH. Cheilocystidia 28–35 × 9–13 µm, clavate to subfusiform, thin-walled, yellowish white to hyaline in 5% KOH. Pleurocystidia not observed. Tube trama composed of 5–15 µm wide parallel hyphae, hyaline to yellowish in 5% KOH. Pileipellis a trichoderm, composed of thin-walled, elongated, and slightly interwoven hyphae, 7–22 µm wide, hyaline to yellowish in 5% KOH; terminal cells 23–100 × 8–22 µm, clavate to subcylindrical, with obtuse apex. Pileal trama made up of hyphae 5–25 µm diam, colourless in 5% KOH. Stipitipellis composed of thin-walled hyphae, 3–8 µm wide, light yellow in 5% KOH. Stipe trama composed
of cylindrical, light yellow in 5% KOH, thin-walled, interwoven hyphae 8–23 μm wide. Clamp connections frequently present in all tissues.

Habitat and distribution: Solitary or scattered on soil under *Castanea mollissima* BL. in subtropical chestnut plantations. Currently only known from Henan Province, China.

Additional specimens examined: CHINA. Henan Province, Xinyang City, Renhua County, alt. 300 m, 22 July 2016, Ming Zhang (GDGM46275, GDGM46509, GDGM46401, GDGM46405); same location, alt. 350 m, 22 July 2016, Xiang-Rong Zhong & Tai-Hui Li (GDGM46419, GDGM46433).

Notes: Phylogenetic analyses shown that the specimens of *G. pallidus* formed a well supported lineage and nested into the sect. *Pallidus*. *Gyroporus alboluteus* and *G. memnonius* are two closely related species in phylogeny. Indeed, *G. memnonius* resembles *G. pallidus* in morphology, but differs in its stronger basidiomata, narrower basidiospores (4–5 μm wide) and smaller basidia 19–26 × 6 μm (Xie et al. 2022). *G. alboluteus* can be easily distinguished by its pileus colour (see above in *G. alboluteus*). Besides, two specimens from China named as “G. cf. castaneus” also closely related to *G. pallidus*. However, the former differs in its larger basidiomata, narrower basidiospores [(4–)4.5–6(–7) μm] with a large Qm value (1.81 ± 0.16), and distributed in the temperate regions of northeastern China (Xie et al. 2022).

Morphologically, *G. pallidus* resembles *G. castaneus*, *G. paramjitii*, *G. punctatus* Lj.N. Vassiljeva and *G. tuberculatosporus*. However, *G. castaneus*, originally reported from Europe, differs in its larger basidiomata (pileus can up to 10 cm broad) and basidiospores [8–12(14) × 4.5–6(7) μm] (Heinemann and Rammeloo 1979; Moser 1983; Castro and Freire 1995); *Gyroporus paramjitii*, originally described from India, differs in its dark brown to red brown basidiomata, smaller basidia (11–16 × 6 μm), and larger basidiospores (7.5) 8–11.6 (13) × 5–6.6 (7) μm (Das et al. 2017; Xie et al. 2022); *Gyroporus punctatus*, originally described from the south of Russian Far East, differs in its rugulose to reticulate pileus, rugulose stipe, and larger basidiospores (up to 12 μm long) (Vassiljeva 1950; Nagasawa 2001); *G. tuberculatosporus*, originally reported from southwestern China, differs in its larger and yellowish brown basidiomata, large and broad basidiospores (9–11.3 × 5–8.7 μm) (Zang 2006).

Two new species *G. porphyreus* and *G. subglobosus* recently reported from China, also similar to *G. pallidus*. However, *G. porphyreus* differs in its yellow-brown, red-brown to purple pileus, brown to red-brown stipe, and narrower basidiospores (4–5.5 μm wide) with a relatively large Q value (1.4–2.56) (Xie et al. 2022); *G. subglobosus* differs in its yellowish brown, red-brown to dark brown pileus, brown to red-brown stipe, and subglobose basidiospores (6.5–9.5 × 5–7 μm) with a small Q value (1.1–1.5), besides, *G. subglobosus* can naturally distributed in northeastern China, and associated with *Pinus koraiensis* Siebold et Zuccarini, *Quercus mongolica* Fischer ex Ledebour, or *Castanopsis kawakami* Hayata (Xie et al. 2022). Additionally, *G. porphyreus* and *G. subglobosus* nested into the sect. *Castaneus*, and can be easily distinguished from *G. pallidus* by the larger genetic distances.

**Discussion**

In this study, a phylogenetic overview of the genus *Gyroporus* was carried out on the basis of the combined sequences ITS-nrLSU and *atp6* datasets, four new sections within the genus were proposed, i.e. G. sect. *Castaneus*, G. sect. *Cyanescens*, G. sect. *Longicystidiatus* and G. sect. *Pallidus*, and five new species, *G. alboluteus*, *G. atrocyanescens*, *G. pseudolongicystidiatus*, *G. pallidus* and *G. subcaerulescens*, were discovered from China.

In sect. *Castaneus*, *G. castaneus* has been widely reported in Europe, North America and eastern Asia. However, the reported collections of “*G. castaneus*” are actually a complex consisting of several different taxa (Das et al. 2017; Davoodian et al. 2018; Xie et al. 2022); for example, the specimens labelled as “*G. castaneus*” represent obviously more than one species in the phylogenetic tree (*Figure 1*). The specimens of this complex from subtropical and tropical regions of Asia or other continents represent different species, such as *G. mcnabii*, *G. memnonius*, *G. naranjus*, *G. paramjitii*, *G. pallidus* etc. It is believed that further studies with more samples will contribute more to reveal the diversity of *G. castaneus* complex.

The sect. *Cyanescens* formed a monophyletic group in the phylogenetic tree (*Figures 1* and *2*), and consisted of species with cyanescent oxidation reactions. *Gyroporus atrocyanescens* and *G. subcaerulescens* are well nested into this section, and closely related to the
Chinese species *G. flavocyanescens*, but they can be separated by the morphological features and the genetic distance. In this section, the species from Southern Hemisphere clustered together, while the species from Northern Hemisphere formed two well supported clades in the *atp6* phylogenetic tree (Figure 2), which was consistent with the previous study by Davoodian et al. (2018). *Gyroporus cyanescens* was reported to be widely distributed in China in the past (Bi and Zheng 1990, 1994; Ying and Zang 1994; Mao 2000; Li et al. 2015), and a recently study proved that the distribution of *G. cyanescens* in China is highly suspectable and specimens fully identical to the European species has not been found yet (Huang et al. 2021). Specimens from temperate regions of China labelled as "*G. cyanescens*" could be *G. alpinus*, and specimens from subtropical or tropical regions of China with obvious cyanescant oxidation reactions could be *G. brunneoflaccosus*, *G. flavocyanescens* or *G. atrocyanescens*.

The sect. *Longicystidiatus* was well supported (Figures 1 and 2; BS/BPP = 99%/1; BS/ BPP = 100%/1), and formed a sister relationship with the sect. *Cyanescens*. However, species in this section lack of cyanescant oxidation reaction and can be easily distinguished from other species in *Gyroporus* by their very large and conspicuous cystidia, especially in *G. longicystidiatus* and *G. pseudolongicystidiatus*, the size of cheilocystidia can up to 100 μm in length.

The sect. *Pallidus* formed a monophyletic clade in the phylogenetic trees (Figures 1 and 2), and four species were included. Species in this section are difficult to distinguish from the species in sect. *Castaneus* in morphology, but they can be easily separated from each other in phylogeny. Besides, species in sect. *Pallidus* usually have paler pileus colour, and without red or purple tinge to compare with species in the sect. *Castaneus*. The species “*G. cf. castaneus*”, described from China in Xie et al. (2022), has been proved to belong to the sect. *Pallidus*, and represents a different species from *G. castaneus*.

As noted in previous studies, species of *Gyroporus* are widely distributed in China and eastern Asia. Although several new species have been reported, there are still a larger number of unidentified specimens waiting to be studied, and numerous additional hidden species would be revealed based on more collections and DNA molecular evidences in the future.

Key to sections and species of *Gyroporus* from China
1. Basidiomata not cyanescant ................................................................. 2
   1. Basidiomata cyanescant ........................................................................ 4 (sect. *Cyanescens*)
2. Cheilocystidia shorter, usually less than 50 μm long ......................................................... 3
   2. Cheilocystidia longer, some much longer than 50 μm, up to 100 μm long ....................... 8 (sect. *Longicystidiatus*)
3. Pileus without red or purple tinge, white, brown, yellow-brown to dark brown, stipe concolourous with pileus or paler; pileipellis as a cutis or trichodermium ............................................................. 9 (sect. *Pallidus*)
3. Pileus always with more or less red or purple tinge, yellow-brown, orange-brown, brown to red brown, stipe concolourous with pileus or darker, pileipellis trichodermium ................................. 12 (sect. *Castaneus*)

Section *Cyanescens*
4. Only hymenophore and pileus context slowly changing to pastel blue when bruised .................................................. 5
   4. All parts of basidiomata changing to blue when bruised ......................................................... 5
5. Pileus and stipe obviously brown, from brownish orange, light brown, light reddish brown to dark brown, with brown floccose-scales and long hairs or villi; context white, turning light turquoise at first, then quickly becoming dark turquoise or dark blue when exposed; basidiospores 8.5–10 × 5–6 μm .......................... 5
   5. Pileus and stipe paler than above, with little or without brown tinge, from white, ivory yellow, greyish-yellow, olive yellow, flavous, grey-yellow to grey-orange; brown floccose-scales and long hairs absent or much less obvious ..........................
6. Basidiomata immediately and intensely turning dark blue to deep blue when bruised; pileus white to greyish yellow, covered with greyish yellow floccose squamules; basidiospores 7.5–10 × 4.8–6 µm .............................................................. G. atrocyaneasens

6. Basidiomata gradually becoming blue to dull blue when bruised .......................................................... 7

7. Pileus ivory yellow to grey-orange or brownish-yellow, covered with scaly to floccose squamules; basidiospores 7–10 × 5.5–7.5 µm; basidia long and slender, 35–55 × 7–12 µm; and distributed in tropical forests .......................................................... 8

7. Pileus flavous, dull yellow, grey-orange to greyish-orange, nearly glabrous or somewhat fibrillose to finely tomentose; basidiospores 8–10 × 5.5–6.5 µm; and distributed in tropical forests dominated by Fagaceae trees .......................................................... G. flavocyanescens

Section Longicystidiatus

8. Cheilocystidia broader, 23–98 × 9–21 µm; pileus 2.7–9 cm broad, subtomentose, drab, yellow-brown to dark yellow-brown; stipe light yellowish brown to brown; basidiospores 7–9 × 3.5–6 µm .............................................................. G. longicystidiatus

8. Cheilocystidia narrower, 37–100 × 6–10 µm; pileus 5–10 cm broad, subglabrous when mature, brownish orange to brownish yellow; basidiospores 8–10 × 5.5–6.5 µm .............................................................. G. pseudolongicystidiatus

9. Pileus white, pale yellow to pale orange, fibrillose or velvet-subtomentose when young and nearly glabrous in age; stipe surface glabrous or with white pruina; basidiospores 8.5–9.5 × 4.5–5 µm; pileipellis a cutis, composed of suberect, interwoven hyphae covered with yellowish brown to brown pigment on surface in 5% KOH; terminal cells 30–95 × 7–10 µm .............................................................. G. alboluteus

9. Pileus never white to pale yellow or pale, without yellowish tinge .............................................................. 2

10. Basidiomata larger, pileus up to 10 cm broad, yellow to yellow-brown; basidiospores 8–10 × 4.5–6 µm; distributed in temperate areas .............................................................. G. cf. castaneus

10. Basidiomata smaller, pileus less than 10 cm broad .............................................................. 11

11. Pileus 4.8–6 cm broad, dark brown; stipe subtomentose, brown-yellow to yellow-brown; basidiospores 8–10 × 4–5 µm, slightly thick-walled; pleurocystidia 17–40 × 4–10 µm, subfusciform or fusiform; pileipellis a trichoderm, composed of thin to slightly thick-walled hyphae, light yellow in KOH; terminal cells 38–105 × 9–15 µm .............................................................. G. memnonius

11. Pileus 3–5 cm broad, usually cracking into small scales when mature or in dry conditions, brownish orange, light brown to brown; stipe concolourous with pileus, slightly paler to yellowish brown to yellowish downward the base; basidiospores 8–10 × 5–6 µm; pileipellis a trichodermium, composed of thin-walled, elongated, and slightly interwoven hyphae, hyaline to yellowish in 5% KOH; terminal cells 23–100 × 8–22 µm .............................................................. G. pallidus

Section Castaneus

12. Basidiomata larger, pileus up to 10 cm broad, yellowish brown to reddish brown; basidiospores 9–11.3 × 5–8.7 µm; distributed in tropical forests .............................................................. G. tuberculatosporus

12. Basidiomata smaller, pileus less than 10 cm broad .............................................................. 13

13. Basidiospores subglobose to ellipsoid (Qm < 1.5) .............................................................. G. subglobosus

13. Basidiospores oval to ellipsoid (Qm > 1.5) .............................................................. 14

14. Pileus yellow-brown, brown to red-brown when young, then purple; stipe brown, pale to red-brown; basidiospores 7–10.5 × 4–5.5 µm .............................................................. G. porphyreus

14. Pileus red-brown, orange brown to dark red-brown; stipe red-brown to dark red-brown; basidiospores 7–9 × 5–6 µm .............................................................. G. paramjiti
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