A Contribution to Knowledge of *Craterellus* (Hydnaceae, Cantharellales) in China: Three New Taxa and Amended Descriptions of Two Previous Species

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Species of *Craterellus* (Hydnaceae, Cantharellales) in China are investigated on the basis of morphological and molecular phylogenetic analyses of DNA sequences from nuc 28S rDNA D1-D2 domains (28S) and nuc rDNA internal transcribed spacer ITS1-5.8S-ITS2 region. Five species are recognized in China, of which three of them are described as new, viz. *C. fulviceps*, *C. minor*, and *C. parvopullus*, while two of them are previously described taxa, viz. *C. aureus*, and *C. lutescens*. A key to the known Chinese taxa of the genus is also provided.

Keywords: East Asia, molecular phylogeny, morphology, new taxa, taxonomy

**INTRODUCTION**

*Craterellus* Pers. (Hydnaceae, Cantharellales), typified by *C. cornucopioides* (L.) Pers., is characterized by a small, funnel-shaped basidioma with a hollow stipe (Petersen, 1979a). Recent molecular phylogenetic data have confirmed the monophyly of the genus (Hibbett et al., 2014). To date, many taxa of *Craterellus* have been discovered in Africa, America, and Asia (Dahman et al., 2000; Matheny et al., 2010; Beluhan and Ranogajec, 2011; Kumari et al., 2012; Wilson et al., 2012; Das et al., 2017; Hembrom et al., 2017; Bijeesh et al., 2018; Zhong et al., 2018; Zhang et al., 2020; Cao et al., 2021a,b). They have received much attention for their edibility and medicinal value; for example, *C. cornucopioides* is considered a highly nutritious edible fungus and has antihyperglycemic, antioxidative, and antitumor activities (Beluhan and Ranogajec, 2011; Liu et al., 2010; Beluhan and Ranogajec, 2011; Kumari et al., 2012; Wilson et al., 2012; Das et al., 2017; Hembrom et al., 2017; Bijeesh et al., 2018; Zhong et al., 2018; Zhang et al., 2020; Cao et al., 2021a,b).
followed Zhang et al. (2021). PCR products were checked for size and purity using 1% (w/v) agarose gel electrophoresis. The amplified PCR products were sequenced using an ABI 3730 DNA Analyzer (BGI, Guangzhou, China) with the PCR primers. Forward or reverse sequences were assembled with BioEdit (Hall, 1999). All newly obtained sequences were deposited in GenBank1.

**Dataset Assembly**

A total of thirty DNA sequences (16 of 28S, 14 of ITS) from 17 collections were newly generated for this study (Table 1). For the concatenated dataset, the 28S and ITS sequences generated in the study were aligned with selected sequences from previous studies and GenBank (Table 1). *Hydnum minus* FHMU2461 and *Hydnum cremelbaldum* FHMU2153 were chosen as outgroups as described by An et al. (2017). Sequences of 28S and ITS were aligned separately to test for phylogenetic conflict. The topologies of the phylogenetic trees based on a single gene were identical, indicating that the phylogenetic signals present in the different gene fragments were not in conflict. Then, the sequences of the different genes were aligned using MUSCLE (Edgar, 2004), and alignments were purged from unreliably aligned positions and gaps using Gblocks (Castresana, 2000). The sequences of the different genes were concatenated using Phyutility v2.2 for further analyses (Smith and Dunn, 2008).

**Phylogenetic Analyses**

The combined nuclear dataset (28S + ITS) was analyzed using maximum likelihood (ML) and Bayesian inference (BI) methods. ML tree generation and bootstrap (BS) analyses were performed using RAxML v7.2.6 (Stamatakis, 2006), running 1,000 replicates combined with the ML search. BI was conducted in MrBayes v3.1 (Huelsenbeck and Ronquist, 2005) on the CIPRES Science Gateway portal (Miller et al., 2011). The best-fit likelihood models of 28S (GTR + I + G) and ITS (HKY + I + G) were estimated in MrModeltest v2.3 (Nylander, 2004) based on the Akaiake information criterion. Bayesian analysis was repeated for 30 million generations and sampled every 1,000 generations. Trees sampled from the first 25% generations were discarded as burn-in, and Bayesian posterior probabilities (PP) were then calculated for a majority-rule consensus tree of the retained sampled trees.

**RESULTS**

**Molecular Data**

The combined dataset (28S + ITS) of *Craterellus* consisted of 161 taxa and 2,173 nucleotide sites (Figure 2), and the alignment was submitted to TreeBase (SB8981). The topologies of the phylogenetic trees based on the combined dataset generated from ML and BI analyses were identical, but statistical support showed slight differences. In this study, we focused on lineages 1–14 from China (Figure 2). Lineage 1, with strong statistical support (BS = 85%, PP = 0.99), comprised of three collections (GDGM46432, GDGM48105, and GDGM49945) of *C. luteus*, and three collections (FHMU2100, FHMU2102, and FHMU2407) from southern China, and two collections (FHMU6549, FHMU6550) from eastern China. Lineage 2, with

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1https://www.ncbi.nlm.nih.gov/genbank
strong statistical support (BS = 82%, PP = 1.0), comprised of two collections (FHMU6551, and FHMU6552) from eastern China. Lineage 3, three collections (FHMU6555, FHMU6556, and FHMU6557) from southern China grouped together with high statistical support (BS = 100%, PP = 0.99). Lineage 4 comprised of the holotype of \textit{C. atrobrunneolus}. Lineage 5, with strong statistical support (BS = 94%, PP = 1.0), comprised of two collections (Yuan 14,520, and Yuan 14,721) of \textit{C. squamatus} from northeastern China. Lineage 6 comprised of the holotype of \textit{C. macrosporus}. Lineage 7, with strong statistical support (BS = 100%, PP = 1.0), comprised of two collections (Yuan 14,623, and Yuan 14,647) of \textit{C. croceialbus} from northeastern China. Lineage 8 comprised of one collection named \textit{C. cornucopioides} from western China. Lineage 9, with strong statistical support (BS = 100%, PP = 1.0), comprised of two collections (Yuan 14,776 and Yuan 14,779) of \textit{C. albidus} from northeastern China. Lineage 10, with strong statistical support (BS = 96%, PP = 1.0), comprised of two collections (HGASM01-10046, and HGASM01-3581) of \textit{C. albidus} from southwestern China. Lineage 11, with strong statistical support (BS = 95%, PP = 1.0), comprised of one collection (FHMU6553) from central China, and one collection labeled as \textit{C. tubaeformis} from Japan. Lineage 12, with strong statistical support (BS = 99%, PP = 1.0), comprised of one collection (FHMU6554) from central China, and one collection labeled as \textit{C. melanoxeros} also from China. Lineage 13 comprised of one collection (ECM90) from eastern China. Lineage 14, with strong statistical support (BS = 90%, PP = 1.0), comprised of seven collections of \textit{C. lutescens} (UPSF-11789, UPSF-11790, UPSF-11791, 104198, SS575, ma023, and TM02_22), five collections labeled as \textit{Craterellus} sp. (RSEM15_01, RSEM16_35, RSEM26, RSEM26_17, and RSEM26_64), and five collections (FHMU6544–FHMU6548) from southwestern China.

**Taxonomy**

\textit{Craterellus aureus} Berk. & M.A. Curtis, Proc. Amer. Acad. Arts & Sci. 4: 123, 1860 \textbf{Figures 3A–E, 4.}

\textbf{Basidiomata} medium-sized. \textbf{Pileus} 1.5–5 cm diam, infundibuliform, broadly infundibuliform with age; surface dry, vivid yellow (1A5) to orange (3A7); margin straight when young, wavy or lobed at maturity. \textbf{Hymenophore} nearly smooth, dirty white (1B2), yellow (4A7) to pale orange (1A2); context 0.1–0.15 cm in thickness, whitish (3A1) to pale yellow (3A2). \textbf{Stipe} 1.2–2.7 × 0.35–0.45 cm, central, hollow, usually curved, without any obvious demarcation between pileus and stipe; surface dry, yellowish-white (3A2), yellow (4A4) to pale orange (1A2). Basal mycelium white. \textbf{Odor} mild. \textbf{Spore print} not obtained.

\textbf{Basidiospores} [60/9/5] (7–)7.5–8.21–9(–9.5) × 5.5–5.97–6.5(–7) µm, Q = (1.17–)1.23–1.55(–1.64), Qm = 1.38 ± 0.1, ellipsoid to broadly ellipsoid, smooth, slightly thick-walled (up to 0.5 µm), hyaline or yellowish in KOH. \textbf{Basidia} 50–83 × 6.5–8.5 µm, cylindro-clavate, with irregular flexuous, slightly thick-walled (up to 0.5 µm), 4–6-spored, pale yellowish in KOH; sterigmata 5–6 µm in length. \textbf{Cystidia} absent. \textbf{Pileipellis} intricate trichoderm composed of cylindrical, 4–9 µm wide, slightly thick-walled (0.5–0.7 µm) hyphae, faintly pale yellow in KOH; terminal cells 27–59 × 4–8 µm, subcylindrical to subclavate with obtuse apex. \textbf{Clamp connections} absent in all tissues.

\textbf{Habitat}: Gregarious, caespitose, or rarely solitary on the ground of forests dominated by \textit{Castanea} spp. and \textit{Quercus} spp. (Zhang et al., 2018).

\textbf{Known distribution}: Eastern China (Jiangxi Province), and southern China (Guangdong and Hainan Provinces, Hong Kong) (Berkeley and Curtis, 1860).

\textbf{Specimens examined}: CHINA. Hainan Province: Jianfengling of Hainan Tropical Rainforest National Park, elev. 850 m, 4 July 2012, N.K. Zeng1057 (FHMU2407); Limushan of Hainan Tropical Rainforest National Park, elev. 850 m, 4 July 2012, N.K. Zeng1057 (FHMU2407); Limushan of Hainan Tropical Rainforest National Park, elev. 850 m, 4 July 2012, N.K. Zeng1057 (FHMU2407); Limushan of Hainan Tropical Rainforest National Park, elev. 850 m, 4 July 2012, N.K. Zeng1057 (FHMU2407); Limushan of Hainan Tropical Rainforest National Park, elev. 850 m, 4 July 2012, N.K. Zeng1057 (FHMU2407).

\textbf{Notes}: Our recent collections and the holotype of \textit{C. lutescens}, a species first described from Guangdong Province, southern China (Zhong et al., 2018), phylogenetically group together with high statistical support (\textbf{Figure 2}), which suggests that these new specimens belong to \textit{C. lutescens}. Morphologically, these newly collected materials easily remind us of \textit{C. aureus}, a species first described in Hong Kong, southern China. When \textit{C. lutescens} was
| Taxon | Voucher | Locality | GenBank accession no. | References |
|-------|---------|----------|-----------------------|------------|
| Craterellus aff. excelsius | G3184 | Guyana | KJ786602 | — | Unpublished |
| C. aff. excelsius | G3279 | Guyana | KJ786625 | — | Unpublished |
| C. aff. tubaeformis | Mushroom Observer # 289652 | Mexico | — | MH168540 | Unpublished |
| C. albids | HGASMF01-3581 | Guizhou, SW China | MT921161 | — | Zhang et al., 2020 |
| C. albids | HGASMF01-10046 | Guizhou, SW China | MT921162 | — | Zhang et al., 2020 |
| C. albostriatus | CAL 1624 | India | MG593194 | — | Biejeeh et al., 2018 |
| C. atratoxides | TH8243 | Guyana | — | KT339209 | Wilson et al., 2012 |
| C. atratoxides | MCA1313 | Guyana | JO915119 | JO915093 | Wilson et al., 2012 |
| C. atratoxides | TH9232 | Guyana | JO915137 | JO915111 | Wilson et al., 2012 |
| C. atratoxides | TH8473 | Guyana | JO915129 | JO915103 | Wilson et al., 2012 |
| C. atratoxides | AMV1965a | Colombia | KT724157 | KT724106 | Unpublished |
| C. atratoxides | AMV1959 | Colombia | KT724156 | — | Unpublished |
| C. atratoxides | AMV1870 | Colombia | — | KT354698 | Unpublished |
| C. atratoxides | AMV1992 | Colombia | — | KT354700 | Unpublished |
| C. atratoxides | AMV1990 | Colombia | — | KT354699 | Unpublished |
| C. atratus | AMV1832 | Colombia | KT724158 | KT724107 | Unpublished |
| C. atratus | TH9203 | Guyana | JO915133 | JO915107 | Wilson et al., 2012 |
| C. atratus | MCA990 | Guyana | JO915126 | JO915100 | Wilson et al., 2012 |
| C. atratus | MCA1070 | Guyana | JO915118 | JO915092 | Wilson et al., 2012 |
| C. atratus | MN21-2006 | Thailand | — | AB445115 | Disyatstat et al., 2016 |
| C. atrobrunneolus | Yuan13878 | Yunnan, SW China | MN894058 | MN902353 | Cao et al., 2021a |
| C. atrobrunneolus | Yuan13878 | Yunnan, SW China | MN894058 | MN902353 | Cao et al., 2021a |
| C. atrocinereus | Arora15001 | United States | — | KR560049 | Frank, 2015 |
| C. atrocinereus | JLF3750 | United States | — | KR560048 | Frank, 2015 |
| C. aureus | N.K. Zeng1057 (FHMU1207) | Hainan, southern China | OL439672 | OM469019 | Present study |
| C. aureus | M.S. Su145 (FHMU1206) | Jiangxi, eastern China | OL439673 | — | Present study |
| C. aureus | N.K. Zeng3141 (FHMU1202) | Hainan, southern China | OL439674 | OM469020 | Present study |
| C. aureus | N.K. Zeng3139 (FHMU1200) | Hainan, southern China | OL439675 | — | Present study |
| C. aureus | M.S. Su196 (FHMU6550) | Jiangxi, eastern China | OL439676 | OL439545 | Present study |
| C. badioligrius | Yuan 14776 | Liaoning, NE China | MW897932 | MW890548 | Cao et al., 2021b |
| C. badioligrius | Yuan 14779 | Liaoning, NE China | MW897933 | MW890549 | Cao et al., 2021b |
| C. caeruleofuscus | MH17001 | United States | MT237468 | MH58300 | Cao et al., 2021a |
| C. calcornucopioides | JLF3744 | United States | — | KR660046 | Frank, 2015 |
| C. calcornucopioides | Arora 15002 | United States | — | KR660047 | Frank, 2015 |
| C. calxculus | Mushroom Observer # 321697 | United States | — | MK970596 | Unpublished |
| C. carolinensis | FLAS-F-59997 | United States | — | KY664712 | Petersen, 1969 |
| C. cf. lutescens | BB 13.048 | Canada | KM484696 | — | Shao et al., 2014 |
| C. cf. lutescens | BB 13.125 | United States | KM484697 | — | Shao et al., 2014 |
| C. cinereofimbriatus | TH9264 | Guyana | JO915138 | JO915112 | Wilson et al., 2012 |
| C. cinereofimbriatus | TH9075 | Guyana | JO915131 | JO915105 | Wilson et al., 2012 |
| C. cinereofimbriatus | TH9264 | Guyana | JO915138 | JO915112 | Wilson et al., 2012 |
| C. cinereofimbriatus | TH9899 | Guyana | JO915130 | JO915104 | Wilson et al., 2012 |
| C. cinereofimbriatus | JOH4 | Colombia | KT724159 | — | Unpublished |
| C. cinereus | 107-08 | India | JF412276 | JF412278 | Kumari et al., 2012 |
| C. cinereus | AST2015 | Pakistan | — | MF374488 | Naseer and Khalid, 2018 |
| C. cinereus | AST12B | Pakistan | — | MF374489 | Naseer and Khalid, 2018 |
| Taxon | Voucher | Locality | GenBank accession no. | References |
|-------|---------|----------|-----------------------|------------|
|       |         |          | 28S                  | ITS        |
| C. cornucopioides | HbO-53302 | Norway | AF105301 | — | Dahlman et al., 2000 |
| C. cornucopioides | UPSF-11792 | Sweden | AF105297 | — | Dahlman et al., 2000 |
| C. cornucopioides | Groc11399 clone 1 | United States | — | KT693262 | Raja et al., 2017 |
| C. cornucopioides | WA0000071019 | Poland | — | MK028881 | Kotowski et al., 2019 |
| C. cornucopioides | AFTOL-ID 286 | United States | AY700188 | DQ205680 | Matheny et al., 2007, 2010 |
| C. cornucopioides | — | Tibet, SW China | AJ279672 | — | Li et al., 1999 |
| C. cornucopioides | CNF 1/7292 | Croatia | — | MK169230 | Mešić et al., 2020 |
| C. croceialbus | Yuan 14623 | Liaoning, NE China | MW979529 | MW980572 | Cao et al., 2021b |
| C. croceialbus | Yuan 14647 | Liaoning, NE China | MW979530 | MW980573 | Cao et al., 2021b |
| C. cornucopioides var. mediosporus | 268-06 | United States | JF412275 | JF412277 | Kumari et al., 2012 |
| C. excelsus | TH8235 | Guyana | JQ915128 | JQ915102 | Wilson et al., 2012 |
| C. excelsus | TH7515 | Guyana | JQ915127 | JQ915101 | Wilson et al., 2012 |
| C. excelsus | MCA3107 | Guyana | JQ915121 | JQ915095 | Wilson et al., 2012 |
| C. falax | PBM3290 | United States | — | GU590923 | Matheny et al., 2010 |
| C. falax | MQ15002 | Canada | — | MH571125 | Unpublished |
| C. falax | FLAS-F-60401 | United States | — | MH281835 | Unpublished |
| C. fulviceps | MHNNU10567 (FHMU6553) | Hunan, central China | OL439678 | OL439548 | Present study |
| C. ignicolor | UPSF-11794 | United States | AF105314 | — | Dahlman et al., 2000 |
| C. indicus | PUN3884 | India | HM113529 | HM113530 | Kumari et al., 2012 |
| C. indicus | MSR6 | India | — | HQ450769 | Kumari et al., 2012 |
| C. inusitatus | CAL 1625 | India | MG593195 | — | Bijeesh et al., 2018 |
| C. lutescens | 104198 (envir. seq.) | Ireland | — | AY082606 | Harrington and Mitchell, 2002 |
| C. lutescens | TM02_22 | Canada | EJ522746 | — | Porter et al., 2008 |
| C. lutescens | UPSF-11790 | Sweden | AF105300 | — | Dahlman et al., 2000 |
| C. lutescens | UPSF-11791 | Spain | AF105304 | — | Dahlman et al., 2000 |
| C. lutescens | SS575 | Sweden | JQ976982 | — | Tibuhwa et al., 2012 |
| C. lutescens | mal023 | Italy | MNS592820 | MNS59294 | Federico et al., 2020 |
| C. lutescens | L.P. Tang1647 (FHMU6547) | Yunnan, SW China | OL439679 | OL439549 | Present study |
| C. lutescens | L.P. Tang1705 (FHMU6546) | Yunnan, SW China | OL439680 | — | Present study |
| C. lutescens | W.H. Zhang441-1 (FHMU6544) | Yunnan, SW China | OL439681 | OL439550 | Present study |
| C. lutescens | W.H. Zhang441-2 (FHMU6545) | Yunnan, SW China | OL439682 | OL439551 | Present study |
| C. lutescens | W.H. Zhang441-3 (FHMU6546) | Yunnan, SW China | OL439683 | OL439552 | Present study |
| C. luteus | GDGM46432 | Guangdong, southern China | MG727898 | MG727897 | Zhong et al., 2018 |
| C. luteus | GDGM48105 | Guangdong, southern China | MG701171 | MG727896 | Zhong et al., 2018 |
| C. luteus | GDGM49495 | Guangdong, southern China | MG806926 | MG806930 | Zhong et al., 2018 |
| C. macrosporus | Yuan 14782 | Liaoning, NE China | MW979531 | MW980574 | Cao et al., 2021b |
| C. melanoxerus | SS576 | Sweden | JQ976983 | — | Tibuhwa et al., 2012 |
| C. melanoxerus | 420526MF0299 | China | MG712381 | — | Unpublished |
| C. minor | MHNNU32505 (FHMU6554) | Hunan, central China | OL439684 | OL439553 | Present study |
| C. odoratus | 14026h2 | United States | MN227279 | — | Unpublished |
| C. odoratus | 14026h1 | United States | MN227278 | — | Unpublished |
| C. odoratus | UPSF-11799 | United States | AF105306 | — | Dahlman et al., 2000 |
| Taxon              | Voucher             | Locality                | GenBank accession no. | References                  |
|--------------------|---------------------|--------------------------|-----------------------|-----------------------------|
|                    |                     |                          | **28S**               | **ITS**                     |
| C. olivaceoluteus  | TH9205              | Guyana                   | JQ915135              | JQ915109                    | Wilson et al., 2012          |
| C. olivaceoluteus  | MCA3186             | Guyana                   | JQ915124              | JQ915098                    | Wilson et al., 2012          |
| C. parvogriseus    | CAL1533             | India                    | MF421098              | MF421099                    | Das et al., 2017             |
| C. parvogriseus    | KNPS_WC18158        | Korea                    | MT974136              | —                           | Ko et al., 2020              |
| C. parvopullus     | N.K. Zeng4913 (FHMU6555) | Hainan, southern China | OL439685              | OM334829                    | Present study                |
| C. parvopullus     | N.K. Zeng4912 (FHMU6555) | Hainan, southern China | OL439686              | OM334828                    | Present study                |
| C. parvopullus     | N.K. Zeng4911 (FHMU6557) | Hainan, southern China | OL439687              | OM334827                    | Present study                |
| C. pleurotoides    | MCA3124             | Guyana                   | JQ915123              | JQ915097                    | Wilson et al., 2012          |
| C. pleurotoides    | TH9220              | Guyana                   | JQ915136              | JQ915110                    | Wilson et al., 2012          |
| C. shoreae         | CAL_F_1396          | India                    | KY290585              | —                           | Cao et al., 2021a            |
| C. sinuosus        | TF1802              | United States            | U87992                | —                           | Feibelman et al., 1997       |
| Craterellus sp.    | Y.J. Hao2080 (FHMU6551) | Anhui, eastern China | —                     | OL439546                    | Present study                |
| Craterellus sp.    | MHHNU32154 (FHMU6552) | Anhui, eastern China | OL439677              | OL439547                    | Present study                |
| Craterellus sp.    | RSEM26_17 (envr. seq.) | Austria                   | EU046070              | —                           | Urban et al., 2008           |
| Craterellus sp.    | RSEM16_35 (envr. seq.) | Austria                   | EU046065              | —                           | Urban et al., 2008           |
| Craterellus sp.    | RSEM15_01 (envr. seq.) | Austria                   | EU046056              | —                           | Urban et al., 2008           |
| Craterellus sp.    | RSEM26 (envr. seq.) | Austria                   | EU046028              | —                           | Urban et al., 2008           |
| Craterellus sp.    | RSEM26_64 (envr. seq.) | Austria                   | EU046073              | —                           | Urban et al., 2008           |
| Craterellus sp.    | RSEM26_17 (envr. seq.) | Austria                   | EU046070              | —                           | Urban et al., 2008           |
| Craterellus sp.    | AWW263              | Malaysia                  | JQ915117              | JQ915091                    | Wilson et al., 2012          |
| Craterellus sp.    | 610723MF0035        | —                        | —                     | —                           | Unpublished                  |
| Craterellus sp.    | LAM 0257           | Malaysia                  | KY091022              | —                           | Unpublished                  |
| Craterellus sp.    | LAM 0254           | Malaysia                  | KY091020              | —                           | Unpublished                  |
| Craterellus sp.    | DOB 2489           | Malaysia                  | KY090820              | —                           | Unpublished                  |
| Craterellus sp.    | NC-8338            | United States            | —                     | AY456340                    | Edwards et al., 2004         |
| Craterellus sp.    | CY14_025_1 (envr. seq.) | New Caledonia        | —                     | KY774189                    | Carriconde et al., 2019     |
| Craterellus sp.    | PGK14_052 (envr. seq.) | New Caledonia        | —                     | KY774191                    | Carriconde et al., 2019     |
| Craterellus sp.    | 16450              | India                     | —                     | MF589901                    | Unpublished                  |
| Craterellus sp.    | Mushroom Observer # 2896663 | Mexico                   | MH223820              | —                           | Unpublished                  |
| Craterellus sp.    | YM226 (envr. seq.) | Japan                     | —                     | AB848480                    | Miyamoto et al., 2014        |
| Craterellus sp.    | CM13_278_1 (envr. seq.) | New Caledonia | —                     | KY774188                    | Carriconde et al., 2019     |
| Craterellus sp.    | OTU_506s (envr. seq.) | Europe                   | —                     | MT095625                    | Arraiano-Castilho et al., 2020 |
| Craterellus sp.    | CMY31E2 (envr. seq.) | New Caledonia            | —                     | KY774190                    | Carriconde et al., 2019     |
| Craterellus sp.    | G3154              | Guyana                    | KJ786597              | KJ786692                    | Unpublished                  |
| Craterellus sp.    | G2070              | Guyana                    | —                     | KJ786682                    | Unpublished                  |
| Craterellus sp.    | G3228              | Guyana                    | KJ786613              | —                           | Unpublished                  |
| Craterellus sp.    | G3237              | Guyana                    | KJ786614              | KJ786704                    | Unpublished                  |
| Craterellus sp.    | G3112              | Guyana                    | KJ786587              | —                           | Unpublished                  |
| Craterellus sp.    | G1340              | Guyana                    | KJ786565              | KJ786670                    | Unpublished                  |
| Taxon | Voucher | Locality | GenBank accession no. | References |
|-------|---------|----------|-----------------------|------------|
| **Craterellus sp.** | BB 09.079 | New Caledonia | KM484695 | — | Shao et al., 2014 |
| **Craterellus sp.** | LM3266 | France | — | KM576330 | Shao et al., 2014 |
| **Craterellus sp.** | AMV1879 | Colombia | KT724161 | — | Unpublished |
| **Craterellus sp.** | M66A9 (envir. seq.) | Mexico | — | EU653479 | Morris et al., 2008 |
| **Craterellus sp.** | LMAO6b-09 | France | — | JF506753 | Unpublished |
| **Craterellus sp.** | YM835 | Japan | — | LC175080 | Miyamoto et al., 2018 |
| **Craterellus sp.** | 14044 | Spain | — | MW282673 | Unpublished |
| **Craterellus sp.** | OTU_236 | Germany | — | MW238032 | Unpublished |
| **Craterellus sp.** | MEL:2382717 | Australia | — | KP012898 | Unpublished |
| **Craterellus sp.** | MEL:2383015 | Australia | — | KP012877 | Unpublished |
| **Craterellus sp.** | ECM90 (envir. seq.) | Zhejiang, eastern China | — | JQ991715 | Unpublished |
| **C. squamatus** | Yuan 14520 | Liaoning, NE China | MW979534 | MW980571 | Cao et al., 2021b |
| **C. squamatus** | Yuan 14721 | Liaoning, NE China | MW979535 | MW980570 | Cao et al., 2021b |
| **C. strigosus** | TH9204 | Guyana | JQ915134 | JQ915108 | Wilson et al., 2012 |
| **C. strigosus** | MCA1750 | Guyana | JQ915120 | JQ915094 | Wilson et al., 2012 |
| **C. strigosus** | JOH116 (envir. seq.) | Colombia | — | KT354701 | Unpublished |
| **C. strigosus** | AMV1885 (envir. seq.) | Colombia | KT724164 | KT724110 | Unpublished |
| **C. tubaeformis** | DAVFP26257 | Canada | — | HM468491 | Zhou et al., 2011 |
| **C. tubaeformis** | MushroomObserver.org/230696 | United States | — | MH298913 | Unpublished |
| **C. tubaeformis** | MushroomObserver.org/312399 | United States | — | MH063270 | Unpublished |
| **C. tubaeformis** | 2A4 | Japan | AB973798 | AB973799 | Unpublished |
| **C. tubaeformis** | 1D3 | Japan | — | AB973729 | Unpublished |
| **C. tubaeformis** | UPS-11797 | United States | AF105311 | — | Dahlman et al., 2000 |
| **C. tubaeformis** | TRTC52516 | Belgium | — | HM468496 | Zhou et al., 2011 |
| **C. tubaeformis** | DM1094 | Denmark | — | MT640258 | Unpublished |
| **C. tubaeformis** | UPS-11793 | Sweden | AF105307 | — | Dahlman et al., 2000 |
| **C. tubaeformis** | BB 07.293 | Slovakia | KF294840 | — | Buyck et al., 2014 |
| **C. tubaeformis** | TRTC52235 | Belgium | — | HM468497 | Zhou et al., 2011 |
| **C. tubaeformis** | BR089347 | Canada | — | HM468493 | Zhou et al., 2011 |
| **C. tubaeformis** | OSC-41280 | United States | AF105313 | — | Dahlman et al., 2000 |
| **C. tubaeformis** | GCB1905 | Belgium | — | MT094784 | Dahlman et al., 2000 |
| **C. tubaeformis** | UPSF-11795 | United States | AF105308 | — | Dahlman et al., 2000 |
| **Hydnum sp.** | N.K. Zeng2819 (FMU2461) | Yunnan, SW China | KY407528 | KY407533 | An et al., 2017 |
| **Hydnum sp.** | N.K. Zeng2511 (FMU2153) | Hainan, southern China | KY407527 | KY407532 | An et al., 2017 |

GenBank numbers in bold indicate the newly generated sequences; SW, Southwest; NE, Northeast.

first described (Zhong et al., 2018), the species looked different from the original diagnosis of *C. aureus* (Berkeley and Curtis, 1860; Corner, 1966): the bright yellow cap, large size, and robust aspect of the basidiomata and the white hymenophore made it impossible to associate *C. luteus* with Berkeley and Curtis’ original description. Our new collections, which share near-identical (BS = 83%, PP = 1.0) sequences with the holotype of *C. luteus*, indicate that this species might be more variable in overall aspect and color, thereby, significantly reducing the morphological differences with the orange *C. aureus*. Our collections also have a near-identical basidiospore size compared with those reported for *C. aureus*, whereas basidiospores of *C. luteus* are longer [(8.5–)9–11(–12.5) µm]. The fact that both species were described from southern China, sharing the same climate and vegetation, suggests *C. luteus* is a synonym of *C. aureus*, but it does not exclude the presence of a larger species complex in southern China within this clade. The phylogenetic analyses also showed that *C. aureus* is closely related to *C. odoratus* (Schwein.) Fr. (Figure 2), a species originally described in North America (Petersen, 1979b;
However, *C. odoratus* has a more fragile basidioma, narrower basidiospores measuring 8.9–11.8 × 4.4–6.3 µm, and a strong pleasant odor (Petersen, 1979b; Knopf, 1981).

*Craterellus fulviceps* N.K. Zeng, Y.Z. Zhang, P. Zhang & Zhi Q. Liang, sp. nov. Figures 3F, 5 MycoBank: MB841969.

Diagnosis: This species is distinguished from others in *Craterellus* by its very small-sized basidioma, a fulvous pileus, a veined hymenophore, an egg-yolk yellow stipe, and a presence of clamp connections in all parts of the basidioma.

Etymology: Latin “*fulvi-*,” meaning fulvous, and “*ceps*,” meaning pileus, refer to the fulvous pileus of our new species.

**Holotype**: CHINA. Hunan Province: Rucheng County, Jiulongjiang Nature Reserve, elev. 600 m, 2 October 2020, P. Zhang MHHNU10567 (FHMU6553). GenBank accession number: 28S = OL439678, ITS = OL439548.

**Basidiomata** very small-sized. **Pileus** 1–3 cm diam, convex to applanate, center slightly depressed; surface nearly smooth, fulvous (2A3); margin decurved; context very thin. **Hymenophore** veined, decurrent; folds about 0.1 cm broad.
Stipe 2–4 × 0.3–0.8 cm, central, slightly concave and curved in the middle; surface dry, egg-yolk yellow (2A4). Basal mycelium white. Odor not distinctive. Spore print not obtained. Basidiospores [40/2/1] 8–9–10 × 6.5–7.6–8.5 µm, Q = 1.06–1.36(–1.38), Qm = 1.19 ± 0.09, ellipsoid, rarely subglobose, smooth, slightly thick-walled (up to 0.5 µm), yellowish in KOH. Basidioles 58–82 × 9–15.5 µm, long, narrow, subcylindrical, slightly thick-walled (up to 0.5 µm), 2–5-spored, yellowish in KOH; sterigmata 3–7 µm in length. Cystidia absent. Pileipellel a cutis composed of mostly cylindrical, 4–10.5 µm wide, slightly thick-walled (0.5–0.7 µm) hyphae, faintly pale yellow in KOH; terminal cells 45–75 × 5–10 µm, subcylindrical to subclavate with obtuse apex. Clamp connections abundant in all parts of the basidioma. Habitat: Solitary, scattered, or gregarious on the ground of forests dominated by fagaceous trees. Known distribution: Central China (Hunan Province). Notes: The collection from central China phylogenetically clustered with one specimen (1D3) identified as _Craterellus tubaeformis_.

**FIGURE 2** Phylogram inferred from a combined dataset (28S + ITS) of _Craterellus_ using RAxML. RAxML bootstrap percentages (BS ≥ 70%) and Bayesian posterior probabilities (PP ≥ 0.95) are indicated above or below the branches as BS/PP.
from Japan with strong statistical support (Lineage 11 of Figure 2). Our molecular phylogenetic data also show that specimens identified as *C. tubaeformis* were present in several different parts of the tree (Figure 2). Although the true position of *C. tubaeformis* in the molecular tree should be defined in the future, now we are sure that the Chinese collection in Lineage 11 (Figure 2) is not true *C. tubaeformis*, for the European species has a fuscous or fuacous umber pileus, larger basidiospores measuring 8–11 × 5.5–8 μm, and narrower basidia 60–90 × 8–11 μm (Corner, 1966), which is morphologically different from the Chinese specimen. And thus, the Chinese collection was proposed as a new species.

**Craterellus lutescens** (Fr.) Fr., Epic. Syst. Mycol. (Upsaliae): 532, 1838 Figures 6A–D, 7.

**Basidiomata** very small-sized. **Pileus** about 3 cm diam, nearly convex to applanate, center slightly depressed; margin inrolled; surface nearly smooth, brown (6D5); context about 0.2 cm in thickness, yellowish (2A3). **Hymenophore** veined, sometimes smooth, decurrent; folds very thin, light orange-yellow (4A4) to orange-yellow (4A6). **Stipe** 4–6 × 0.5–0.8 cm, central, cylindrical, hollow; surface dry, sunflower yellow (3A8) to dark yellow (4B8); context yellowish-white (4A2). **Odor** pleasant, milky. **Spore print** not obtained.

**Basidiospores** [240/12/5] (8–)8.5–9.7–11(–11.5) × (6.5–)7–7.8–9(–9.5) μm, Q = 1.13–1.36(–1.46), Qₘ = 1.23 ± 0.16, ellipsoid, smooth, slightly thick-walled (up to 0.5 μm), pale yellowish in KOH. **Basidia** 61–84 × 7.5–10 μm, long, narrow, subcylindrical, thin to slightly thick-walled (up to 0.5 μm), 4–6-spored, yellowish in KOH; sterigmata 5.5–7 μm in length. **Cystidia** absent. **Pileipellis** a cutis composed of 5.5–10.5 μm wide, slightly thick-walled (0.5–0.7 μm) hyphae, yellowish in KOH; terminal cells 30–58 × 4–8.5 μm, subcylindrical to subclavate with obtuse apex. **Clamp connections** abundant in all parts of the basidioma.

**Habitat:** Solitary, scattered, or gregarious on the ground of forests dominated by *Pinus yunnanensis* Franch. and *Quercus* L.

**Known distribution:** Southwestern China (Yunnan Province); Europe (Dahlman et al., 2000).

**Specimens examined:** CHINA. Yunnan Province: Jianchuan County, Shibaoshan Nature Reserve, near the grotto parking lot, elev. 2,499 m, 16 August 2014, L.P. Tang164 (FHMU6547); same location, elev. 2,542 m, 19 August 2014, L.P. Tang1705 (FHMU6548); Lijiang City, bought from a market, 19 August 2020, W.H. Zhang441-1, 441-2, 441-3 (FHMU6544, FHMU6546, and FHMU6545).

**Notes:** Our collections and three Swedish specimens (UPSF-11789, UPSF-11790, and SS575) of *C. lutescens* phylogenetically group together with strong statistical support (Figure 2). Morphologically, the Chinese specimens match well with those of *C. lutescens* provided by Petersen (1969). Therefore, the specimen from China is recognized as *C. lutescens*.

**Craterellus minor** N.K. Zeng, Y.Z. Zhang, P. Zhang & Zhi Q. Liang, sp. nov. Figures 6E,F, 8 MycoBank: MB841974.

**Diagnosis:** This species is distinguished from others in *Craterellus* by its very small-sized basidioma, a grayish yellow pileus without dark pigments, a veined hymenophore, a lemon-yellow stipe, and the presence of clamp connections in all parts of the basidioma.

**Etymology:** Latin “*minor*”, refers to very small-sized basidioma of the new species.

**Holotype:** CHINA. Hunan Province: Sangzhi County, Badagong Mountain, Tianping Mountain, elev. 750 m, 15
FIGURE 4 | Microscopic features of Craterellus aureus (FHMU2407). (A) Basidiospores. (B) Basidia. (C) Pileipellis. Scale bars = 10 µm. Drawings by Y.-Z. Zhang.

FIGURE 5 | Microscopic features of Craterellus fulviceps (FHMU6553, holotype). (A) Basidiospores. (B) Basidia. (C) Pileipellis. Scale bars = 10 µm. Drawings by Y.-Z. Zhang.

September 2020, P. Zhang MHHNU32505 (FHMU6554). GenBank accession number: 28S = OL439684, ITS = OL439553.

**Basidiomata** very small-sized. **Pileus** about 1.7 cm in diam, center strongly depressed; margin inrolled, with irregular small crenulate; surface dry, grayish-yellow (1B2); context very thin, white or whitish (2A1). **Hymenophore** veined, decurrent; folds about 0.1 cm broad, forking gill-folds, white to pale (5A1). **Stipe** 2.6 × 0.3 cm, central, hollow, cylindrical, slightly concave and curved in the middle; surface dry, pale lemon yellow (1A4) with white base (3A1). **Odor** indistinct. **Spore print** not obtained.

**Basidiospores** [40/1/1] (8–)8.5–9.4–10.5 × 7–7.7–8.5 µm, Q = (1.07–)1.12–1.4, Qm = 1.23 ± 0.08, ellipsoid to broadly ellipsoid, smooth, inamylloid, slightly thick-walled (up to 0.5 µm), yellowish in KOH. **Basidia** 56–75 × 8–13 µm, long, narrow, subcylindrical, slightly thick-walled (up to 0.5 µm), 2–5-spored, yellowish in KOH; sterigmata 4.5–8 µm in length. **Cystidia** absent. **Pileipellis** a cutis composed of mostly cylindrical, 5–10 µm wide, slightly thick-walled (up to 0.5 µm) hyphae, faintly pale yellow in KOH; terminal cells 35–85 × 5–7 µm, subcylindrical to subclavate with obtuse apex. **Clamp connections** present in all parts of the basidioma.

Habitat: Solitary to scattered on the ground of forests dominated by fagaceous trees.

Known distribution: Central China (Hunan Province).

Notes: The new collection from central China phylogenetically clustered with one specimen labeled as *C. melanoxeros* (Desm.) Pérez-De-Greg (420526MF0891) also from China with strong statistical support (Figure 2). The Chinese species is morphologically related to European *C. melanoxeros* (SS576). However, *C. melanoxeros* has a large basidioma, a presence of dark pigments, and narrower basidiospores (Dahlman et al., 2000; Akata and Kumbasli, 2014).

Craterellus parvopullus N.K. Zeng, Y.Z. Zhang & Zhi Q. Liang, sp. nov. Figures 6G–I, 9 MycoBank: MB841977.

Diagnosis: This species is distinguished from others in *Craterellus* by its basidioma without any obvious demarcation between pileus and stipe, a blackish brown to blackish pileus, a smooth grayish hymenophore, subglobose to ellipsoid or broadly ellipsoid basidiospores, hyphae in pileipellis more or less inflated, but obviously slender in terminations, an absence of clamp connections in all parts of the basidioma, and it is associated with the trees of Dipterocarpaceae.

Etymology: Latin “parvo,” meaning small, and “pullus,” meaning blackish, refer to the small and blackish pileus of our new species.

Holotype: CHINA. Hainan Province: Wanning County, Bofangling, elev. 80 m, 29 August 2020, N.K. Zeng4913 (FHMU6555). GenBank accession number: 28S = OL439685, ITS = OM334829.
Basidiomata very small to small-sized. Pileus 1.8–4.6 cm diam, infundibuliform; margin slightly incurved, wavy, irregularly folded; surface dry, blackish brown (6F7) to black (5F1); context very thin, grayish (1E1). Hymenophore smooth to slightly folded, ashen gray (4B1). Pileus 1.8–4.6 cm diam, infundibuliform; margin slightly incurved, wavy, irregularly folded; surface dry, blackish brown (6F7) to black (5F1); context very thin, grayish (1E1). Hymenophore smooth to slightly folded, ashen gray (4B1). Stipe 1.2–2.6 × 0.15–0.4 cm, confluent with pileus, hollow; surface dry, ashen gray (4B1); context very thin, grayish (1E1). Odor not distinctive. Spore print not obtained.

Basidiomata very small to small-sized. Pileus 1.8–4.6 cm diam, infundibuliform; margin slightly incurved, wavy, irregularly folded; surface dry, blackish brown (6F7) to black (5F1); context very thin, grayish (1E1). Hymenophore smooth to slightly folded, ashen gray (4B1). Stipe 1.2–2.6 × 0.15–0.4 cm, confluent with pileus, hollow; surface dry, ashen gray (4B1); context very thin, grayish (1E1). Odor not distinctive. Spore print not obtained.

Basidiomata very small to small-sized. Pileus 1.8–4.6 cm diam, infundibuliform; margin slightly incurved, wavy, irregularly folded; surface dry, blackish brown (6F7) to black (5F1); context very thin, grayish (1E1). Hymenophore smooth to slightly folded, ashen gray (4B1). Stipe 1.2–2.6 × 0.15–0.4 cm, confluent with pileus, hollow; surface dry, ashen gray (4B1); context very thin, grayish (1E1). Odor not distinctive. Spore print not obtained.

Basidiomata very small to small-sized. Pileus 1.8–4.6 cm diam, infundibuliform; margin slightly incurved, wavy, irregularly folded; surface dry, blackish brown (6F7) to black (5F1); context very thin, grayish (1E1). Hymenophore smooth to slightly folded, ashen gray (4B1). Stipe 1.2–2.6 × 0.15–0.4 cm, confluent with pileus, hollow; surface dry, ashen gray (4B1); context very thin, grayish (1E1). Odor not distinctive. Spore print not obtained.

Basidiomata very small to small-sized. Pileus 1.8–4.6 cm diam, infundibuliform; margin slightly incurved, wavy, irregularly folded; surface dry, blackish brown (6F7) to black (5F1); context very thin, grayish (1E1). Hymenophore smooth to slightly folded, ashen gray (4B1). Stipe 1.2–2.6 × 0.15–0.4 cm, confluent with pileus, hollow; surface dry, ashen gray (4B1); context very thin, grayish (1E1). Odor not distinctive. Spore print not obtained.

Basidiomata very small to small-sized. Pileus 1.8–4.6 cm diam, infundibuliform; margin slightly incurved, wavy, irregularly folded; surface dry, blackish brown (6F7) to black (5F1); context very thin, grayish (1E1). Hymenophore smooth to slightly folded, ashen gray (4B1). Stipe 1.2–2.6 × 0.15–0.4 cm, confluent with pileus, hollow; surface dry, ashen gray (4B1); context very thin, grayish (1E1). Odor not distinctive. Spore print not obtained.

Basidiomata very small to small-sized. Pileus 1.8–4.6 cm diam, infundibuliform; margin slightly incurved, wavy, irregularly folded; surface dry, blackish brown (6F7) to black (5F1); context very thin, grayish (1E1). Hymenophore smooth to slightly folded, ashen gray (4B1). Stipe 1.2–2.6 × 0.15–0.4 cm, confluent with pileus, hollow; surface dry, ashen gray (4B1); context very thin, grayish (1E1). Odor not distinctive. Spore print not obtained.

Basidiomata very small to small-sized. Pileus 1.8–4.6 cm diam, infundibuliform; margin slightly incurved, wavy, irregularly folded; surface dry, blackish brown (6F7) to black (5F1); context very thin, grayish (1E1). Hymenophore smooth to slightly folded, ashen gray (4B1). Stipe 1.2–2.6 × 0.15–0.4 cm, confluent with pileus, hollow; surface dry, ashen gray (4B1); context very thin, grayish (1E1). Odor not distinctive. Spore print not obtained.

Basidiomata very small to small-sized. Pileus 1.8–4.6 cm diam, infundibuliform; margin slightly incurved, wavy, irregularly folded; surface dry, blackish brown (6F7) to black (5F1); context very thin, grayish (1E1). Hymenophore smooth to slightly folded, ashen gray (4B1). Stipe 1.2–2.6 × 0.15–0.4 cm, confluent with pileus, hollow; surface dry, ashen gray (4B1); context very thin, grayish (1E1). Odor not distinctive. Spore print not obtained.

Basidiomata very small to small-sized. Pileus 1.8–4.6 cm diam, infundibuliform; margin slightly incurved, wavy, irregularly folded; surface dry, blackish brown (6F7) to black (5F1); context very thin, grayish (1E1). Hymenophore smooth to slightly folded, ashen gray (4B1). Stipe 1.2–2.6 × 0.15–0.4 cm, confluent with pileus, hollow; surface dry, ashen gray (4B1); context very thin, grayish (1E1). Odor not distinctive. Spore print not obtained.
grow in temperate regions (Cao et al., 2021b); all of them are not associated with trees of Dipterocarpaceae (Cao et al., 2021a,b). Moreover, *C. atrobrunneolus* has smaller basidiospores measuring (6.2–)6.5–7.8(–8) × (4.2–)4.5–6(–6.2) µm (Cao et al., 2021a); *C. badiogriseus* has larger basidiospores measuring (7.5–)8–10.5(–11) × (6.5–)6.8–7.5(–8) µm, and a pileipellis composed of thick-walled hyphae without slender terminations (Cao et al., 2021b); *C. croceialbus* has a brown pileus with an orange-white margin, larger basidiospores measuring (9–)10–12(–12.5) × (6.5–)6.8–8(–8.2) µm, and a pileipellis composed of hyphae without slender terminations (Cao et al., 2021b); *C. macrosporus* has a brown pileus, larger basidiospores measuring (12.5–)12.8–14.5(–15) × (8.8–)9–11(–11.5) µm, and a pileipellis composed of thin-walled hyphae without slender terminations (Cao et al., 2021b); *C. squamatus* has a squamulose pileus, larger basidiospores measuring (11.5–)12–13.8(–14) × (8.2–)8.5–9.5(–10) µm, and a pileipellis composed of thick-walled hyphae without slender terminations (Cao et al., 2021b).

Besides the five species found in China, Malaysian *C. cornucopioides* var. *mediosporus* Corner and *C. verrucosus* Massée, European *C. cornucopioides*, North American *C. atrocinereus* D. Arora & J.L. Frank, *C. calicornucopioides* D. Arora & J.L. Frank and *C. fallax* A.H. Sm are also morphologically similar to *C. parvopullus*. However, *C. verrucosus* has a rugulose hymenophore, larger basidiospores measuring 8–10 × 6.5–8 µm, and wider hyphae (up to 20 µm) more or less vertically arranged in the pileipellis (Corner, 1966); *C. cornucopioides* var. *mediosporus* has larger basidiospores measuring 8–10 × 6.5–7.5 µm, and a pileipellis composed of uninflated hyphae (Corner, 1966); *C. cornucopioides* s.s. has larger basidiospores measuring (7–)11–15(–20) × (5–)7(–11) µm, and its distribution in temperate areas (Pilz et al., 2003); *C. atrocinereus* has larger basidiospores measuring 8–10 × 4.5–6 µm, a prominently folded, distinctly thick hymenium, and groups on the ground under hardwoods, especially *Quercus* and *Neolithocarpus* (Frank, 2015); *C. calicornucopioides* has larger basidiospores measuring 11–14 × 8–10 µm, a presence of abundant clamp connections, and is mainly distributed with *Quercus*, *Arctostaphylos*, *Vaccinium* and *Arbutus* (Frank, 2015); *C. fallax* has larger basidiospores measuring 10–13 × 7–9 µm, and is mainly distributed in a broad host range, including Pinaceae (*Pinus* and *Tsuga*) and Fagaceae (*Quercus* and *Castanea*) (Matheny et al., 2010). Phylogenetically, *C. parvopullus* is not closely related to *C. atrobrunneolus*, *C. atrocinereus*, *C. calicornucopioides*, *C. cornucopioides*, and *C. fallax* (Figure 2).

**Key to Known Craterellus Species in China**

1. Without any obvious demarcation between pileus and stipe
2. Pileus vivid yellow to orange

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**FIGURE 7** | Microscopic features of *Craterellus lutescens* (FHMU6544). (A) Basidiospores. (B) Basidia. (C) Pileipellis. Scale bars = 10 µm. Drawings by Y.-Z. Zhang.

**FIGURE 8** | Microscopic features of *Craterellus minor* (FHMU6554, holotype). (A) Basidiospores. (B) Basidia. (C) Pileipellis. Scale bars = 10 µm. Drawings by Y.-Z. Zhang.
8. Basidiomata brown, yellow, hyphal clamp connections
9. Pileus brown, hymenophore veined, sometimes smooth..............................................................C. lutescens
9. Pileus fulvous, grayish-yellow, hymenophore veined, never smooth..............................................10
10. Stipe egg-yolk yellow..............................................................C. fulviceps
10. Stipe pale lemon yellow..............................................................C. minor

DISCUSSION

Craterellus cornucopioides and Craterellus tubaformis Complexes

Craterellus cornucopioides, originally described in Europe, was previously considered a widely distributed species (Akata and Kumbasli, 2014). However, recent studies have indicated that C. cornucopioides represents a species complex rather than a single widespread species (Dahlman et al., 2000). Our molecular phylogenetic data also show that specimens identified as C. cornucopioides were present in several different parts of the tree (Figure 2). Interestingly, collections of C. cornucopioides from Europe were present in more than one part of the tree (Figure 2). The species concept of C. cornucopioides should be confirmed by obtaining collections and DNA sequences from the holotype locality. Craterellus cornucopioides s. str. likely occurs in fewer areas of Europe; one specimen identified as C. cornucopioides from Tibet, western China (Lineage 8 in Figure 2), might represent another species. Craterellus tubaformis was also present in several parts of the tree (Figure 2), which indicates that C. tubaformis represents a species complex rather than a single widespread species; the collections identified as C. tubaformis in China from previous studies should be re-evaluated.

Species Diversity of Craterellus in China

High species diversity of Craterellus in China was revealed in this study, with fourteen species-level lineages identified (Figure 2). Three lineages (3, 11, and 12) were described as new species, viz. C. minor, C. parvopullus, and C. fulviceps. Eight lineages (1, 4–7, 9, 10, and 14) represent previously described species, viz. C. albidus, C. atrobrunneolus, C. aureus, C. badiogriseus, C. croceialbus, C. lutescens, C. macrosporus, and C. squamatus. Three lineages (2, 8, and 13) remain undescribed because of insufficient materials. Five additional species have been reported from China, viz. C. cornucopioides, C. cornucopioides var. parvisporus, C. luteus, C. odoratus, and C. tubaformis. Craterellus luteus is a synonym of C. aureus, and the occurrence of C. cornucopioides, C. cornucopioides var. parvisporus, C. odoratus, and C. tubaformis has not yet been confirmed in China.

Phylogenetic Relationships and Geographic Divergence of Craterellus

Our molecular phylogenetic data based on two-locus DNA sequences (28S + ITS) with a large number of collections from China have uncovered useful information regarding the phylogeny and geography of Craterellus. Our data indicate
that the affinities of *Craterellus* species between China and Europe, North America, and Australia are evident (Figure 2); for example, *C. lutescens* (Lineage 14 in Figure 2) is found in China, Europe, and North America; *C. badiogriseus* (Lineage 9 in Figure 2) is associated with one specimen (LMAC6b-09) from Europe; *C. aureus* (Lineage 1 in Figure 2), and two Chinese specimens (FHMU6551 and FHMU6552) (Lineage 2 in Figure 2) of *Craterellus* are closely related to North American *C. odoratus; C. parvopullus* (Lineage 3 in Figure 2) is closely related to two specimens (GMB-2014 MEL:2382717 and GMB-2014 MEL:2383015) from Australia; *C. macrosporus* (Lineage 6 in Figure 2), *C. squamatus* (Lineage 5 in Figure 2), and two North American specimens (NC-8338 and FLAS-F-60401) labeled as C. sp. and *C. fallax*, respectively, are in the same clade; a Chinese specimen (ECM90) labeled as C. sp. (Lineage 13 in Figure 2) is closely related to one collection (M66A9) from Mexico. Moreover, *C. fulviceps* (lineage 11 in Figure 2) is found in China and Japan; *C. parvopullus* (Lineage 3 in Figure 2) is associated with two specimens (LAM 0254 and AWW263) from Malaysia.

We also noted that there is little or no statistical support in some deeper nodes of the phylogeny, although the molecular data provided new insights into the phylogeny and geography of *Craterellus* with a large number of collections from China included. In the future, with more genes investigated and more *Craterellus* species discovered, a molecular phylogenetic tree of *Craterellus* should be constructed on the basis of the present data, which will provide more interesting information.

**DISCLOSURE**

All the experiments undertaken in this study comply with the current laws of the People’s Republic of China.

**DATA AVAILABILITY STATEMENT**

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: National Center for Biotechnology Information (NCBI) GenBank, https://www.ncbi.nlm.nih.gov/genbank/, OL439672–OL439687, OM334827–OM334829, OL439545–OL439553, OM469019–OM469020 and MycoBank, https://www.mycobank.org/, MB841969, MB841974, MB841977.

**AUTHOR CONTRIBUTIONS**

Z-QL and N-KZ: conceptualization and writing—original draft preparation. Y-ZZ: methodology, performing the experiment, and formal analysis. N-KZ, PZ, L-PT, Z-HC, M-SS, Y-JH, H-YH, and W-HZ: resources. N-KZ, BB, Z-QL, PZ, H-YH, and W-HZ: writing—review and editing. N-KZ and Z-QL: supervision. N-KZ: project administration and funding acquisition. All authors contributed to the article and approved the submitted version.

**FUNDING**

This study was supported by the National Natural Science Foundation of China (No. 32160001).

**ACKNOWLEDGMENTS**

We are very grateful to Professor Z. L. Yang, Kunming Institute of Botany, Chinese Academy of Sciences, and H. S. Yuan, Institute of Applied Ecology, Chinese Academy of Sciences, for providing valuable literature; G. Lu, L. X. Yuan, and L. Li, Haikou Duotan Wetlands Institute, the forest rangers of Liji Qingpilin Nature Reserve of Hainan and Hainan Tropical Rainforest National Park, for their help during the field investigations. We would like to thank TopEdit (www.topeditisci.com) for linguistic assistance during the preparation of this manuscript.

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The handling editor BD declared a past co-authorship with the author BB.

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