Multigene Phylogeny and Morphology Reveal Unexpectedly High Number of New Species of *Cantharellus* Subgenus *Parvocantharellus* (Hydnaceae, Cantharellales) in China

Ming Zhang ¹, Chao-Qun Wang ¹, Bart Buyck ², Wang-Qiu Deng ¹ and Tai-Hui Li ¹,*

¹ 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 510070, China; zhangming_1985@163.com (M.Z.); dayangtutu@163.com (C.-Q.W.); dengwq@gdim.cn (W.-Q.D.)
² Institut Systématique, Evolution, Biodiversité (ISYEB), UMR 7205, Muséum National d’Histoire Naturelle, Sorbonne Université, CNRS, Case Postale 39, 12 rue Buffon, F-75005 Paris, France; bart.buyck@mnhn.fr

* Correspondence: lith@gdim.cn

Abstract: The genus *Cantharellus*, commonly known as chanterelles, has recently been divided into six subgenera; however, wider sampling approaches are needed to clarify the relationships within and between these groups. A phylogenetic overview of *Cantharellus* subgenus *Parvocantharellus* in China was inferred based on the large subunit nuclear ribosomal RNA gene (nrLSU), the DNA-directed RNA polymerase II subunit 2 (rpb2), and the transcription elongation factor 1-alpha (tef1). A total of nine species from China were assigned to the subgenus, including seven novel species, namely *Cantharellus aurantinus*, *C. austrosinensis*, *C. galbanus*, *C. luteolus*, *C. luteovirens*, *C. miniobalus*, and *C. sinominior*, and two known species, namely *C. albus* and *C. zangii*. The detailed descriptions and illustrations were provided based on the newly obtained data, with the comparisons to closely related species. *C. zangii* was restudied based on the paratype specimens and multiple new collections from the type locality. Furthermore, the Indian species *C. sikkimensis* was identified as a synonym of *C. zangii* based on the morphological and molecular analyses. A key to the Chinese species belonging to the subg. *Parvocantharellus* is also provided.

Keywords: chanterelles; molecular phylogeny; morphology; seven new taxa; taxonomy

1. Introduction

*Cantharellus* Adans. ex Fr., typified by *C. cibarius* Fr., is an important genus of wild edible mushrooms and is renowned for its high culinary, economic, and ecological value. Chantarelles have a global distribution and are especially rich in subtropical to tropical zones, demonstrating ectomycorrhizal associations with a variety of plants [1]. Approximately 300 species have been estimated to exist worldwide, and nearly 180 species have been described thus far [1,2]. *Cantharellus* species possess a colourful pileus, nearly smooth to evidently lamellate-folded hymenophore with variously forked or anastomosing veins, and smooth basidiospores [1,3,4]. It is easy to recognise *Cantharellus* species at the genus level in the field solely based on their morphological features. However, the determination of their taxonomic positions at the species level is extremely complicated owing to overlaps in phenotypic variation among species. With the development of molecular biology, molecular-based studies have provided a basis for species identification and taxonomic development, especially for the molecular review of some type specimens and for re-classification of some old species based on new collections, so as to make species recognition more effective and accurate [5–10]. Molecular phylogenetic studies have delimited several species and revealed an unexpected species diversity. The tef1 gene has been identified as a suitable DNA barcoding marker to determine terminal relationships among closely related *Cantharellus* species [1,6,11–14].
Recently, within the genus *Cantharellus*, six subgenera (subg. *Afrocantharellus* Eyssart. & Buyck, subg. *Cantharellus* Adans. ex Fr., subg. *Cinnabarinus* Buyck & V. Hofst., subg. *Parrocantharellus* Eyssart. & Buyck, subg. *Pseudocantharellus* Eyssart. & Buyck, and subg. *Rubrinus* Eyssart. & Buyck) were proposed based on a phylogenetic analysis of widely distributed samples [1]. The subgenus *Parrocantharellus*, typified by *C. romagnesianus* Eyssart. & Buyck, was described as a monophyletic assemblage of mostly markedly small, yellow, orange, pink, or red species, presenting with a lilac-purple or brownish tinge in certain cases, particularly in the pileus centre, and exhibiting principally thin-walled hyphal endings and abundant clamp connections [1,15]. Species in subg. *Parrocantharellus* are mainly distributed in the northern hemisphere [16].

The names of the European and American species, such as *C. cibarius* Fr., *C. cinnabarinus* Schwein., and *C. minor* Peck, are often misapplied in Chinese samples, and a large number of undescribed taxa exist in China [17,18]. Thus far, only the following 10 species have been originally described from China: *C. albus* S.P. Jian & B. Feng, *C. hainanensis* N.K. Zeng, Zhi Q. Liang & S. Jiang, *C. hygrophoroides* S.C. Shao, Buyck & F.Q. Yu, *C. macrocarpus* N.K. Zeng, Y.Z. Zhang & Zhi Q. Liang, *C. phloginus* S.C. Shao & P.G. Liu, *C. tuberculosporus* M. Zang, *C. vaginatus* S.C. Shao, X.F. Tian & P.G. Liu, *C. versicolor* S.C. Shao & P.G. Liu, *C. yunnanensis* W.F. Chiu, and *C. zangii* X.F. Tian, P.G. Liu & Buyck [2,19–27].

In our survey of the species diversity of *Cantharellus* in China, we discovered some distinct *Cantharellus* samples. The subsequent morphological and molecular analyses of their *tef1* and LSU + *tef1* + *rpb2* gene sequences confirmed that these samples belong to the subg. *Parrocantharellus*, representing nine independent species, including seven new species, which are described and illustrated herein.

2. Materials and Methods

2.1. Morphological Studies

Photographs of the basidiomata were taken in the field before they were collected. The macro-morphological descriptions were based on field notes and colour photographs. The colour codes that were used followed Kornerup and Wanscher [28]. The microscopic measurements were carried out on dried tissue sections that were stained with 5% KOH and 1% aqueous Congo red under a light microscope (Olympus BX51, Tokyo, Japan) with magnification up to 1000×. For basidiospore descriptions, the abbreviation [n/m/p] denotes n spores measured from m basidiomata of p collections; the notation (a–)b–c(–d) describes the basidiospore dimensions, where the range ‘b–c’ represented 90% or more of the measured values and ‘a’ and ‘d’ are the extreme values; \(L_m\) and \(W_m\) indicate the average length and width (±standard deviation) of the measured basidiospores, respectively; the Q value refers to the length/width ratio of an individual basidiospore; and \(Q_m\) refers to the average Q value of all of the measured basidiospores ± standard deviation. All of the line-drawings of the microstructures were made free-hand and were based on the rehydrated materials. The studied specimens were deposited in the Fungarium of Guangdong Institute of Microbiology (GDGM).

2.2. DNA Extraction, PCR Amplification and Sequencing

The 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 LR0R/LR7 [29], *tef1F/tef1R* or *tef-1Fcanth/tef-1Rcanth* [1,30] and *RPB2-5FCanth/RPB2-7cRCanth* [1] were used to amplify the LSU, *tef1*, and *rpb2* genes, respectively. The PCR reactions were performed in a total volume of 25 \(\mu\)L containing 0.5 \(\mu\)L template DNA, 11 \(\mu\)L distilled water, 0.5 \(\mu\)L of each primer, and 12.5 \(\mu\)L PCR mix [DreamTaq™ Green PCR Master Mix (2×), Fermentas, USA]. The 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 60 s, annealing at 53 °C (LSU) /50 °C (tef1) /52 °C (rpb2) for 60 s, and extension at 72 °C for 60 s; with a final extension at 72 °C for 8 min.
The PCR products were electrophoresed on a 1% agarose gel with known standard DNA markers and the sequencing was performed on an ABI Prism® 3730 Genetic Analyzer (PE Applied Biosystems, Foster, CA, USA) at the Beijing Genomic Institute using the same primers. The raw sequences were assembled with SeqMan implemented in Lasergene v7.1 (DNASTAR, Madison, USA). The newly generated sequences in this study were submitted to GenBank.

2.3. Phylogenetic Analyses

Data on the generated sequences and the homologous sequences that were downloaded from GenBank were used to reconstruct the phylogenetic trees. Detailed sample information, including species names, voucher specimens, localities, GenBank accession numbers, and references, are listed in Table 1. The sequences of the three loci (LSU, tef1, and rpb2) were separately aligned using MAFFT [31] and examined in Bioedit v7.0.9 [32]. Missing sequences were coded as “N”, and the ambiguously aligned bases and introns of the protein-coding genes were retained in the final analyses. The final sequence alignments were deposited in TreeBase (ID 28589).

Table 1. Information on the specimens that were used in the phylogenetic analyses. Sequences that were newly generated in this study are indicated in black bold.

| Taxa                  | Voucher | Locality       | GenBank Accession No. | Reference  |
|-----------------------|---------|----------------|-----------------------|------------|
| Cantharellus afrocarthus | BB 96.236   | Zambia         | KF294669 JX192994 KF294747 | [5]        |
| C. afrocarthus        | BB 96.235   | Zambia         | KF294668 JX192993 KF294746 | [5]        |
| C. albicolutescens    | BB 08.070   | Madagascar     | KF294646 JX192982 KF294723 | [5]        |
| C. albidosquamosus    | PC0142511   | Cameroon       | MT002285 MT002270 MT004806 | [33]       |
| C. alborafescens      | AH44223     | Spain          | KR677531 KX828816 KX828735 | [34]       |
| C. albus              | HKAS107047  | China          | MT782542 MT776017 MT776013 | [2]        |
| C. albus              | HKAS107045  | China          | MT782540 MT776015 MT776012 | [2]        |
| C. albus              | GDGM56646   | China          | MZ605071 MZ613974 MZ614019 Present study |
| C. albus              | GDGM81299   | China          | MZ605074 MZ613977 MZ614022 Present study |
| C. albus              | GDGM81064   | China          | MZ605073 MZ613976 MZ614021 Present study |
| C. albus              | GDGM77819   | China          | MZ605072 MZ613975 MZ614020 Present study |
| C. altipes            | BB 07.019    | USA            | KF294627 GQ914939 KF294702 | [1]        |
| C. appalachiensis     | GRSM77088   | USA            | DQ898690 – – DQ898748 | [35]       |
| C. appalachiensis     | BB 07.123    | USA            | KF294635 GQ914979 KF294711 | [1]        |
| C. aurantinus         | GDGM46278   | China          | MZ766517 MZ766560 Present study |
| C. aurantinus         | GDGM46279   | China          | MZ766518 MZ766561 MZ766571 Present study |
| C. aurantinus         | GDGM84974   | China          | MZ766521 MZ766564 MZ766572 Present study |
| C. aurantinus         | GDGM84978   | China          | MZ766522 MZ766565 Present study |
| C. aurantinus         | GDGM81889   | China          | MZ766519 MZ766562 MZ766574 Present study |
| C. aurantinus         | GDGM81899   | China          | MZ766520 MZ766563 MZ766573 Present study |
| C. austrosinensis     | GDGM60305   | China          | MZ605077 MZ613980 MZ614023 Present study |
| C. austrosinensis     | GDGM79507   | China          | MZ605078 MZ613981 MZ614024 Present study |
| C. austrosinensis     | GDGM81303   | China          | MZ605084 MZ613986 MZ614029 Present study |
| C. austrosinensis     | GDGM81249   | China          | MZ605082 MZ613983 MZ614027 Present study |
| C. austrosinensis     | GDGM80616   | China          | MZ605081 MZ613982 MZ614026 Present study |
| C. austrosinensis     | GDGM80211   | China          | MZ605080 MZ613984 MZ614025 Present study |
| C. austrosinensis     | GDGM81381   | China          | MZ605086 MZ613988 MZ614031 Present study |
| C. austrosinensis     | GDGM81379   | China          | MZ605085 MZ613987 MZ614030 Present study |
| C. austrosinensis     | GDGM81271   | China          | MZ605083 MZ613985 MZ614028 Present study |
| C. austrosinensis     | GDGM82877   | China          | MZ605088 MZ613990 MZ614033 Present study |
| C. austrosinensis     | GDGM80151   | China          | MZ605079 – – – Present study |
| C. austrosinensis     | GDGM81985   | China          | MZ605087 MZ613989 MZ614032 Present study |
| C. avellaneus         | 1217/ER     | Madagascar     | KX857093 – – KX856997 | [17]       |
| C. cerinoalbus        | AV 06.051   | Malaysia       | KF294663 KF294741 | [1]        |
| C. cibarius           | GE 07.025   | France         | KF294658 GQ914949 KF294736 | [1]        |
## Table 1. Cont.

| Taxa            | Voucher | Locality          | GenBank Accession No.               | Reference |
|-----------------|---------|-------------------|-------------------------------------|-----------|
|                 |         |                   | LSU | tef1  | rpb2 |               |
| C. cibarius     | BB 07.300 | Slovakia         | KF294641 | GQ919490 | KF294718 | [1] |
| C. cinnabarinus | BB 07.053 | USA              | KF294630 | GQ919484 | KF294705 | [1] |
| C. cinnabarinus | BB 07.001 | USA              | KF294624 | GQ919485 | KF294698 | [1] |
| C. congolensis  | 1645/BB16.044 | Saharan Africa | KX857102 | KX857075 | KX857006 | [17] |
| C. congolensis  | 1676/BB16.123 | Saharan Africa | KX857106 | KX857078 | KX857010 | [17] |
| C. aff. congolensis | BB 06.176 | Madagascar | KF294606 | – | KF294680 | [1] |
| C. aff. congolensis | BB 06.197 | Madagascar | KF294608 | – | KF294683 | [1] |
| C. curatus      | BRNM:825749 | South Korea | MW124390 | – | – | [33] |
| C. cyphelloides | TNS F-61721 | Japan          | NG059027 | – | – | [36] |
| C. decolorans   | BB 08.278 | Madagascar | KF294654 | GQ919498 | KF294731 | [1] |
| C. galbanus     | GDGM86249 | China           | ZM766516 | MZ766568 | MZ766577 | Present study |
| C. gueanensis   | 1517/MR | Guyane          | KX857095 | KX857061 | KX856999 | [17] |
| C. gueanensis   | 1501/MRG07 | Guyane        | KX857094 | KX857060 | KX856998 | [17] |
| C. parvoflavus  | BB 06.176 | Madagascar | KF294608 | – | KF294683 | [1] |
| C. parvoflavus  | BB 06.197 | Madagascar | KF294608 | – | KF294683 | [1] |
| C. luteolus     | GDGM44258 | China           | ZM766514 | MZ766566 | MZ766570 | Present study |
| C. luteolus     | GDGM60393 | China           | ZM766515 | MZ766566 | MZ766575 | Present study |
| C. luteolus     | GDGM86247 | China           | ZM766513 | MZ766567 | MZ766576 | Present study |
| C. luteovirens  | GDGM45899 | China           | MZ605095 | – | – | Present study |
| C. luteovirens  | GDGM80296 | China           | MZ605089 | MZ613991 | MZ614034 | Present study |
| C. luteovirens  | GDGM81395 | China           | MZ605093 | MZ613995 | MZ614037 | Present study |
| C. luteovirens  | GDGM81079 | China           | MZ605092 | MZ613994 | MZ614036 | Present study |
| C. luteovirens  | GDGM80672 | China           | MZ605090 | MZ613992 | MZ614035 | Present study |
| C. luteovirens  | GDGM80680 | China           | MZ605091 | MZ613993 | – | Present study |
| C. minioalbus   | GDGM78910 | China           | MZ605098 | MZ613999 | MZ614043 | Present study |
| C. minioalbus   | GDGM78934 | China           | MZ605102 | MZ614003 | MZ614047 | Present study |
| C. minioalbus   | GDGM78883 | China           | MZ605096 | MZ613997 | MZ614041 | Present study |
| C. minioalbus   | GDGM78901 | China           | MZ605097 | MZ613998 | MZ614042 | Present study |
| C. minioalbus   | GDGM78916 | China           | MZ605100 | MZ614001 | MZ614045 | Present study |
| C. minioalbus   | GDGM78915 | China           | MZ605099 | MZ614000 | MZ614044 | Present study |
| C. minioalbus   | GDGM78926 | China           | MZ605101 | MZ614002 | MZ614046 | Present study |
| C. minioalbus   | GDGM78955 | China           | MZ605103 | – | – | Present study |
| C. minioalbus   | GDGM78997 | China           | MZ605104 | – | – | Present study |
| C. minor        | BB 07.057 | USA              | KF294632 | JX192979 | KF294707 | [1] |
| C. minor        | BB 07.002 | USA              | KF294625 | JX192978 | KF294699 | [1] |
| C. pallens      | AH39124 | Morocco          | KX828804 | KX828834 | KX828735 | [9] |
| C. platyphyllos | BB 98.126 | Tanzania         | KF294620 | JX192975 | KF294694 | [1] |
| C. pseudominimus| JV 01.663 | Portugal        | KF294657 | JX192991 | KF294735 | [18] |
| C. rhodophyllus | BB 16.126 | Congo            | MK422958 | MG450965 | – | [10] |
| C. rhodophyllus | BB 16.006 | Congo            | MK422957 | MG450966 | – | [10] |
| C. romagnesianus | AH44218 | Spain            | KX828807 | KX828836 | KX828757 | [9] |
| C. roseofagetorum | AH44789 | Georgia         | KX828812 | KX828839 | KX828760 | [9] |
| C. sebosus      | BB 08.234 | Madagascar       | KF294652 | JX192986 | KF294729 | [1] |
| C. sikkimensis  | AB-2015 | India            | KP398966 | – | – | [39] |
| C. sinominor    | GDGM80791 | China           | MZ605106 | MZ614005 | MZ614049 | Present study |
| C. sinominor    | GDGM80788 | China           | MZ605105 | MZ614004 | MZ614048 | Present study |
| C. sinominor    | GDGM80842 | China           | MZ605107 | MZ614006 | MZ614050 | Present study |
| C. sinominor    | GDGM80885 | China           | MZ605108 | MZ614007 | MZ614051 | Present study |
| C. splendens    | BB 96.306 | Zambia           | KF294670 | – | KF294748 | [1] |
| C. subalbidus    | OSC81782 | USA              | KX828814 | KX828841 | KX828762 | [9] |
Table 1. Cont.

| Taxa                      | Voucher | Locality     | GenBank Accession No. | Reference |
|---------------------------|---------|--------------|-----------------------|-----------|
|                           |         |              | LSU                   | tef1      | rpb2       |           |
| C. aff. subcyanoxanthus   | BB 98.014 | Tanzania     | KF294615              | JX192973  | KF294689   | [1]       |
| C. subincarnatus subsp.   | BB 06.080 | Madagascar   | KF294602              | JX192963  | KF294676   | [1]       |
| rubrosalmonicus           | C. symoensii | Tanzania     | KF294619              | JX192974  | KF294693   | [1]       |
|                           | C. tabernensis | USA         | KF294634              | GQ914976  | KF294709   | [1]       |
|                           | C. tabernensis | USA         | KF294631              | GQ914974  | KF294706   | [1]       |
|                           | C. tenuithrix  | USA         | JN940600              | GQ914947  | KF294712   | [1,40]    |
|                           | C. texensis  | USA         | KF294626              | GQ914988  | KF294701   | [1]       |
|                           | C. texensis  | USA         | BB 07.018             | KF294626  | GQ914988   | KF294701   | [1]       |
|                           | C. tomentosus | Tanzania     | KF294672              | JX192955  | KF294750   | [1]       |
|                           | C. tricolor  | USA         | BB 06.180             | JN940604  | JX192969   | KF294682   | [1,7]     |
|                           | C. zangii    | China       | GDGM83171             | MZ605113  | MZ614012   | MZ614056   | Present study |
|                           | C. zangii    | China       | GDGM83173             | MZ605114  | MZ614013   | MZ614057   | Present study |
|                           | C. zangii    | China       | GDGM83186             | MZ605117  | MZ614016   | MZ614060   | Present study |
|                           | C. zangii    | China       | GDGM82399             | MZ605112  | MZ614011   | MZ614055   | Present study |
|                           | C. zangii    | China       | GDGM82389             | MZ605110  | MZ614009   | MZ614053   | Present study |
|                           | C. zangii    | China       | GDGM83176             | MZ605115  | MZ614014   | MZ614058   | Present study |
|                           | C. zangii    | China       | GDGM83181             | MZ605116  | MZ614015   | MZ614059   | Present study |
|                           | C. zangii    | China       | GDGM82393             | MZ605111  | MZ614010   | MZ614054   | Present study |
|                           | C. zangii    | China       | GDGM82374             | MZ605109  | MZ614008   | MZ614052   | Present study |
|                           | C. zangii    | China       | GDGM83193             | MZ605118  | MZ614017   | MZ614061   | Present study |
|                           | C. zangii    | China       | GDGM83228             | MZ605119  | MZ614018   | MZ614062   | Present study |
| Craterellus cornucopioides | AFTOL-ID 286 | USA         | –                     | DQ366287  | –          | [41]       |
| Cr. tubaeformis           | BB 07.293  | Slovakia     | KF294640              | GQ914989  | KF294717   | [1,11]     |

Phylogenetic analyses were performed following the methods that were described by Zhang et al. [42]. A maximum likelihood (ML) analysis was performed using RAxML v.7.2.6 [43] and Bayesian inference (BI) was performed using MrBayes 3.1.2 [44]. For both the ML and BI analyses, the most suitable substitution model for each gene partition was determined based on the Akaike Information Criterion (AIC) using MrModeltest v2.3 [45]. The default parameters were included for the ML analysis, except for selecting GTR+GAMMAI as the model, and the statistical data were obtained by performing rapid non-parametric bootstrapping with 1000 replicates. A BI analysis using four chains was conducted using 30 million generations and the stoprule command with stopval set to 0.01. Bayesian trees were sampled every 100 generations, the first 25% of the generations were discarded as a burn-in, and the Bayesian posterior probabilities (BPP) were calculated from the posterior distribution of the retained Bayesian trees. The bootstrap support (BS) of ≥50% in the ML tree and BPP of ≥0.90 indicated statistical significance. The phylogenetic trees were visualised using FigTree v1.4.23.

3. Results

3.1. Molecular Phylogeny

In the concatenated dataset (LSU + tef1 + rpb2), 304 sequences (108 for LSU, 101 for tef1, and 95 for rpb2) from 114 fungal collections were included. The alignment length was 3135 characters including gaps (1536 characters for LSU, 723 characters for tef1, and 876 characters for rpb2), of which 1847 characters were conserved, 226 were variable and parsimony-uninformative, and 1062 were parsimony-informative. *Craterellus cornucopioides* (L.) Pers. and *Cr. tubaeformis* were selected as outgroups based on recent studies [1,2,46]. The best models for the BI analysis of the concatenated dataset were GTR + I + G for LSU, K2P + I for tef1, and GTR + I for rpb2, respectively. The ML analysis resulted in a similar topology to the Bayesian analysis, and only the ML topology has been depicted in Figure 1.
Figure 1. The phylogenetic tree of the representative species of *Cantharellus* that was inferred from a multigene (LSU + *tef1* + *rpb2*) dataset by means of both ML and BI methods. *Craterellus cornucopioides* BB 07_293 and *Cr. tubaeformis* AFTOL ID_286 were used as outgroups. The maximum likelihood tree is depicted. The bootstrap supports (BS ≥ 50%) and Bayesian posterior probabilities (BPP ≥ 0.90) are shown on the supported branches. The species generated in this study are in black bold.
Phylogenetic analyses that were based on the multi-locus dataset (LSU + \textit{tef1} + \textit{rpb2}) showed that \textit{C. subg. Parvocantharellus} formed a distinct clade in the genus \textit{Cantharellus}, and seven new well-supported lineages were nested in this subgenus. Lineage I formed a well-supported terminal clade (100\% BS and 1.00 BPP) and was closely related to \textit{C. appalachiensis} R.H. Petersen and \textit{C. tabernensis} Feib. \& Cibula. Lineages II, III, and IV formed three isolated terminal branches with robust evidence (100\% BS and 1.00 BPP). Lineage V formed sister relationships with \textit{C. parvoflavus} M. Herrera, Bandala, \& Montoya and \textit{C. minor} Peck, and was also closely related to \textit{C. romagnesianus} Eyssart. \& Buyck. Lineage VI formed a sister relationship with \textit{C. albus} S.P. Jian \& B. Feng. Finally, Lineage VII was closely related to \textit{C. himalayensis} D. Kumari, Ram. Upadhyay \& Mod.S. Reddy and \textit{C. curvatus} Buyck, R. Ryoo \& Antonin. In addition, two known species, \textit{C. albus} and \textit{C. zangii}, that were originally reported from China, were strongly supported (100\% BS and 1.00 BPP) in the phylogenetic trees, but a sequence named \textit{C. sikkimensis} K. Das, Buyck, D. Chakr., Baghela, S.K. Singh \& V. Hofst. was clustered with \textit{C. zangii} in the multi-locus phylogenetic tree.

In the \textit{tef1} dataset, 74 sequences from the 18 species were selected for the phylogenetic analyses. The length of the dataset was 706 characters including gaps, of which 448 characters were conserved, 22 were variable and parsimony-uninformative, and 236 were parsimony informative. \textit{Cantharellus cinnabarinus} (Schwein.) Schwein. was selected as the outgroup based on the above multi-locus analyses. K2P + G4 was selected as the best model for BI. The ML and Bayesian analyses produced similar estimates of tree topologies, and only the tree that was inferred from the ML analysis is displayed (Figure 2). Species in the \textit{C. subg. Parvocantharellus} formed three main subclades but without significant support. The seven new lineages were also strongly revealed in the phylogenetic tree and generated similar results with the multi-locus phylogenetic analysis.
Figure 2. Phylogenetic tree of the representative species of the *Cantharellus* subgenus *Parvocantharellus* that was inferred from the *tef1* dataset by means of both ML and BI methods. *Cantharellus cinnabarinus* BB 07_001 is used as the outgroup. The maximum likelihood tree is depicted. Bootstrap supports (BS ≥ 50%) and Bayesian posterior probabilities (BPP ≥ 0.90) are shown on the supported branches. The species generated in this study are in black bold.
3.2. Taxonomy

*Cantharellus albus* in Jian, S.P.; Feng, B. Jian, Feng & Yang. *Phytotaxa* 2020, 470, 137; Figures 3a–c and 4.

Figure 3. Species of *Cantharellus* subg. *Parvocantharellus* from China. (a–c) *C. albus* (a) GDGM56646; (b) GDGM73460; (c) GDGM81399; (d–f) *C. aurantinus* (d) GDGM46278 holotype (e) GDGM46279; (f) GDGM81889; (g–j) *C. austrosinensis* (g) GDGM81249 holotype (h) GDGM80151; (i) GDGM80211; (j) GDGM80296.
Basidiomata small-sized. Pileus 18–42 mm broad, convex when young, then gradually to nearly applanate with a central shallow depression or broadly infundibuliform at maturity; surface dry, with appressed fibrillose squamules, white to yellowish white (4A1–4A2); margin wavy, incurved when young, decurved to slightly upturned at maturity, slightly changing to yellowish when handled, yellowish white to pale orange when dried (4A2–5A2, 4A3–5A3). Context white, 1–3 mm thick in the center of the pileus, sharply attenuate towards margin, unchanging or slightly changing to yellowish when cut. Hymenophore decurrent, close, poorly developed, composed of bifurcate and strongly interconnected low veins, usually less than 1 mm high, white to yellowish white, unchanging or slightly changing to yellowish when bruised. Stipe 20–60 × 2–8 mm, central, cylindrical or slightly tapering towards base, solid, smooth or with faintly scaly, concolourous with pileus, but in the lower part usually yellowish, slightly changing to yellowish when handled. All parts of basidioma becoming yellowish with 5% KOH solution. Odour milk fragrance, pleasant. Taste a little spicy.

**Figure 4.** Cantharellus albus (GDGM56646). (a) Basidia, basidiola and elements of the subhymenium. (b) Basidiospores. (c) Pileipellis. Bars: (a,b) = 10 μm; (c) = 20 μm.

Basidiospores (100/4/4) 5.5–7.5 × (4–) 4.5–6 μm, \( L_m \times W_m = 6.38 (±0.54) \times 4.89 (±0.38) \) μm, \( Q = (1.1) 1.2–1.45 (1.62) \), \( Q_m = 1.31 ± 0.11 \), broadly ellipsoid to subglobose, smooth,
guttulate. Basidia 43–60 × 8–12 µm, 4–6-spored, narrowly clavate, colourless to hyaline in KOH; sterigmata 3–5 µm long. Pilepellis a cutis with long, repent and occasionally interwoven hyphae, subcylindrical cells that are 5–13 µm wide, thin-walled. Stipitpellis a cutis of cylindrical, parallel hyphae, 3–9 µm wide. Clamp connections abundant in all tissues.

Habitat and distribution—Growing in groups or gregariously under Fagaceae plants [Castanopsis fissa (Champ. ex Benth., and Castanopsis sp.) Rehd. et Wils.], mixed with other broadleaf trees in subtropical broadleaf forests. Known from southwest and southern China.

Specimen examined—CHINA. Guangdong Province, Guangzhou City, Baiyunshan, National Forest Park, alt. 160 m, 14 May 2016, Ming Zhang (GDGM45932); Same location, 15 June 2018, Ming Zhang (GDGM73460); Same location, 15 June 2019, Yong He (GDGM56646); Same location, 27 August 2019, Yong He (GDGM77819).

Notes—Cantharellus albus was recently described from southwest China [2] and exhibits small white basidiomata and slightly changes to a yellowish colour when it is bruised or treated with 5% KOH solution. They have poorly-developed gill-like folds with strongly bifurcate and interconnected low veins, a distinct creamy aroma and a slightly spicy taste. They have a white-coloured basidiomata that changes to yellowish-white to pale orange colour when it is dried, and have broadly ellipsoid to subglobose basidiospores. The distinct morphological characteristics and the well-supported monophyletic lineage render it easily distinguished from other the Cantharellus species. In the present study, C. albus was redescribed based on the specimens that were from Guangdong province, which were compared to the description of C. albus in Jian et al. [2], and the macro- and micro-characteristics were almost identical. However, the size of the basidiospores in Jian’s specimens [6–8 × 5–7 µm, Lm × Wm = 6.9 (±0.48) × 5.92 (±0.62) µm] were larger than those in our specimens [5.5–7.5 × 4.5–6 µm, Lm × Wm = 6.38 (±0.54) × 4.89 (±0.38) µm]. The minor difference in the size of the basidiospores in Jian et al. [2] and the present study could be explained by small quantitative differences between the geographically distant populations or the number of measured basidiospores; this has often been noted in other Cantharellus species.

**Cantharellus aurantinus** Ming Zhang, Z.H. Zhang & T.H. Li sp. nov. Figures 3d–f and 5. MycoBank: MB840837.

Etymology—refers to the greyish-orange pileus colour.

Diagnosis—This species is characterized by its small basidiomata, light orange pileus, relatively well-developed hymenophore, and broadly ellipsoid basidiospores (6.5)7–9 × (4.5)5–6 µm in size.

Type—CHINA. Henan Province, Xinyang City, Nanwan Lake Scenic Area, 420 m, N 32°11′, E 113°96′, on soil in Castanopsis spp. dominated forests, 18 July 2016, Ming Zhang (GDGM46278).

Basidiomata small-sized. Pileus 15–40 mm broad, convex when young, then gradually to nearly applanate with a central shallow depression at maturity; surface dry, smooth, light yellow, light orange, greyish yellow to greyish orange (2A5–6A5, 2B5–6B5), margin even, incurved when young, decurved to slightly upturned at maturity, unchanged when handled. Context white to yellowish white, 1.5–2.5 mm thick in the center of the pileus, sharply attenuate towards margin, unchanged when exposed. Hymenophore decurrent, relatively well developed, composed of bifurcate and interconnected low veins, in particular toward the cap margin, usually less than 1 mm high, pale yellow (2A3–4A3), unchanged when bruised. Stipe 20–40 × 8–12 mm, central, cylindrical or slightly tapering towards base, solid, smooth or with faintly scaly, pale yellow to pale orange (2A3–5A3), unchanged when handled. Odour not distinct.
Figure 5. *Cantharellus aurantinus* (GDGM46278, Holotype!). (a) Basidia, basidiola and elements of the subhymenium. (b) Basidiospores. (c) Pileipellis. Bars: (a, b) = 10 μm; (c) = 20 μm.

Basidiospores (100/4/4) (6.5–)7–9 × (4.5–)5–6 μm, Lm × Wm = 7.95(±0.57) × 5.51(±0.42) μm, Q = (1.16)1.3–1.6(1.7), Qm = 1.45±0.13, broadly ellipsoid, smooth, guttulate. Basidia 48–70 × 8–10 μm, 4–6-spored, narrowly clavate, colourless to hyaline in KOH; sterigmata 3–8 μm long. Pileipellis a cutis with long, repent and occasionally interwoven hyphae, subcylindrical cells that are 5–10 μm wide, thin-walled, obtusely rounded at the top. Stipitipellis a cutis of cylindrical, parallel hyphae, 3–12 μm wide. Clamp connections abundant in all tissues.

Habitat and distribution—Growing in solitary or scattered under Fagaceae trees that are mixed with other broadleaf trees in subtropical broadleaf forests. Known from Henan and Jiangsu Province, China.

Specimen examined—CHINA. Henan Province, Xiyang City, Nanwan Lake Scenic Area, alt. 420 m, on soil under broadleaf forests, 18 July 2016, Ming Zhang (GDGM46279, GDGM46413). Jiangsu Province, Nangjing City, Tzu-chin Mountain Scenic Area, alt. 300 m, 5 September 2020, Zi-Han Zhang (GDGM81888, GDGM81889, GDGM81899); Same location,
Notes—The distinctive morphological features of *C. aurantinus* are the light orange to greyish-orange pileus, the pale yellow, gill-like folds with bifurcate and interconnected low veins, the broadly ellipsoid basidiospore, and the thin-walled hyphae of the pileipellis. The phylogenetic analyses supported *C. aurantinus* as an isolated lineage (Lineage VII) that is closely related to *C. curvatus* and *C. himalayensis*. However, *C. curvatus*, recently reported from South Korea, differs by its small and slender basidiomata, dull yellow to orangish-yellow pileus, and shorter basidia (42–55 × 9.5–12 µm) [33]. *Cantharellus himalayensis*, that is reported from India, differs by its large basidiomata, yellowish pileus with pecan-brown scales at the center, relatively small basidiospores (6–8 × 4.5–6 µm), and partially gelatinous pileipellis [38].

In the field, *C. aurantinus* is easily misidentified as *C. cibarius*, as both species share a yellow-orange pileus. However, *C. cibarius* belongs to the subg. *Cantharellus*, and differs by its relatively large basidiomata, well-developed hymenophore of up to 3 mm in depth, longer basidia (80–105 × 7–9 µm) and thick-walled pileipellis hyphae [9,18].

*Cantharellus austrosinensis* Ming Zhang, C.Q. Wang & T.H. Li sp. nov. Figures 3g–j and 6. MycoBank: MB840652.

Etymology—refers to the distribution of this species in southern China.

Diagnosis—This species is characterized by its small basidiomata, pastel yellow to greyish-yellow pileus with a greyish-orange to brownish-orange center, pale yellow to light yellow hymenophore that is composed of bifurcate and interconnected low veins, elliptical to broadly elliptical basidiospores 6–8 × 4.8–6 µm, and the thin-walled hymenophore of the pileipellis.

Type—CHINA. Guangdong Province, Shaoguan City, Renhua County, Danxiashan National Nature Reserve, alt. 199 m, on soil under *Pinus massoniana*, 4 June 2020, Ming Zhang (GDGM81249).

Basidiomata small-sized. Pileus 12–30 mm broad, planate with center depressed, not perforate, margin incurved when young, planate or slightly reflexed with age, obscure striated on surface; subfleshy to slightly membranous; surface dry, glabrous or tomentosus at central, pastel yellow, light yellow to greyish yellow at mass (3A5–5A5, 3B5–4B5), with a greyish orange to brownish orange center (5B5–6B5, 5C5–6C5), often with reddish brown tinge in some specimens (8D7–9D7). Context thin, 0.5–1.5 mm thick in the center of pileus, fibrous, pale yellow to light yellow (3A3–3A5), unchanging when bruised. Hymenophore decurrent, but with a clearly delimited from the stipe surface, gill-like, well or poorly developed, ridges 1–2 mm high, composed of bifurcate and interconnected low veins, pale yellow to light yellow (3A3–4A3, 3A5–4A5), unchanging when bruised. Stipe 10–40 mm long, 2–5 mm thick, subcylindrical, enlarged downward, smooth or with faintly scaly, hollow, concoloured with pileus, darker and more somber than lamellae. Odour not special. Taste mild.

Basidiospores (100/4/4) 6–8 × 4.8–6 µm, $L_m \times W_m = 7.05(\pm 0.51) \times 5.192(\pm 0.34)$ µm, $Q = (1.08)1.2–1.45(1.6)$, $Q_m = 1.36 \pm 0.097$, elliptical to broadly elliptical. Basidia 50–55 × 7–9 µm, clavate, with 5–6(-7) sterigmata. Pileipellis a cutis, composed of interwoven hyphae 5–12 µm in diam., colourless, thin-walled. Hymenophoral trama composed of cylindrical hyphae 7–10 µm in diam. Stipitipellis a cutis of cylindrical, parallel hyphae, 4–12 µm wide, branched, septate. Clamp connections abundant in all tissues.
Habitat and distribution—Solitary or scattered under *Pinus massoniana* Lamb. mixed with other broadleaf trees. Known from southern China.

Specimen examined—CHINA. Guangdong Province, Shaoguan City, Renhua County, Danxiashan National Natural Reserve, alt. 103 m, 1 May 2020, Ming Zhang (GDGM79507); same location, alt. 92 m, 5 June 2020, Li-Qiang Wu (GDGM81247); Feihuashui, alt. 152 m, 3 June 2020, Ming Zhang (GDGM81616); Guanyinshan, alt. 187 m, 27 May 2020, Ming Zhang (GDGM80151); Ruyuan County, Nanling National Natural Reserve, alt. 550 m, 10 June 2020, Ming Zhang (GDGM80211).

Notes—The presence of small basidiomata, a pastel yellow to greyish-yellow pileus with a greyish-orange to brownish-orange centre, thin-walled hyphae, and abundant clamp connections enable the classification and placement of *C. austrosinensis* in the subg. *Parocantharellus*. In the phylogenetic trees, the new species was closely related to *C. appalachiensis*,
C. koreanus Buyck, Antonín & Ryoo, and C. tabernensis. However, C. appalachiensis and C. tabernensis, that are both described from North America, can be distinguished by their relatively large and more robust basidiomata, with a pileus that is usually up to 50 mm in width. Additionally, C. appalachiensis differs in the existence of its drab yellow to dull brown pileus, its relatively large and narrow basidiospores (6.6–8.9 × 4.4–5.9 µm or 6–10.5 × 4–6 µm), and its association with oaks and other hardwoods [47,48]. Cantharellus tabernensis also differs in the presence of its dull orange-yellow to yellowish-brown pileus, vivid orange-yellow hymenophore, its well-developed gills that are up to 3 mm in depth, vivid orange-yellow stipe that is up to 8 mm in diameter, narrow basidiospores with a large Q value (1.49–1.52), and narrow hymenophoral trama hyphae (3–6 µm in diameter) [49]. Cantharellus koreanus, originally described from the temperate region of the Republic of Korea, differs in the presence of its dirty yellow-brown to pale brown pileus with a brown to dark brown centre, yellow to greyish stipe, relatively narrow basidiospores (4.2–5.5 µm in breadth), and its association with various deciduous trees (Carpinus laxiflora, Castanea crenata, and Quercus mongolica) mixed with coniferous trees (Pinus densiflora) [16]. In contrast, C. austrosinensis is distributed in subtropical regions of China and is currently only known to be associated with Pinus massoniana.

Cantharellus quercophilus Buyck, D.P. Lewis, Eyssart. & V. Hofst., belonging to the subg. Cantharellus, resembles a C. austrosinensis with small basidiomata, however, C. quercophilus, that was originally reported in the USA, differs in the presence of its pale brown to greyish-yellow pileus, cream to pale yellowish hymenophore that is sparsely forked, its greyish-buff with a lilac tinged context that changes to a yellow to reddish-brown colour when it is bruised, and its association with Quercus stellata [50].

Cantharellus galbanus Ming Zhang, C.Q. Wang & T.H. Li sp. nov. Figures 7a–c and 8. MycoBank: MB840835.

Etymology—refers to the greenish-yellow basidiomata.

Diagnosis—This species is characterized by its small basidiomata, greenish-yellow to yellow pileus, well-developed gill-like ridges that are usually forked at the margin, relatively small basidiospores 6–7.5 × 4.8–5.5 µm, and thin-walled hyphae of the pileipellis.

Type—CHINA. Hainan Province, Ledong County, Jianfengling National Nature Reserve, alt. 950 m, on soil under Fagaceae trees mixed with other broadleaf trees in tropical broadleaf forests, 13 July 2021, Ming Zhang (GDGM86249).
Figure 7. Species of Cantharellus subg. Parvocantharellus from China. (a-c) C. galbanus (a) GDGM86429 holotype! (b) GDGM43100; (c) GDGM60568); (d-f) C. luteolus (d) GDGM60393 holotype! (e,f) GDGM86247); (g–i) C. luteovirens (g,h) GDGM80672 holotype! (i) GDGM81079.
Basidiomata small-sized. Pileus 5–10 mm broad, convex when young, then gradually to nearly planate with a central shallow depression or finally broadly infundibuliform at maturity; surface dry, glabrous to subtomentos, hygrophanous when wet, greenish yellow (1A6), light yellow (1A5–3A5), yellow (2A6–2B6) to greyish yellow (2B5–3C5), margin incurved and irregularly wavy. Context less than 1 mm thick, yellowish, unchanging when bruised. Hymenophore distant, well developed, composed of decurrent and usually forked gill-folds, less than 1 mm depth, yellowish white to pale yellow (1A2–2A2, 1A3–2A3). Stipe 10–15 × 1–2 mm, cylindrical, or gradually slender towards base, central, hollow, surface smooth, slightly waxy, concolourous with pileus or paler to pastel yellow (1A4–2A4), greenish yellow to yellowish grey (1B2–2B2). Taste mild. Odour fruity.

Basidiospores (50/2/2) 6–7.5 × 4.8–5.5 μm, Lm × Wm = 6.77(±0.36) × 5.19(±0.32) μm, Q = (1.18)1.27–1.4, Qm = 1.31±0.07, elliptical to broadly elliptical, uniguttulate to multiguttulate, smooth, hyaline, inamyloid, with refringent contents. Basidia 52–76 × 7–8 μm, 4–6-spored, narrowly clavate with large number of vacuoles, sterigmata 4–6 μm long; basidiola 50–80 × 7–10 μm, numerous, clavate. Hymenial cystidia absent. Hymenophoral trama filamentous, composed of colourless and branched hyphae, hyphae up to 13 μm in diam., septate, thin-walled. Pileipellis a cutis, composed of horizontal to ascending, subparallel, cylindrical and branched, thin-walled hyphae arranged mostly in irregular pattern; septa clamped; terminal cells 5–17 μm wide, mostly cylindrical to subclavate, slightly appendiculate. Stipitipellis a cutis of cylindrical, parallel hyphae, 5–13 μm wide, branched, septate, mostly cylindric with clavate to subfusoid. Stipe trama with hyphae 3–15 μm wide, clamped, septate. Clamp connections abundant in all tissues.

Figure 8. Cantharellus galbanus (GDGM86249, Holotype!). (a) Basidiospores. (b) Basidia, basidiola and elements of the subhymenium. (c) Pileipellis. Bars: (a,b) = 10 μm; (c) = 20 μm.
Habitat and distribution—Growing in groups or gregariously under Fagaceae trees mixed with other broadleaf trees in tropical broadleaf forests. Known from southern China.

Specimen examined—CHINA. Hainan Province, Changjiang County, Bawangling National Natural Reserve, 942 m, 7 July 2013, Ming Zhang (GDGM43100); Hainan Province, Ledong County, Jianfengling National Natural Reserve, 950 m, 17 June 2017, Ming Zhang (GDGM60568).

Notes—*Cantharellus galbanus* is characterized by the presence of its small basidiomata, greenish-yellow pileus, distant and well-developed hymenophore, and relatively small basidiospores (6–7.5 × 4.8–5.5 µm). The molecular phylogenetic analysis that was based on a single specimen showed that *C. galbanus* formed an independent clade (Lineage IV) and was clearly distinguished from the other species in the subg. *Parvocantharellus*, fully supporting the identification of *C. galbanus* as a distinct species. *Cantharellus citrinus* Buyck, R. Ryoo & Antonin, recently reported from South Korea, is morphologically similar to *C. galbanus*, as both species share small, lemon-yellow basidiomata. However, *C. citrinus* belongs to the subg. *Cinnabarini* and differs in its relatively poorly-developed hymenophore with transversely irregular anastomosis, and large basidiospores (7.6–8.4 × 5.4–5.9 µm) [33].

*Cantharellus luteolus* Ming Zhang, C.Q. Wang & T.H. Li sp. nov. Figures 7d-f and 9. MycoBank: MB840836.

Etymology—refers to the yellowish-orange pileus colour.

Diagnosis—This species is characterized by its small basidiomata, yellow to orange pileus, well-developed gill-like ridges mostly forked at the margin, elliptical to subglobose basidiospores, and thin-walled hyphae of pileipellis.

Type—CHINA. Hainan Province, Ledong County, Jianfengling National Nature Reserve, alt. 950 m, on soil under Fagaceae trees that are mixed with other broadleaf trees in tropical broadleaf forests, 17 June 2017, Ming Zhang (GDGM60393).

Basidiomata small-sized. Pileus 20–32 mm broad, convex when young, then applanate with center depressed at mature, surface dry, tomentosus, pastel yellow, yellow, light yellow, yellowish orange, greish orange, light orange to orange (3A4–5A4, 3A6–6A6, 3B4–5B4), margin incurved and irregularly wavy. Hymenophore well developed, composed of decurrent, mostly forked and strongly interveined gill-folds, less than 1 mm depth, light yellow (3A5–4A5), greyish yellow to greyish orange (3B5–5B5). Stipe 20–30 × 3–7 mm, cylindrical, or gradually slender towards base, central, hollow, surface smooth, slightly waxy, concolourous with pileus or paler to light yellow, greyish yellow (3A5–4B5) to light orange (4A5). Context white to yellowish, 1–2 mm thick, unchanging when bruised. Taste mild. Odour fruity.
Basidiospores (75/3/3) 7–8 × 5.2–6.5 μm, $L_m \times W_m = 7.44(\pm0.46) \times 6.04(\pm0.29) \mu m$, $Q = (1.12)1.16–1.33(1.36)$, $Q_m = 1.23 \pm 0.07$, elliptical to subglobose, uniguttulate to multiguttulate, smooth, hyaline, inamyloid, with refringent contents. Basidia 60–85 × 7–10 μm, 4–6-spored, narrowly clavate with large number of vacuoles, sterigmata 5–10 μm long; basidiole 51–85 × 6–10 μm, numerous, clavate. Hymenial cystidia absent. Hymenophoral trama filamentous; hyphae 3–9 μm diam., branched, septate. Pileipellis a cutis, composed of horizontal to ascending, subparallel, cylindrical and branched, thin-walled hyphae arranged mostly in irregular pattern; septa clamped; terminal cells mostly cylindrical to subclavate, up to 150 μm long, slightly appendiculate. Stipitipellis a cutis of cylindrical, parallel hyphae, 3–12 μm wide, branched, septate, mostly cylindrical with clavate to subfusoid. Stipe trama with hyphae 3–9 μm wide, clamped, septate. Clamp connections abundant in all tissues.

Habitat and distribution—Growing solitary or scattered under Fagaceae trees that are mixed with other broadleaf trees in tropical broadleaf forests. Known from southern China.

Specimen examined—CHINA. Hainan Province, Changjiang County, Bawangling National Natural Reserve, 942 m, 6 July 2013, Ming Zhang (GDGM44258); Hainan Province, Ledong County, Jianfengling National Natural Reserve, 942 m, 13 July 2021, Ting Li (GDGM86247).

Notes—The following combination of characteristics that included small basidiomata, yellow to orange pileus, greyish-yellow to greyish-orange hymenophores, elliptical to subglobose basidiospores, and thin-walled hyphae of the pileipellis, made *C. luteolus* easily distinguishable from the other species in *Cantharellus*. Genetically, *C. luteolus* is
a monophyletic taxon (Lineage VI) that is significantly related to the Chinese species *C. albus*, together forming a significantly monophyletic clade. However, *C. albus* can be easily distinguished by the presence of its robust, white basidiomata that slightly changes to a yellowish colour when it is bruised, with a strongly bifurcate and interconnected hymenophore, and relatively small basidiospores [2], above study in *C. albus*.

**Cantharellus luteovirens** Ming Zhang, C.Q. Wang & T.H. Li sp. nov. Figures 7g–i and 10. MycoBank: MB840653.

Etymology—refers to the yellowish-orange basidiomata.

Diagnosis—This species is characterized by its small, yellow to yellowish-orange basidiomata, hygrophanous pileus surface, poorly-developed hymenophore that is composed of strongly bifurcate and interconnected low veins, and broadly ellipsoid basidiospores that measure 6–7(–7.5) × (4.5–)4.8–5.5(–6) μm.

Type—CHINA. Guangdong Province, Guangzhou City, Baiyun Mountain, alt. 130 m, 16 June 2020, Ming Zhang (GDGM80672).

Basidiomata small-sized. Pileus 15–42 mm broad, convex when young, then gradually to nearly planatel with a central shallow depression or broadly infundibuliform at maturity; surface dry to hygrophanous, smooth, pastel yellow (2A4–4A4), light yellow (2A5–4A5), yellow to yellowish orange (3A6–4A6), usually with greyish yellow (3C5–4C5) tint at center, margin wavy, incurved when young, decurved to slightly upturned at maturity, unchanging when handled. Context yellowish white, 1–1.3 mm thick in the center of the pileus, usually less than 1 mm high, yellowish white to pale yellow (2A2–3A2, 2A3–3A3), unchanging when bruised. Stipe 20–30 × 2–3 mm, central, cylindrical or slightly tapering towards base, hollow, smooth, concolourous or paler than pileus, unchanging when handled. Odour none, taste mild.

Basidiospores (100/4/4) 6.0–7.0(7.5) × (4.5)4.8–5.5(6) μm, \( L_m \times W_m = 6.79(\pm 0.40) \times 5.07(\pm 0.30) \) μm, \( Q = (1.15)1.27–1.5(1.55), Q_m = 1.34(\pm 0.093), \) broadly ellipsoid to subglobose, smooth, guttulate. Basidia 40–70 × 6–10 μm, 2–6-spored, narrowly clavate, colourless to hyaline in KOH; sterigmata 3–7 μm long. Pileipellis a cutis, composed of repent and occasionally branched hyphae, subcylindrical cells that are 6–13 μm wide, up to 200 μm long, thin-walled. Stipitipellis a cutis of cylindrical, parallel hyphae, 4–8 μm wide, occasionally up to 12 μm wide. Clamp connections abundant in all tissues.

Habitat and distribution—Growing in groups or gregariously under *Acacia auriculiformis* A. Cunn. ex Benth and *Acacia mangium* mixed other broadleaf trees in subtropical forests. Currently only known from Guangdong Province in southern China.

Specimen examined—CHINA. Guangdong Province, Guangzhou City, Baiyun Mountain, alt. 100 m, 8 May 2020, Xi-Shen Liang (GDGM81079); Same location, alt. 136 m, 14 May 2016, Ming Zhang (GDGM45899); Same location, alt. 218 m, 28 May 2020, Ming Zhang (GDGM81395); Same location, alt. 183 m, 12 June 2020, Jun-Yan Xu (GDGM80296).

Notes—**Cantharellus luteovirens** is characterised by the presence of its small pastel yellow to yellowish-orange basidiomata, poorly-developed hymenophore with bifurcate and strongly interconnected low veins, broadly ellipsoid to subglobose basidiospores, and thin-walled pileipellis hyphae. These traits enable the classification and placement of *C. luteovirens* into the subg. *Parvothelarrellus*. The molecular phylogenetic analyses showed that all of the *C. luteovirens* specimens formed a distinct lineage (Lineage III) close to *C. minioalbus* (Lineage II). However, *C. luteovirens* is morphologically different from *C. minioalbus* by its pastel yellow to yellowish-orange basidiomata, poorly-developed hymenophore, and relatively large basidiospores.

**Cantharellus galbanus** is extremely morphologically similar to *C. luteovirens*. However, *C. galbanus* differs by its small basidiomata, greenish pileus colour, relatively distant and well-developed hymenophore, and tropical distribution. In the phylogenetic trees, the two species formed two distinct monophyletic taxa and could easily be separated from each other owing to their branch lengths.
Additionally, *C. koreanus*, *C. minor*, and *C. tabernensis* are also morphologically similar to *C. luteovirens*, owing to the presence of small basidiomata and a yellowish to orange tinct pileus. However, the former three species can be distinguished from *C. luteovirens* in the field by their relatively distant and well-developed hymenophores. Additionally, *C. koreanus* differs by the presence of its dirty yellowish-brownish to pale brown pileus, with a brown centre, and relatively large but narrow basidiospores [6–8(–9) × 4.2–5.5(–6.5) μm] [16]. *Cantharellus minor* differs by the presence of its egg-yellow to orange pileus, long stipe, and large basidiospores 8–11 × 5–7 μm [51–53]. *Cantharellus tabernensis* differs by the presence of its dull orange-yellow to yellowish-brown pileus, vivid orange-yellow hymenophore and stipe, relatively large basidiospores (6–9 × 4–6 μm), and small basidia (35–55 × 5–8 μm) [49].

**Figure 10.** *Cantharellus luteovirens* (GDGM80672 Holotype!). (a) Basidiospores. (b) Basidia, basidiola and elements of the subhymenium. (c) Pileipellis. Bars: (a,b) = 10 μm; (c) = 20 μm.

*Cantharellus minioalbus* Ming Zhang, C.Q. Wang & T.H. Li sp. nov. Figures 11a–d and 12. MycoBank: MB840654.

Etymology—refers to the small white basidiomata.

Diagnosis—This species can be easily distinguished from others in *Cantharellus* by its small and white-coloured basidiomata, gill-like hymenophore that is well-developed with bifurcate and interconnected low veins, and growing in groups or gregariously under broadleaf trees.
Type—CHINA. Yunnan Province, Puer City, Taiyanghe National Forest Park, alt. 1616 m, N 22°36′24.8″, E 101°05′21.6″, 24 September 2019, Ming Zhang (GDGM78901).}

Figure 11. Species of *Cantharellus* subg. *Parvocantharellus* from China. (a–d) *C. minioalbus* (a) GDGM78926; (b) GDGM78901 holotype; (c) GDGM78934; (d) GDGM78910; (e–g) *C. sinominor* (e) GDGM80842 holotype (f) GDGM80788; (g) GDGM80885; (h–i) *C. zangii* (h) GDGM83181; (i) GDGM83193.
Basidiomata small-sized. Pileus 3–10 mm broad, convex when young, then gradually to nearly applanate with a central shallow depression or finally broadly infundibuliform at maturity; surface dry, with appressed fibrillose scales, white to yellowish white, margin wavy, incurved when young, decurved to slightly upturned with maturity, unchanging when handled. Context yellowish white, unchanging when exposed. Hymenophore decurrent, but with a clearly delimitation from the stipe surface, distant, with well-defined gill-like folds, relatively well developed, frequently forking towards pileus margin, with lower irregular anastomosis amongst the folds, white to pale yellow, unchanging when bruised. Stipe 15–30 × 1.5–2.5 mm, central, cylindrical or slightly inflated towards base, solid, smooth or faintly scaly, concolourous with pileus, unchanging when handled. Odour not distinct.

Basidiospores (100/4/4) 4.5–7 × 4–5.5(–6.2) μm, L_m × W_m = 5.71(±0.64) × 4.87(±0.49) μm, Q = (1)1.1–1.27(1.37), Q_m = 1.17 ± 0.07, broadly ellipsoid to subglobose, smooth, guttulate. Basidia 44–66 × 6–8 μm, 2–6-spored, narrowly clavate, colourless to hyaline in KOH, with 2–6 sterigmata; sterigmata 3–7.5 μm long. Hymenophoral trama irregular, composed of colourless and branched hyphae, 3–20 μm wide, septate, thin-walled. Pileipellis a cutis with long, repent, branched, and usually interwoven hyphae, subcylindrical cells that are
3–13 µm wide, thin-walled; terminal cells appressed to suberect, mostly cylindrical, up to 200 µm long and 5–13 µm wide. Stipitipellis a cutis of cylindrical, parallel hyphae, 3–7 µm wide, terminal cells clavate or cylindrical, 5–10 µm wide. Clamp connections abundant in all tissues.

Habitat and distribution—Growing in groups or gregariously under Castanopsis sp. and Fagus sp. in tropical broadleaf forests. Currently only known from Yunnan Province, Southwest China.

Specimen examined—CHINA. Yunnan Province, Puer City, Simao District, Taiyanghe National Forest Park, alt. 1616 m, 24 September 2019, Ming Zhang (GDGM78915, GDGM78916, GDGM78926, GDGM78934), Jun-Yan Xu (GDGM78901); Same locality, alt. 1662 m, 25 September 2019, Ming Zhang (GDGM78955), Jun-Yan Xu (GDGM78997).

Notes—Cantharellus minioalbus is characterised by the presence of its small white basidiomata, broadly infundibuliform pileus that is covered with fibrillose scales, distant and well-defined gill-like hymenophore that are frequently forking towards the pileus margin, with the existence of few abnormal anastomosis among the folds, broadly ellipsoid to subglobose basidiospores, and thin-walled hyphae of pileipellis. These traits enable the classification and placement of C. minioalbus into the subg. Parvocantharellus. The molecular phylogenetic analyses showed that the new species formed an isolated lineage in the subg. Parvocantharellus and was genetically distinct from all of the other Cantharellus taxa with sequence data.

Cantharellus albus is similar to C. minioalbus, as both species share white basidiomata. However, C. albus, redescribed above, differs by the alteration of the basidiomata colour from white to yellow when it is bruised, and by the presence of a poorly-developed hymenophore with variously forked or strongly anastomosing veins, and relatively large basidiospores [5.5–7.5 × (4–) 4.5–6 µm].

Cantharellus sinominor Ming Zhang, C.Q. Wang & T.H. Li sp. nov. Figures 11e–g and 13. MycoBank: MB840655.

Etymology—refers to the species described from China and is similar to C. minor.

Diagnosis—This species is characterized by its small and light yellow basidiomata with a relatively longer stipe, the stipe is usually longer than the diameter of the pileus. It has well-developed gill-like ridges that are mostly forked at the margin, as well as elliptical to elongate elliptical basidiospores, and thin-walled hyphae of the pileipellis.

Type—CHINA. Guizhou Province, Longli Town, Longjiaoshan Forest Park, alt. 1000 m, on soil under Keteleeria sp. and Picea sp. dominated forests, 5 July 2020, Ming Zhang (GDGM80842).
Basidiomata small-sized. Pileus 10–23 mm broad, applanate with center depressed, not perforate, margin incurved when young, applanate or slightly reflexed with age, obscure striate on surface; subfleshy to slightly membranous; surface dry, subtomentosus, greyish yellow to greyish orange at central (3B4–5B4), gradually fading to light yellow to light orange toward margin (3A4–5A4). Context thin, 0.5–1.2 mm thick in the center of the pileus, fibrous, pale yellow to pale orange (3A3–5A3), unchanging when bruised. Hymenophore decurrent, distant to subdistant, well developed, gill-liked ridges 1–1.5 mm high, mostly forked at margin, greyish yellow to greyish orange (3B5–5B5), unchanging when bruised. Stipe 30–50 mm long, 2–3 mm thick, subcylindrical, slightly tapering downward, smooth or with faintly scaly, hollow, concolourous to pileus. Odour none, Taste mild.
Basidiospores (100/4/4) (6–)6.5–8.5(–9) × (4.5–)5–6 µm, \( L_m \times W_m = 7.55(\pm 0.61) \times 5.56(\pm 0.34) \) µm, \( Q = (1.2)1.27–1.5(1.6) \), \( Q_m = 1.34 \pm 0.09 \), elliptical to elongate elliptical. Basidia 37–74 × 7–9 µm, clavate, 5–6-spored, slender, narrowly clavate; sterigmata 5–7 µm long. Hymenophoral trama subparallel to regular, composed of colourless and branched hyphae, 4–10 µm wide, septate. Pileipellis a cutis, composed of ascending to erect and occasionally branched hyphae, 3–12 µm wide; terminal cell 38–120 × 7–10 µm, mostly cylindrical to subclavate, thin-walled. Stipitipellis a cutis of cylindrical, parallel hyphae, 3–8 µm wide, branched, septate, mostly encrusted with golden reflective substance. Stipe trama with hyphae 9–15 µm wide, clamped, septate. Clamp connections abundant in all tissues.

Habitat and distribution—Growing in groups or gregariously under mixed forests that are dominated by *Keteleeria* sp. and *Picea* sp. Currently known from southwest China.

Specimen examined—CHINA. Guizhou Province, Qiannan Buyi and Miao Autonomous Prefecture, Longli County, bought from Guanyin village mushroom market, 1 July 2020, alt. 1080 m, Ming Zhang (GDGM80788); Guiyang City, bought from a mushroom market, 1 July 2020, alt. 1080 m, Ming Zhang (GDGM80824); Longli County, Longjiashan National Forest Park, alt. 1000 m, 5 July 2020, Ming Zhang (GDGM80885).

Notes—*Cantharellus sinominor* is one of the most commonly documented *Cantharellus* species in subtropical coniferous forests in southwest China, and it can be found in local wild edible mushroom markets. In the field, *C. sinominor* is easily confused with *C. minor*, a species with small yellow basidiomata. The molecular phylogenetic analyses showed that they are closely related, but independent species. *Cantharellus minor* differs by the presence of its glabrous, bright yellow-orange to orange pileus, that is usually fading to pale orange-buff or pale orange, and its relatively large basidiospores (8–11 × 5–7 µm) [51–53]. Additionally, *C. minor* is reportedly associated with oaks and other hardwoods, whereas *C. sinominor* is associated with coniferous trees.

*Cantharellus parvoflavus* M. Herrera, Bandala & Montoya, that is recently described from Mexico, is similar to *C. sinominor*. However, the former presents with a bright yellow-orange pileus with appressed fibrils at the centre, relatively narrow basidiospores (6–9 × 4.5–5 µm), and narrow hymenophoral trama hyphae (4–5 µm in diameter) [30].

*Cantharellus alboroseus* Heinem. and *C. tenuis* Heinem., two small species that were originally reported in the Congo, are morphologically similar to *C. sinominor*. However, *C. alboroseus* belongs to subg. *Rubrinus* and differs by the presence of its bright orange to pale pink pileus, small basidiospores \( [7.1–7.7(7.9) \times (4–)4.1–4.7(–5) \) µm], and the absence of clamp connections [17]. *Cantharellus tenuis*, may belong to the subg. *Cinnabarinus* and differs by the presence of its tiny, bright orange basidiomata and small basidiospores \( 7–8 \times 5–5.7 \) µm) [3,17].

*Cantharellus zangii* X.F. Tian, P.G. Liu & Buyck, *Mycotaxon* 2012, 120, 100; Figures 11h–i and 14.

Synonym—*Cantharellus sikkimensis* K. Das, Buyck, D. Chakr., Baghela, S.K. Singh & V. Hofst., in Das, Hofstetter, Chakraborty, Baghela, Singh & Buyck, *Phytotaxa* 2015, 222(4), 273.
Figure 14. Cantharellus zangii (GDGM83193). (a) Basidiospores. (b) Basidia, basidiola and elements of the subhymenium. (c) Pileipellis. Bars: (a) = 10 μm; (b,c) = 20 μm.

Basidiomata small-sized. Pileus 10–40 mm broad, convex when young, then planate with center depressed at mature, surface dry, brown to dark brown (6E6–7E6, 6F6–7F6) at first, gradually fading to light brown to brownish orange (5C5–6C5, 5D5–6D5), glabrous, irregularly wrinkled, hygrophanous when wet, margin incurved and irregularly wavy. Hymenophore decurrent, subdistant, gill-like, well developed, ridges 1.5–2 mm, composed of bifurcate and interconnected low veins, in particular toward pileus margin, veins usually less than 1 mm broad between ridges, light yellow (3A5), olive yellow (3C6), greyish yellow (4B6) to pale orange (5A4). Stipe 50–130 × 3–6 mm, subcylindrical, or gradually broader towards base, central, hollow, mostly twisted or longitudinally ridged or fluted, surface smooth, slightly waxy, brownish orange (5C5) to light orange (6A5) on upper half, greyish yellow (4B5) on lower half. Context 1–3 mm thick, greyish yellowish to olive brown (4B4–4D4), unchanging when bruised. Odour pleasant. Taste mild.
Basidiospores (100/4/4) 8–11(–12) × 5.5–7(–8) μm, $L_m \times W_m = 9.25(\pm 0.94) \times 6.16(\pm 0.45) \mu m$, $Q = (1.23)1.33–1.67(1.75)$, $Q_m = 1.5\pm 0.12$, ellipsoid to sub-reniform, smooth, thin-walled, hyaline, sometimes with tiny oil drops. Basidia 70–90 × 8–11 μm, 5–6-spored, slender, narrowly clavate, with large number of vacuoles, sterigmata 5–8 μm long; basidioles 65–100 × 7–10 μm, numerous, clavate. Hymenial cystidia absent. Hymenophoral trama irregular to subparallel, composed of colourless and loose hyphae, 3–5 μm wide, branched, septate. Pileipellis a cutis, composed of repent to ascending and occasionally branched hyphae, 5–18 μm wide, subcylindrical; terminal cell 40–85 × 7–14 μm, mostly cylindrical to subclavate, thin-walled. Stipitipellis a cutis of cylindrical, parallel hyphae, 3–9 μm wide, branched, septate, mostly cylindric with clavate to subfusoid or rounded apices. Stipe trama with hyphae 9–15 μm wide, clamped, septate. Clamp connections abundant in all tissues.

Habitat and distribution—Growing in groups or gregariously under Abies georgei Orr and A. densa Griff. in subalpine coniferous forests or mixed forests. Known from southwest China and northern districts of India.

Specimen examined—CHINA. Yunnan Province, Shangrila, Big Ravine, alt. 3030 m, 16 September 2007, Y.C. Li 537 (HKAS55743); Haba Snowy Mountains, alt. 3000 m, 30 September 2007, Feng Bang 182 (HKAS 55824); Bitahai National Natural Reserve, alt. 3850 m, 3 September 2020, Ming Zhang (GDGM82399, GDGM82389); Same location, 4 September 2020, Ming Zhang (GDGM83193, GDGM82374, GDGM83171, GDGM83173, GDGM83186).

Notes—As the type specimen of C. zangii was unavailable, two paratype specimens were carefully examined and compared with the newly collected specimens from the type locality in this study. The macro- and micro-morphological characteristics were observed to be well-matched. Therefore, data on new ITS, LSU, tef1, and rpb2 gene sequences of C. zangii that were derived from our newly collected specimens are provided in this study.

The molecular phylogenetic analyses showed that C. zangii formed a distinct and well-supported lineage, and a sample named C. sikkimensis AB-2015 nested into the well-supported C. zangii lineage (100% BS and 1.00 BPP) in the multi-locus phylogenetic tree. Cantharellus sikkimensis, originally reported from India, is characterized by its dark brown pileus, light yellow hymenophore, long and hollow stipe, ellipsoid to sub-reniform basidiospores (8–11 × 5–7 μm) [39], which is highly consistent with C. zangii in morphology. Furthermore, a BLAST search that was based on the ITS sequence of C. zangii showed 99.14% identity percent to the sequence (accession no: KR001903) from the type specimen of C. sikkimensis AB-2015. Both of these species show distributions in subalpine coniferous forests and are associated with Abies plants. Thus, C. sikkimensis is a late synonym of C. zangii, and the distribution of C. zangii extends to the south of the Himalayas.

3.3. Key to Species of Subgenus Parvotharellus in China

1 Basidiomata white to yellowish-white.................................................................2
2 Pileus 20–50 mm wide, changing to yellowish when it is bruised; basidiospores 5.5–7.5 × (4) 4.5–6 μm.............................................................................................................C. albus
3 Pileus 3–10 mm wide, unchanging in colour when it is bruised; basidiospores 4.5–7 × 4–5.5(–6.2) μm.................................................................C. mini-oalbus
4 Pileus relatively larger, usually >50 mm wide...............................................C. appala-chiensis
5 Pileus smaller, usually <50 mm wide..............................................................C. aus-trosinensis
6 Growing under coniferous trees.................................................................5
4' Growing under broadleaf trees.................................................................8
5 Basidiospores 6–9 μm long, average length <8 μm...........................................6
5' Basidiospores 8–12 μm long, average length >8 μm......................................7
6 Pileus pastel yellow, light yellow to greyish-yellow, with a brownish-orange or reddish-brown center, glabrous or tomentosus at centre; basidiospores 6–8 × 4.8–6 μm; $L_m \times W_m = 7.05(\pm 0.51) \times 5.192(\pm 0.34) \mu m$.................................................................C. aus-trosinensis
### Discussion

In our multi-locus phylogenetic analyses, the ingroup sequences resulted in the formation of six main subgenera that is largely consistent with the most recent phylogenetic studies [1,2,8,9,26,34,46]. Thus, we adopted the treatment of Buyck et al. [1] and treated C. subg. *Parvocantharellus* as a monophyletic group, sister to the subg. *Cinnabarinus*. Apart from C. aff. *subcyanoxanthus*, the species of the subg. *Parvocantharellus* formed a well-supported (93% BS and 0.99 BPP) clade in the multi-locus phylogenetic tree. A total of nine species from China nested into this well-supported clade, including the seven new species that are described above: *C. aurantinus*, *C. austrosinensis*, *C. galbanus*, *C. luteolus*, *C. luteovirens*, *C. minioalbus*, and *C. sinominor*, and two previously reported species *C. albus* and *C. zangii*. In the phylogenetic analyses of the tef1 dataset, species in the subg. *Parvocantharellus* formed similar interspecific relationships in the multi-locus dataset, the seven new species were also well-supported, and further proved that the tef1 gene is suitable to determine the interspecific relationships for most species in *Cantharellus*.

In this study, nine species were discovered from China, and they all belong to the C. section *Flavobrunnei*, which is characterized by the presence of medium-sized to extremely small basidiomata, a yellowish to brownish pileus, a long stipe, and abundant clamp connections. Phylogenetic analyses in our study all support the sect. *Flavobrunnei* as a monophyletic subclade in the subg. *Parvocantharellus*. In addition to the nine species that were introduced above, *C. appalachensis* and *C. minor* belonging to the subg. *Parvocantharellus* have also been reported in China [47,54–56]. *C. appalachensis* was proposed to demonstrate a geographically disjunct distribution from southeastern North America to eastern Asia [47]. However, only the LSU sequences of *C. appalachensis* that were derived from the Chinese samples were available, and these were not included in the phylogenetic analyses owing to the markedly low levels of genetic variation and the challenges that were encountered in distinguishing them among most of the species [57]. Thus, to determine the distribution of *C. appalachensis* in China, additional useful gene sequences from more samples are warranted. *C. minor* is considered a broad species and is widely distributed in most parts of China [54–56], including northeast, central, southern, and southwest China. Unfortunately, there were no specimen vouchers that were available for these records. The name "*Cantharellus minor*" is a collective name and has been misapplied to almost any small yellow *Cantharellus* species in China. The four new species *C. austrosinensis*, *C. galbanus*, *C. luteovirens*, and *C. sinominor* are easily misidentified as *C. minor* based on their morphological characteristics. However, phylogenetic analyses indicated that they represented five distinct species and *C. minor*, originally reported from North America.
under oaks and other hardwoods, can be distinguished by the presence of its large basidiospores (8–11 × 5–7 µm) [51–53]. In the present study, no samples of *C. minor* from China were detected in the phylogenetic analyses, and further studies with extensive sampling are warranted to determine the distribution of the species in China. The distribution of *C. minor* may be similar to that of *C. cibarius* in China. A recent study has shown that the distribution of *C. cibarius* is limited to northeast China, and the popular edible mushroom that is marketed in Yunnan, Guizhou, and Sichuan Provinces is, in fact, the native species *C. yunnanensis* W.F. Chiu [18].

Geographically, the species that are in the *C.* subg. *Parvocantharellus* are mainly distributed in the northern hemisphere and are especially diverse in Asia [16,35,38]. Except for *C. zangii* which has been reported in the subalpine regions of China and India, the remaining eight species were all reported in the subtropical and tropical regions of southern China, revealing an unexpectedly large number of new *Cantharellus* species in China, with a considerable number of species remaining to be discovered. Remarkably, in the phylogenetic trees, specimens that were from the northern hemisphere were clustered together in the well-supported sect. *Flavobrunnei* of subg. *Parvocantharellus*, representing a distinct northern hemisphere distribution clade. Meanwhile, three species, namely *C. avellaneus*, *C. congoensis*, and *C. subcyanoxanthus*, from the southern hemisphere formed the basal and sub-basal branches in the subgenus. *C. avellaneus* and *C. congoensis*, which belong to the sect. *Congolenses* Heinem., formed an isolated sub-basal clade in the subgenus and were characterized by their strongly blackening context and strong reaction with most macrochemical reagents. These distinct morphological characteristics make the species in this section easily distinguishable from *Flavobrunnei*, demonstrating a unique tropical African geographic distribution clade. *C. subcyanoxanthus*, which is characterized by its strong blue-violet-lilac to vinaceous basidiomata and yellow context, formed a monospecific sect. *Cyanomaculati* Buyck & V. Hofstetter, was located in the basal clade of subg. *Parvocantharellus*, but without significant support in the multi-locus phylogenetic tree. Based on molecular correlations, Buyck et al. [1] roughly divided the two sections in the subg. *Parvocantharellus*, but their morphological characteristics are not well-matched with the definition of the subg. *Parvocantharellus*. Thus, their distinct morphological characteristics and relatively independent phylogenetic positions may result in their assignment to a new subgenera level in the future as more related species continue to be discovered.

**Author Contributions:** Conceptualization, M.Z. and T.-H.L.; methodology, M.Z. and C.-Q.W.; performing the experiment, M.Z.; phylogenetic analysis, M.Z. and B.B.; validation, M.Z., C.-Q.W., B.B., W.-Q.D. and T.-H.L.; writing—original draft preparation, M.Z.; writing—review and editing, C.-Q.W., B.B., W.-Q.D., and T.-H.L.; visualization, M.Z.; supervision, T.-H.L.; project administration, M.Z.; funding acquisition, M.Z. All authors have read and agreed to the published version of the manuscript.

**Funding:** This research was funded by the National Natural Science Foundation of China (Nos. 32070020, 31970016), the Science and Technology Planning Project of Guangdong Province, China (No. 2019B121202005), and the Science and Technology Planning Project of Guizhou Province, China [No. Qian Ke He Fu Qi (2019) 4007].

**Institutional Review Board Statement:** Not applicable.

**Informed Consent Statement:** Not applicable.

**Data Availability Statement:** In Publicly available datasets were analyzed in this study. This data can be found here: [https://www.ncbi.nlm.nih.gov/](https://www.ncbi.nlm.nih.gov/); [https://www.mycobank.org/](https://www.mycobank.org/); [https://www.treebase.org/treebase-web/home.html](https://www.treebase.org/treebase-web/home.html), accessed on 28 July 2021.

**Acknowledgments:** The authors sincerely thank the editors and anonymous reviewers for their efforts and contributions towards this manuscript. Sincere acknowledgments are expressed to S.C. Shao (Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences), L.Q. Wu, Y. He (Institute of Microbiology, Guangdong Academy of Sciences), and J.W. Liu (Kunming Institute of Botany, Chinese Academy of Sciences) for their assistance.

**Conflicts of Interest:** The authors declare that there are no conflicts of interest.
