

cryptogamie

Mycologie

2021 • 42 • 3

New insights into the taxonomy of the genus
Cantharellus in China: epityfication
of *C. yunnanensis* W.F. Chiu and
the first record of *C. cibarius* Fr.

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- Science Citation Index
- Publications bibliographiques du CNRS (Pascal).

Cryptogamie, Mycologie est distribué en version électronique par / *Cryptogamie, Mycologie is distributed electronically by*:

- BioOne® (<http://www.bioone.org/loi/crym>)

Cryptogamie, Mycologie est une revue en flux continu publiée par les Publications scientifiques du Muséum, Paris

Cryptogamie, Mycologie is a fast track journal published by the Museum Science Press, Paris

Les Publications scientifiques du Muséum publient aussi / *The Museum Science Press also publishes*: *Adansonia, Geodiversitas, Zoosystema, Anthropozoologica, European Journal of Taxonomy, Naturae, Cryptogamie* sous-sections *Algologie, Bryologie, Comptes Rendus Palevol*.

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diff.pub@mnhn.fr / <http://sciencepress.mnhn.fr>

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ISSN (imprimé / *print*): 0181-1584/ ISSN (électronique / *electronic*): 1776-100

New insights into the taxonomy of the genus *Cantharellus* in China: epitypification of *C. yunnanensis* W.F. Chiu and the first record of *C. cibarius* Fr.

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Submitted on 20 April 2020 | Accepted on 13 January 2021 | Published on 19 March 2021

Shao S.-C., Liu P.-G., Wei T.-Z. & Herrera M. 2021. — New insights into the taxonomy of the genus *Cantharellus* in China: epitypification of *C. yunnanensis* W.F. Chiu and the first record of *C. cibarius* Fr. *Cryptogamie, Mycologie* 42 (3): 25–37. <https://doi.org/10.5252/cryptogamie-mycologie2021v42a3>. <http://cryptogamie.com/mycologie/42/3>

ABSTRACT

Yellow chanterelles are one of the most common edible mushrooms found in Yunnan Province, China. Previous studies identified the species of these mushrooms as *Cantharellus cibarius* Fr. based on morphology alone. However, the diversity of yellow chanterelles comprises many species within the *C. cibarius* complex, including *C. yunnanensis* W.F. Chiu. We hypothesized that the latter species is widely marketed in Yunnan Province and does not actually belong to *C. cibarius*. Hence, to confirm the species identity, taxonomic re-evaluation using integrated taxonomic approaches is required. Herein, samples collected from different markets and from near the type locality were subjected to morphological and molecular analyses. We generated *tef-1α* sequences and analyzed them using the maximum likelihood and Bayesian inference methods. The study revealed that the specimens previously identified as *C. cibarius* with a wide distribution in southwestern China are indeed *C. yunnanensis*. Our morphological assessment was markedly influenced by the revision of the type specimen (*C. yunnanensis*) and its original description, as some characteristics of the specimen did not match the description (e.g., the size and shape of the spores). Similarly, our single-locus phylogenetic analysis strongly supported the identification of the marketed species in Southwestern China (Guizhou and Yunnan Provinces) as *C. yunnanensis* instead of *C. cibarius*. Following our findings, we epitypified *C. yunnanensis*. Additionally, we collected, identified, and confirmed the presence of *C. cibarius* in northeastern China.

KEY WORDS

Hydnaceae,
Cantharellus cibarius
complex,
epitypification,
taxonomic revision,
tef-1α.

RÉSUMÉ

Nouveaux aperçus sur la taxonomie du genre Cantharellus en Chine : épitypification de C. yunnanensis W.F. Chiu et le premier enregistrement de C. cibarius Fr.

La chanterelle jaune est l'un des champignons comestibles le plus courant dans la province du Yunnan, en Chine. Des études antérieures ont identifié l'espèce de ces champignons comme étant *Cantharellus cibarius* Fr. sur la base de la seule morphologie. Cependant, la diversité des chanterelles jaunes comprend de nombreuses espèces au sein du complexe *C. cibarius*, dont *C. yunnanensis* W.F. Chiu. Nous avons émis l'hypothèse que cette dernière espèce est largement commercialisée dans la province du Yunnan et n'appartient pas réellement à *C. cibarius*. Par conséquent, pour confirmer l'identité de l'espèce, une réévaluation taxonomique utilisant des approches taxonomiques intégrées est nécessaire. Dans ce but, des échantillons prélevés sur différents marchés et à proximité de la localité type ont été soumis à des analyses morphologiques et moléculaires. Nous avons généré des séquences *tef-1α* et les avons analysées en utilisant les méthodes de maximum de vraisemblance et d'inférence bayésienne. L'étude a révélé que les spécimens précédemment identifiés comme *C. cibarius* avec une large distribution dans le sud-ouest de la Chine sont bien *C. yunnanensis*. Notre évaluation morphologique a été fortement influencée par la révision du spécimen type (*C. yunnanensis*) et sa description originale, car certaines caractéristiques du spécimen ne correspondaient pas à la description (par exemple, la taille et la forme des spores). De même, notre analyse phylogénétique des séquences *tef-1α* a fortement appuyé l'identification des espèces commercialisées dans le sud-ouest de la Chine (provinces du Guizhou et du Yunnan) comme étant *C. yunnanensis* au lieu de *C. cibarius*. Suite à nos découvertes, nous avons épitypié *C. yunnanensis* W.F. Chiu. De plus, nous avons collecté, identifié et confirmé la présence de *C. cibarius* dans le nord-est de la Chine.

MOTS CLÉS
Hydnaceae,
Cantharellus cibarius
complexe,
épitypification,
révision taxonomique,
tef-1α.

INTRODUCTION

Chinese chanterelles have been studied since the 20th century, with the description of the first new species, *Cantharellus yunnanensis* W.F. Chiu (Chiu 1973), followed by the subalpine species *C. tuberculosporum* M. Zang (Zang 1980). Since then, several studies have recorded the diversity of this genus in China, concentrating primarily on the classification using morphological features. (e.g., Shao et al. 2011; Tian et al. 2012). Morphologically, the species within the subgenus *Cantharellus* (Buyck et al. 2014) usually develop yellow fruiting bodies with brown, vinaceous, or lilac-purple pigments at the cap surface, which is generally smooth or sometimes exhibits appressed squamae. The main microscopic characteristics are the wall thickness of the terminal hyphae of the pileipellis, abundant clamps, and basidiospore size (Buyck et al. 2014). Studies conducted by the first author in tropical and subalpine areas of Yunnan Province, using morphological and molecular data, resulted in the description of several new species (Shao et al. 2014, 2016a, 2016b). These results gave rise to further taxonomic studies that led to the description of new species of this subgenus, such as *C. hainanensis* N.K. Zeng, Zhi Q. Liang & S. Jiang (An et al. 2017) along with new records for known species in subg. *Cantharellus* from China, such as for the American *C. lateritius* (Berk.) Singer, and European *C. cibarius* Fr. and *C. ferruginascens* P. D. Orton (Fang et al. 2019). Despite the prominence of this group, the identity of some species of *Cantharellus* reported in China needs to be re-evaluated with morphological and molecular techniques.

Cantharellus cibarius Fr. is the type species of the genus and was initially described from Northern Europe. The species is characterized in the field by its yellowish color, veined

hymenophore, and apricot scent. However, recent studies supported by molecular data have described new species within this *cibarius*-complex, mainly from North America and Asia (Arora & Dunham 2008; Buyck & Hofstetter 2011; Foltz et al. 2013; Leacock et al. 2016; Olariaga et al. 2016; Shao et al. 2016b; Thorn et al. 2017). Furthermore, Olariaga et al. (2016) suggested that the main distribution area of *C. cibarius* s.s. might be the northern parts of Europe and perhaps the most northern parts of North America and Asia. However, further studies to evaluate and confirm this distribution pattern are necessary. Presently, the known distribution of *C. cibarius* is limited to Europe and East Asia, with collections confirmed by molecular evidence from Estonia, France, Slovakia, Spain, Norway, Switzerland (Eyssartier & Buyck 2000; Olariaga et al. 2016; Thorn et al. 2017) and Japan (Ogawa et al. 2018). *Cantharellus cibarius*, together with some other yellow chanterelles, has been recorded among the edible mushrooms sold in markets in China (Wang et al. 2014; Wu et al. 2019) and is commonly referred to as *Ji-You-Jun*, meaning chicken fat, due to its yellow color (Shao et al. 2016b).

Ongoing studies have revealed that the diversity within the *C. cibarius* complex in China is relatively high (unpublished data), including genuine *C. cibarius* in northeastern China, as well as *C. yunnanensis* (Chiu 1973) and some undescribed species in Southwestern China. We suspect that most of the chanterelles sold in edible mushroom markets in Yunnan Province are not *C. cibarius* but are instead *C. yunnanensis*. We will show here that the original description of *C. yunnanensis* (Chiu 1973) is ambiguous and makes correct identification difficult. Nevertheless, Chiu's species has been included in checklists but without data on morphology or support from molecular analyses. Therefore, the objectives of this paper are to 1) redescribe

the micromorphological characteristics of popularly marketed *C. yunnanensis*; 2) designate a suitable epitype for *C. yunnanensis*; and 3) provide robust morphological and molecular evidence of the presence and distribution of *C. cibarius* in China.

MATERIAL AND METHODS

SAMPLING AND MORPHOLOGICAL STUDY

Yellow chanterelles were collected from various sites and markets in Guizhou, Jilin and Yunnan Provinces from 2007 to 2019. Descriptions of morpho-anatomical characteristics based on fresh samples were obtained following Largent (1986). The color notations indicated in the descriptions were according to Kornerup & Wanscher (1978). Basidiomes were dried in a hot air dehydrator at 45°C for further analyses. We conducted microscopic assessments under a Leica DM2500 compound light microscope after tissues were rehydrated in 3% potassium hydroxide (KOH). In this study, 35 basidiospores per collection were measured (length and width). The results of the basidiospore measurements are presented as follows: (a-)b-c(-d), with b-c containing at least 90% of all values and the extremes (a, d) enclosed in parentheses. The mean range is denoted as *Xm*, and the length/width ratio (Q) of basidiospores in side view is defined as the interval of the mean values per collection. The form of the basidiospores was interpreted after calculating the Q values following Bas (1969). In this study, voucher specimens for the epitype of *C. yunnanensis* and other materials examined were deposited in the Herbarium of Cryptogams, Kunming Institute of Botany, Chinese Academy of Sciences (KUN-HKAS).

DNA EXTRACTION, PCR AND SEQUENCING

Total genomic DNA was obtained using a modified cetyltrimethylammonium bromide (CTAB) procedure of Gardes & Bruns (1993). We amplified the transcription elongation factor 1- α (*tef-1 α*) gene with the primers *tef1F* and *tef1R* (Morehouse *et al.* 2003). PCR was performed with an initial denaturation at 94°C for 3 min; 35 cycles of 30 sec at 94°C, 30 sec at 55°C, and 2 min at 72°C; and a final elongation at 72°C for 5 min. The PCR products were purified using a Sangon purification kit, and sequencing was performed by the Sangon Company (Shanghai, China) on an ABI 3730XL automatic sequencer using the same primers. The obtained sequences were assembled and trimmed in BioEdit (Hall 1999). Finally, accession numbers (Table 1) were attached to the clean sequences deposited in GenBank (<http://www.ncbi.nlm.nih.gov>).

PHYLOGENETIC ANALYSES

To address the phylogenetic relationships within the genus, we used a total dataset of 50 *tef-1 α* sequences. The dataset included the four new *tef-1 α* sequences and 45 sequences of the subgenus *Cantharellus* (Buyck *et al.* 2014) downloaded from GenBank. Among these 45 sequences, only the paired-end raw reads of the complete genome data of *C. cibarius* (Accession number: MG75) were available in the raw

sequence read archive of NCBI (<https://www.ncbi.nlm.nih.gov/sra/?term=SRR5803930>). Herein, we performed de novo assembly using GetOrganelle (Jin *et al.* 2020). Thereafter, the *tef-1 α* region was extracted from the assembled genome, which included the sequence employed in our analyses. Additionally, the *tef-1 α* sequence of *Craterellus tubaeformis* (Fr.) Quél. was retrieved from NCBI and used as an outgroup in this study. Then, we generated a dataset of aligned *tef-1 α* single loci (50 sequences) using the data editor Phyde (v.9971) (Müller *et al.* 2010) with alignment using MUSCLE (Edgar 2004), in which inconsistencies were corrected manually. The phylogenetic relationships were inferred according to maximum likelihood (ML) and Bayesian inference (BI) methods using IQ-TREE (Nguyen *et al.* 2014) and MrBayes on XSEDE (v.3.2.6) at the CIPRES Science Gateway portal (Miller *et al.* 2010), respectively. The best evolutionary model for both datasets was determined with ModelFinder (Kalyaanamoorthy *et al.* 2017). The TNe+G model was used for ML and BI analyses. The ML analysis was performed in ultrafast mode with 1000 bootstrap (-bb) replicates, while the BI analysis was estimated with two independent runs of 1 000 000 generations. Four chains were employed for each run, and one tree was sampled every 1000 generations. Sampling points collected before stationarity (convergence of likelihood scores) were eliminated as burn-in (10%). We determined the posterior probabilities for the supported clades on the basis of a 50% majority-rule consensus of the trees retained after burn-in. The phylogenies from ML and BI analyses were displayed using FigTree (v.1.3.1) (Rambaut 2009). Bootstrap values (BS) $\geq 70\%$ and Bayesian posterior probabilities (BPPs) ≥ 0.95 were considered significant.

RESULTS

The two phylogenetic analyses (ML and BI) are largely congruent, showing both species in terminal clades supported by high bootstrap and posterior probability values (Fig. 1). *C. yunnanensis* clusters in a clade that is sister to, but independent of, the Japanese species *C. anzutake* W. Ogawa, N. Endo, M. Fukuda & A. Yamada. The specimen KU720330 (WangXH2580) collected in northeastern China clusters together with the Japanese samples of *C. cibarius* (LC085476, LC085477).

Family HYDNACEAE Kalichman
Genus *Cantharellus* Adans. ex Fr.

Cantharellus yunnanensis W.F. Chiu
(Figs 2-3)

In Acta Microbiologica Sinica 13 (2): 129 (1973).

MYCOBANK. — 310378.

HOLOTYPE. — (design. Chiu, 1973): Kunming, Yunnan, China. S.C. Shen (8090).

TABLE 1. — Voucher table. List of species of the subgenus *Cantharellus* included in phylogenetic analyses indicating voucher specimen, location and GenBank accession numbers of *tef-1α* gene. The sequences generated in this study are in **bold**.

Taxon	Voucher Specimen	Location	Genbank
<i>C. altipes</i> Buyck & V. Hofstetter	BB 07.019	United States	tef-1α
<i>C. altipes</i>	BB 07.005	United States	GQ914939
<i>C. amethysteus</i> (Qué.) Qué.	BB 07.284	Slovakia	GQ914938
<i>C. amethysteus</i>	BB 07.309	Slovakia	GQ914953
<i>C. anzutake</i> W. Ogawa, N. Endo, M. Fukuda & A. Yamada	C-2	Japan	GQ914954
<i>C. anzutake</i>	C-84	Japan	LC085470
<i>C. camphoratus</i> R.H. Petersen	12.09.06.av01	United States	LC179800
<i>C. chicaoensis</i> Leacock, J. Riddell, Rui Zhang & G.M. Muell.	1073/JJ MO-CANT-1	United States	KX592735
<i>C. cibarius</i> Fr.:Fr.	WXH 2296	Finland	KX857025
<i>C. cibarius</i>	BB 07.300	Slovakia	KM893842
<i>C. cibarius</i>	GE 07. 025	France	GQ914950
<i>C. cibarius</i>	AFTOL-ID 607		GQ914949
<i>C. cibarius</i>	WXH 2580	NE China	DQ059050
<i>C. cibarius</i>	MG75	SW China	KM893847
<i>C. deceptivus</i> Buyck, Justice & V. Hofst.	1079/JJ NC-CANT-5	United States	KM893847
<i>C. flavolateritius</i> Buyck & V. Hofst.	1078/JJ NC-CANT-4	United States	KX857030
<i>C. flavolateritius</i>	1076/JJ NC-CANT-2	United States	KX857029
<i>C. hainanensis</i> N.K. Zeng, Zhi Q. Liang & S. Jiang	N.K.Zeng2739	China	KX857027
<i>C. hainanensis</i>	N.K.Zeng2289	China	KY407537
<i>C. iuventateviridis</i> Buyck, Looney, Harsch & V. Hofst.	1542/SH13.7.2012	United States	KY407536
<i>C. iuventateviridis</i>	1543/SH14.7.2012	United States	KX857063
<i>C. lateritius</i> (Berk.) Singer	BB 07.025	United States	KX857064
<i>C. lateritius</i>	BB 07.058	United States	GQ914957
<i>C. lewisii</i> Buyck & V. Hofstetter	BB 02.197	United States	GQ914959
<i>C. lewisii</i>	BB 07.003	United States	GQ914961
<i>C. lilacinopruinatus</i> Hermitte, Eyssart. & Poumarat	BB 07.221	Slovakia	GQ914962
<i>C. pallens</i> Pilát	BB 09.441	Italy	GQ914951
<i>C. pallens</i>	BB 09.430	Italy	KX834411
<i>C. phasmatis</i> Foltz & T.J. Volk	CO57	United States	KX834410
<i>C. phasmatis</i> Foltz & T.J. Volk	CO74	United States	JX030417
<i>C. quercophilus</i> Buyck, Lewis, Eyssart. & V. Hofstetter	BB 07.097	United States	JX030418
<i>C. roseocanus</i> (Redhead, Norvell & Danell) Redhead, Norvell & Moncalvo	MO 245717		JX192981
<i>C. spectaculus</i> Foltz & T.J. Volk	CO81	United States	MF784581
<i>C. tenuithrix</i> Buyck & V. Hofstetter	BB 14.099	United States	JX030414
<i>C. velutinus</i> Buyck & V. Hofst.	DM WV13.36	United States	KX857054
<i>C. velutinus</i>	WR WV07.074	United States	KX857070
<i>C. versicolor</i> S.C. Shao & P.G. Liu	Yu 24	China	KX857068
<i>C. versicolor</i>	Tian 160	China	KM893856
<i>C. violaceovinosus</i> M. Herrera, V.M. Bandala & L. Montoya	Bandala 4513	Mexico	KM893857
<i>C. violaceovinosus</i>	Corona 648	Mexico	MF616520
<i>C. yunnanensis</i> W.F. Chiu	SSC 1	SW China	MF616521
<i>C. yunnanensis</i>	XieXD174	SW China	KM893834
<i>C. yunnanensis</i>	Herrera 263C	SW China	KU720337
<i>Cantharellus</i> sp	C-106	Japan	MT252010
<i>Craterellus tubaeformis</i> (Fr.) Qué.	BB 07.293	Slovakia	LC085473
			GQ914989

ORIGINAL DESCRIPTION. — Pileus 1.5-2.5 cm, curved; shallowly depressed in the center; faint yellow (capucine buff), very fine pubescence on the pileus; waves on the margin, decurved. Hymenophore pale to pale salmon depending on age, ridge-like gill folds, distant, dichotomous branching. Stipe 0.5-1 × 3-5 cm, irregular dimples, and fibrous tints, slightly tapering toward the base, pale. Basidiospores ellipsoid, slight olive color, 2-2.5 × 0.5-0.8 μm.

MYCOBANK. — 393369.

ADDITIONAL MATERIAL EXAMINED. — **China**. Yunnan Prov., Kunming, 11.VIII.1942, S. C. Shen 8090 (HKAS[HMAS 4090], holotype); Yunnan Prov., Kunming, China, 2100 m alt., 19.VIII.2007, XieXD174 (HKAS[HKAS 55817]); Yunnan Prov., Dali, 2550 m alt., 18.VIII.2007, ShiXF 126 (HKAS[HKAS 55749]), ShiXF 134 (HKAS[HKAS 55750]), ShiXF 137 (HKAS[HKAS 55751]); Guizhou Prov., Bijie, China, 2300 m alt., 12.VII.2008, TianXF 298 (HKAS[HKAS 55771]); Guizhou Prov., Bijie, China, 2300 m alt., 20.VIII.2008, TianXF351 (HKAS[HKAS 55782]); Yunnan Prov., Kunming, China, 2000 m alt., 29.VII.2008, TianXF

12 (HKAS[HKAS 55804]), TianXF 13 (HKAS[HKAS 55805]), TianXF 5 (HKAS[HKAS 55810]); Guizhou Province, Bijie, China, 2300 m alt., 01.VII.2009, ShaoSC 1 (HKAS[HKAS 58195]), ShaoSC 2 (HKAS[HKAS 58196]); Yunnan Prov., Kunming, China, 2100 m alt., 30.VII.2009, ShaoSC 6 (HKAS[HKAS 58200]), ShaoSC 7 (HKAS[HKAS 58201]); Yunnan Prov., Xishuangbanna, China, 680 m alt., 29.VIII.2009, ShaoSC 76 (HKAS[HKAS 58205]); Yunnan Prov., Puer, 900 m alt., 26.VII.2009, ShaoSC 100 (HKAS[HKAS 58210]); Yunnan Prov., Kunming, China, 2050 m alt., 26.VIII.2009, ZhangJP 17 (HKAS[HKAS 58215]); Yunnan Prov., Chuxiong, China, 2200 m alt., 11.IX.2009, ZhangJP 117 (HKAS[HKAS 58225]); Yunnan Prov., Kunming China, 2100 m alt., 03.IX.2019, Herrera 263C (HKAS[HKAS 107313], *epitypus hic designatus*), Herrera 264C (HKAS[HKAS 107314]), Herrera 265C (HKAS[HKAS 107315]), Herrera 266C (HKAS[HKAS 107316]).

EPITYPE DESCRIPTION

Basidiomata

Obviously fleshy, medium-sized, 20-60 mm in height.

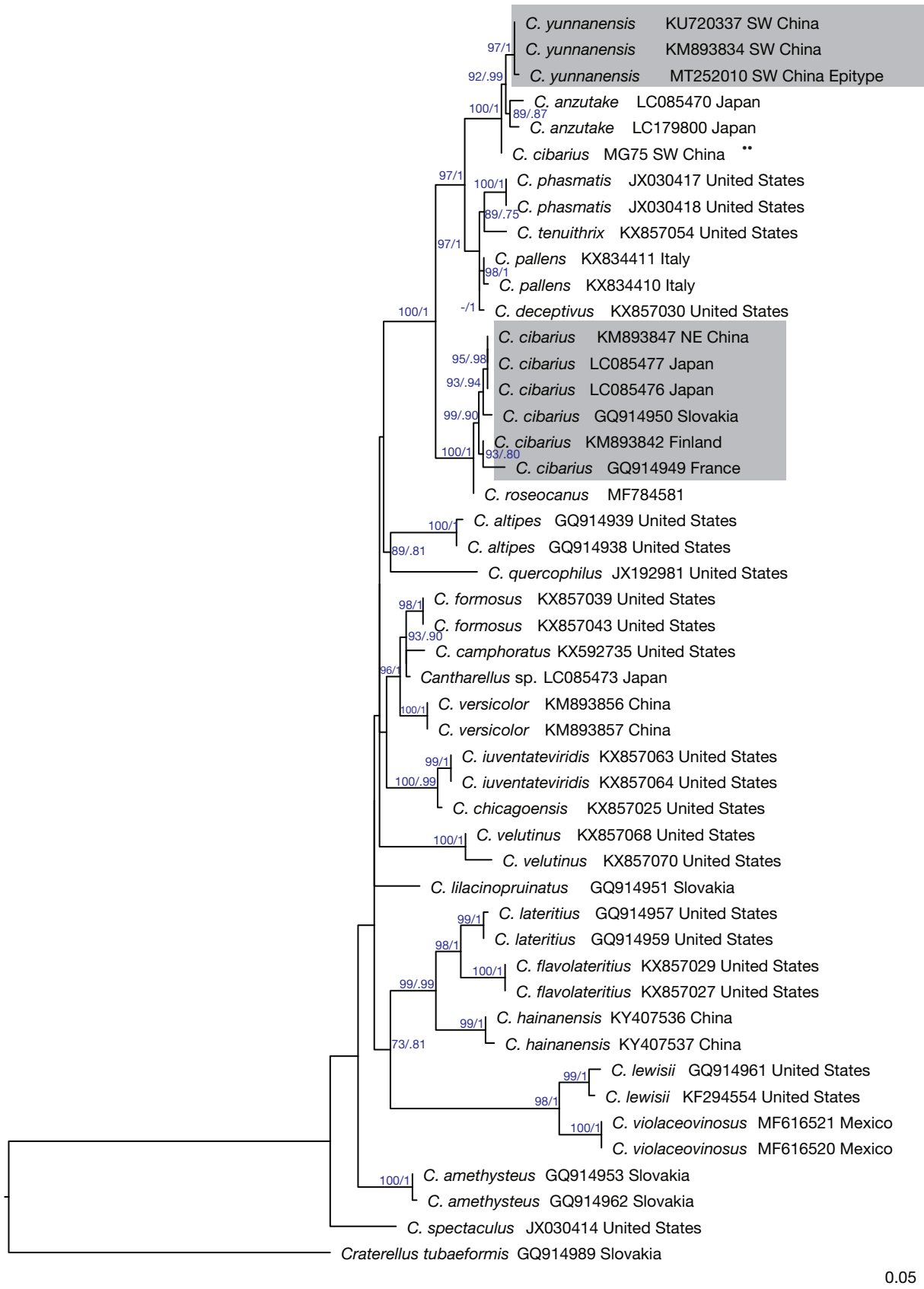


FIG. 1. — Molecular phylogenetic analysis by maximum likelihood of a *tef-1a* sequence dataset of species of the subgenus *Cantharellus* Adans. ex Fr. Bootstrap values and posterior probabilities (BS/BPPs) are indicated on the tree branches. *Craterellus tubaeformis* (Fr.) Quél. was used as the outgroup. Double dots (**) are used to indicate that the sequence was formerly identified as *C. cibarius* Fr. by Li et al. 2018.



FIG. 2. — *Cantharellus yunnanensis* W.F. Chiu: **A**, basidiomes Herrera 263C (epitype); **B**, **C**, surface of the pileus; **D**, hymenophore; **E**, surface of the stipe. Scale bars: A, 10 mm; B-E, 2 mm.

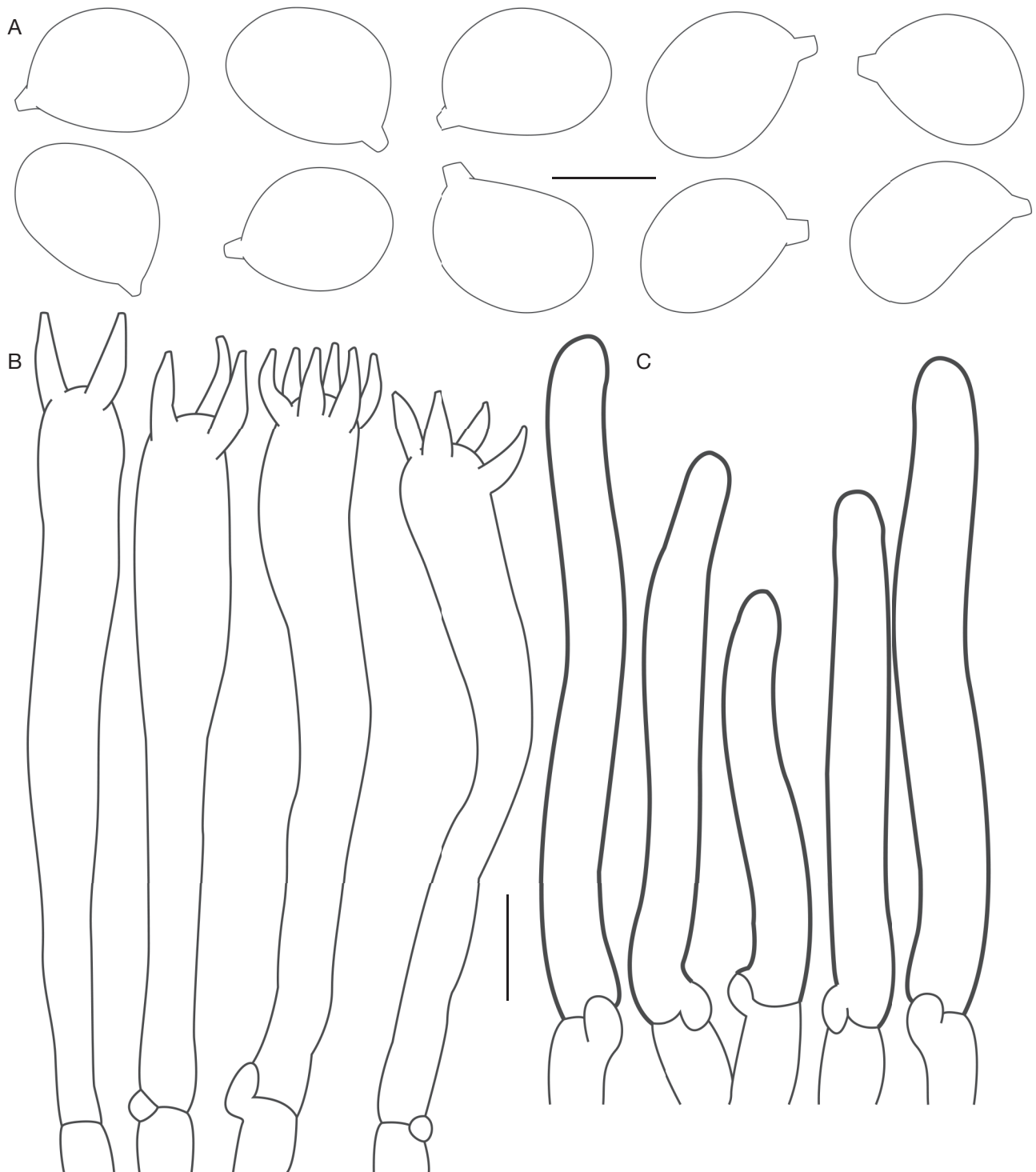


FIG. 3. — *Cantharellus yunnanensis* Herrera 263C: **A**, spores; **B**, basidia; **C**, terminal hyphae of the pileipellis. Scale bars: A, 25 µm; B-C, 10 µm.

Pileus

30-100 mm in diam., initially slightly convex to convex-planar, later becoming more or less planar with age; margin incurved or straight, regular or folded, smooth, thin; with surface smooth to minutely pubescent, yellow (4A2, 4A3, A4A, A45).

Hymenophore

With well-defined gill-like folds, up to 3 mm and 0.8-1.5 mm intervals decurrent, forking and anastomosing only near the cap margin, bright yellow (3A8, 4A5, 4A6, 4A7) at the insertion with the margin and pale yellow (4A2, 4A3) at the insertion with the stipe.

Context

Solid, fleshy, whitish (3A3), at mid-radius much thinner, 2-15 mm thick, unchanging.

Stipe

20-60 × 5-15 mm solid, subcylindrical tapering downwards, concolorous with the hymenophore (4A2, 4A3), surface glabrous to pubescent mainly in the insertion with the hymenophore.

Odor

Mild, agreeable, fruity.

Taste

Mild, agreeable.

Spore print

No color.

Basidiospores

Broadly ellipsoid or ellipsoid, smooth, colorless, and hyaline, thin-walled, (6.5-) 7-8 (-8.5) × 5-6 (-6.5) μm . $X_m = 7.85-8.17 \times 5.88 \mu\text{m}$, $Q = 1.30-1.55$.

Basidia

60-95 × 7-12 μm long and slender, narrowly clavate to subcylindrical, with 2-6 sterigmata, most commonly 4 sterigmata.

Cystidia

Absent.

Hymenophoral trama

Composed of filamentous hyphae (2.5-) 3-5 (-6.0) μm diam., colorless, thin-walled in an irregular arrangement.

Pileipellis

Mainly of the cutis type, in some areas of the surface, the terminal hyphae can be erected, forming an intricate trichoderm and cluster of hyphae. The hyphae of the pileipellis are 3-9 μm diam., intermingled in a compact (cutis) or slightly loose (trichoderm) arrangement, cylindrical, hyaline to yellowish, often with light yellow contents in some, light yellow-colored in groups, slightly thick-walled (<1 μm thick); distinctive terminal elements 25-77 × 5-10 μm broad, slightly thick-walled (<1 μm thick).

Pileus trama

Composed of cylindrical to inflated hyphae, 3-6 μm diam., slightly thick-walled (<1 μm thick), hyaline, yellowish in mass, some of the hyphal segments filled with yellow contents.

Clamp connections

Present in all tissues examined.

HABIT, HABITAT AND DISTRIBUTION. — Single to caespitose, forming ectomycorrhizae with *Pinus kesiya* var. *langbianensis*, *P. armandii* and *Fagaceae* spp. Widely distributed in Yunnan and Guizhou Provinces, Southwestern China.

NOTES

Cantharellus yunnanensis was described as showing pale to pale salmon coloration with ridge-like gill folds, while our samples displayed a bright yellow, well-defined gill-like folds of up to 3 mm high and 0.8-1.5 mm wide. However, it is possible that the original description was based on dried material (Fig. 4). Additionally, the original description lacks some morphological information that is of taxonomic significance for the subgenus *Cantharellus*, e.g., the presence of clamp connections and thick-walled hyphal extremities in the pileipellis (Buyck *et al.* 2014). A cautious check of the holotype revealed important differences in the shape (ovoid, smooth, and pale olive) and size (7.5-8.0 × 6.5-7.0 μm) of the spores, compared to the original description (Chiu 1973). Additionally, we found smaller basidiospores that we interpreted as immature spores from young fruit bodies. Unfortunately, we could not obtain a sequence from the holotype due to the long period of preservation in the herbarium. *Cantharellus yunnanensis* is one of the most popular chanterelles in the edible mushroom markets of Yunnan Province. The lack of an accurate description or sequence allowed us to select a suitable collection as the epitype.

Cantharellus cibarius Fr.

(Figs 5-6)

In Systema Mycologicum (Lundae) 1: 318 (1821).

Agaricus chantarellus L., *Species Plantarum* 2: 1171 (1753). — *Merulius chantarellus* (L.) Scop., *Flora Carniolica*, ed. 2, 2: 461 (1772) "*cantharellus*". — *Cantharellus flavescens* Lam., *Encyclopedie* 1 (2): 694 (1785) [nom. nov. based on *Agaricus chantarellus* L.]. — *Cantharellus edulis* Pers., *Neues Magazin für die Botanik* 1: 106 (1794) [nom. illeg. Art. 52.1]. — *Cantharellus vulgaris* Gray, *Natural Arrangement of British Plants* 1: 636 (1821) [nom. illeg. Art. 52.1]. — *Craterellus cibarius* (Fr.: Fr.) Quéf., *Flore mycologique de la France et des pays limitrophes*: 37 (1888). — *Alectorocephoides cibarius* (Fr.: Fr.) Earle, *Bulletin of the New York Botanical Garden* 5: 407 (1909). — *Cantharellus cibarius* f. *pallidus* R. Schulz in Michaël, *Führer für Pilzfreunde* 1: no. 82 (1923). — *Cantharellus cibarius* var. *inodorus* Velen., *Novitates Mycologicae*: 36 (1939). — *Cantharellus cibarius* var. *atlanticus* Romagn., *Docums Mycology* 25 (98-100): 421 (1995). — *Cantharellus parviluteus* Fern. Sas., Pérez-de-Greg. & Eyssart., *Bulletin de la Société mycologique de France* 119 (3-4): 262 (2003).

MYCOBANK. — 201371.

NEOTYPE. — United Kingdom, England, Devon, Bovey Tracey, Tradbere Down, on the ground near *Betula*, 3.X.1992, N.W. Legon, K(M)22132. (Olariaga *et al.* 2016).

MATERIAL EXAMINED. — Tuan County, Jilin Prov., China. Changbai Mountain Natural Reserve, 7.VIII.2010, Wang XH2580, (HKAS[HKAS 58234]).

HABIT, HABITAT AND DISTRIBUTION. — Single to caespitose, forming ectomycorrhizae with *Pinus koraiensis* or *Quercus mongolica*. Present in Jilin Province, northeastern China.



FIG. 4. — *Cantharellus yunnanensis* W.F. Chiu, holotype S.C. Shen (8090).

DESCRIPTION OF THE CHINESE COLLECTION

Basidiomata

Fleshy, medium-sized.

Pileus

Convex-planar, later becoming more or less planar with age; margin incurved or straight, regular or folded, smooth, thin; with surface smooth to minutely pubescent, orange-yellow (3A7, 3A8) to bright yellow at the margin (1A7, 2A6).

Context

Solid.

Hymenophore

With well-defined gill-like folds, up to 3 mm, decurrent, forking and anastomosing only near the cap margin, pale yellow to light yellow (3A2, 3A3).

Stipe

Solid, subcylindrical tapering downwards, concolorous with the hymenophore with a yellow tint (2A6).

Odor

Mild, agreeable, sometimes fruity.

Taste

Mild, agreeable.

Spore print

No color.

Basidiospores

Oblong to reniform, smooth, colorless, and hyaline, thin-walled, $8-10 \times 5-6 \mu\text{m}$. $Xm = 9.14 \times 5.08 \mu\text{m}$, $Q = 1.60-2.0$.

Basidia

$80-105 \times 7-9$ (-10) μm , long and slender, 5-6 sterigmata.

Cystidia

Absent.

Hymenophoral trama

Composed of intermingled filamentous hyphae $3.0-5.0 \mu\text{m}$ diam., colorless, thin-walled in an irregular arrangement.

Pileipellis

Mainly of the cutis type, in some areas of the surface, the terminal hyphae may be erect, forming an intricate trichoderm and cluster of hyphae. Hyphae of the pileipellis $4.0-6.0 \mu\text{m}$



FIG. 5. — *Cantharellus cibarius* Fr., basidiomes WangXH2580 (By Xiang-Hua Wang).

diam., intermingled in a compact (cutis) or slightly loose (trichoderm) arrangement, cylindrical, hyaline to yellowish, often with light yellow contents in some, decidedly light yellow-colored, slightly thick-walled ($<1\ \mu\text{m}$ thick); distinctive terminal elements $28\text{--}76 \times 5\text{--}7\ \mu\text{m}$ broad, thick-walled ($1\ \mu\text{m}$ thick), smooth, hyaline to light yellow.

Pileus trama

Composed of cylindrical to inflated hyphae, $4\text{--}6\ \mu\text{m}$ diam., slightly thick-walled ($<1\ \mu\text{m}$ thick), hyaline, yellowish in mass.

Clamp connections

Present in all tissues examined.

DISCUSSION

Cantharellus cibarius was previously reported by Li *et al.* (2018) as a popular edible mushroom marketed in Yunnan and Sichuan Provinces, China. Their study did not include a morphological description of the collections; thus, there was no evidence available for the identified species. Herein, our phylogenetic analyses based on *tef-1 α* (Fig. 1) strongly sup-

ported (100/1) the sister relationships of *C. cibarius* (MG75, Li *et al.* 2018) with *C. anzutake* and *C. yunnanensis*, which together belong to the same clade and not the *C. cibarius* clade. These two clades were found to be distinct and distantly located in this study (Fig. 1); therefore, our results disagree with a previous report on *C. cibarius* (*sensu* Li *et al.* 2018) in China. Nevertheless, we recommend further collections and analyses involving more loci to confirm the identity of the species. In this work, we present a new and accurate record of *C. cibarius* from the northeastern part in China, based on morphological and molecular evidence. We thus confirm that the distribution of *C. cibarius* is not restricted to northern Europe and America.

The epithet “*yunnanensis*” refers to the distribution of these species in different areas of Yunnan Province, China. The Herrera 263C collection (Fig. 2) was selected as the epitype, as it was collected at the same locality (Kunming, China) where the holotype was previously described. The additional material examined herein was collected in different parts of the province and another province in the vicinity, Guizhou.

Due to the short morphology described for the type specimen of *C. yunnanensis*, Ogawa *et al.* (2018) suggested that



FIG. 6. — *Cantharellus cibarius* Fr. Wang XH2580. **A**, spores; **B**, basidia; **C**, terminal hyphae of the pileipellis. Scale bars A, 25 µm; B, C, 10 µm.

this species belongs to the subgenus *Parvocantharellus* (Buyck *et al.* 2014). This is contrary to our findings based on the epitypification of *C. yunnanensis* and supported by molecular

phylogenetic analyses, as the sequences of the *C. yunnanensis* epitype clustered with other species in subg. *Cantharellus* (*C. anzutake* + *C. phasmatis* + *C. tenuithrix* + *C. deceptivus* +

C. pallens). The distinct wall thickness ($<1\ \mu\text{m}$ thick) of the terminal hyphae of the pileipellis observed in the epitype (Fig. 3C) additionally supported its placement in the subgenus *Cantharellus*, as species within the subgenus *Parvocantharellus* display typically thin-walled hyphal ends (Buyck *et al.* 2014).

Our phylogenetic analyses (Fig. 1) placed the Chinese sample of *C. cibarius* together with samples collected from Japan (LC085476, LC085477), Slovakia (GQ914950), Finland (KM893842) and France (GQ914949) with strong support values (100/0.9). Moreover, the description of the Chinese sample of *C. cibarius* in this study is largely consistent with the existing description of the epitype from Sweden provided by Olariaga *et al.* (2016). In contrast, the Chinese collection possessed pale yellow to light yellow gill-folds instead of the typical ochre-yellow to orange-yellow or slightly pinkish forked veins of the hymenophore.

The close morphological similarities between *C. cibarius* and *C. yunnanensis* underlie the difficulties in the identification of the two species. Herein, we propose the general coloration as a key feature for identifying and delimiting both species: *C. cibarius* (Fig. 5) displays an orange-yellow to bright yellow color and a plane pileus, while *C. yunnanensis* (Fig. 2) displays paler basidiomata and a convex pileus. Similarly, a detailed microscopic examination revealed useful quantitative characteristics for delimiting the species. For instance, *C. yunnanensis* exhibits ellipsoid spores ($Q = 1.30\text{--}1.55$), long and wide basidia ($60\text{--}95 \times 7\text{--}12\ \mu\text{m}$), and terminal hyphae of the pileipellis that are long and wide ($22\text{--}77 \times 5\text{--}10$) and slightly thick-walled ($<1\ \mu\text{m}$ thick). In contrast, in *C. cibarius* (Fig. 6C), the spore shape is oblong to reniform ($Q = 1.80$), basidia are long and slender ($80\text{--}105 \times 7\text{--}9\ \mu\text{m}$), and the terminal hyphae of the pileipellis are long and slender ($28\text{--}76 \times 5\text{--}7$) and have thicker walls ($1\ \mu\text{m}$).

Our single-locus phylogenetic analyses (Fig. 1) showed the sister relationships of *C. yunnanensis* and Japanese *C. anzutake* W. Ogawa, N. Endo, M. Fukuda & A. Yamada, 2017. We suspect that the latter species has also been misidentified and recorded as *C. cibarius* (Kawamura 1908) in Japan, possibly because of its bright color. Notably, there are distinct morphological differences between *C. anzutake* and *C. yunnanensis* (Figs 1, 2). For example, different spore shapes (globose to oblong [$Q = 1.1\text{--}1.8$] vs. ellipsoid [$Q = 1.30\text{--}1.55$]) and shorter and slender basidia ($55\text{--}74 \times 7\text{--}10$ vs $60\text{--}95 \times 7\text{--}12$) may be autapomorphic of *C. anzutake* and *C. yunnanensis*, respectively. Based on the newly inferred evolutionary relationships, *C. anzutake* and *C. yunnanensis* appear to constitute sister clades, which are together sister to the clade containing other N. American species (*C. deceptivus* Buyck, Justice & V. Hofst., + *C. pallens* Pilát, *C. phasmatis* Foltz & T.J. Volk, + *C. tenuithrix* Buyck & V. Hofst.), which are distantly located to the *C. cibarius* clade (Fig. 1).

The multiyear survey conducted in Yunnan markets confirmed the presence of *C. yunnanensis* in different areas of this province and included some samples from both Guizhou Province and Yunnan Province in China. Taken together, our morphological and molecular methods (based on *tef-1 α* sequences) confirmed that the edible yellow chanterelles com-

monly sold in the mushroom markets of Yunnan Province are not *C. cibarius* and are instead *C. yunnanensis*. However, the occurrence of *C. cibarius* in China is limited to Northern China. On this note, more explorations are imperative to confirm and understand the distribution range of the species in China. However, Yunnan Province is one of the ecologically most diverse regions in China because of its geographical characteristics. Its mountainous elevations in the northwest and low elevations in the southeast provide highly diverse habitats for macrofungi such as *Cantharellus* species and could serve as a barrier to their diversification. This study contributes to the elucidation of the taxonomy of the *Cantharellus cibarius* complex in China. Therefore, we suggest an integrative taxonomic method that will yield a well-resolved delineation boundary between species complexes and reveal new species in this genus. Finally, our study provided a clear concept for understanding the resolution power of integrative taxonomy (morphology and molecular) in species identification and classification. This combined approach substantially resolved the uncertainty regarding the two species (*C. yunnanensis* and *C. cibarius*) previously described and reported in China.

Acknowledgements

The first author wishes to thank Dr Xiang-Hua Wang (Kunming Institute of Botany, CAS) for help with basidiospore observation in some samples. M. Herrera wants to thank the China-Latin America Young Scientists Exchange Program (2017), Ran Wang and Peng Zhang (Kunming Institute of Botany, CAS) for assistance in the field and markets, and Prof Fu-Qiang Yu (Kunming Institute of Botany, CAS) for his valuable support during the field work and for the taxonomic and molecular analysis of some samples. We are grateful to Dr Brian Schwartz, Dr Felipe Wartchow (associate editor) and an anonymous reviewer for a revision and helpful comments that improved the manuscript. We also wish to thank Biol. David Ramos (Instituto de Ecología, A.C., Xalapa, Mexico) for technical suggestions and image editing. This work was supported by the National Key R & D Program of China (2017YFC0505204) and the National Natural Science Foundation of China (Grant Nos. U1202262 and 31270075).

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Submitted on 20 April 2020;
accepted on 13 January 2021;
published on 19 March 2021.