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Finding correct names for economically important chanterelles (*Cantharellus*, Hydnaceae, Cantharellales) in southwestern China: a plea for third party annotation of sequences in GenBank

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Abstract

One might think that the use of DNA sequences in species recognition will soon have solved all taxonomic confusions. This scenario, however, is not what happened in the taxonomy of chanterelles in the eastern and southern parts of Asia. To solve the name problems associated with chanterelles in southwestern China, we sequenced the loci ITS, LSU, *rpb2* and(or) *tef1* of 68 *Cantharellus* specimens collected in China and South Korea, including the holotypes of *C. albovenosus, C. tuberculosporus, C. versicolor* and *C. zangii*. We used these sequences to link species described from China, India, Japan and South Korea. We took an in-depth look at available sequence data for Indian *Cantharellus* that have caused a lot of taxonomic confusions. We found most DNA data related with Asian chanterelles have flaws concerning either wrong sequences, unreliable base pairs, or confusing metadata. These problems, together with over-interpretation of genetic and morphological variation, are responsible for many synonyms. Taxonomically, we reached the following conclusions: *C. yunnanensis* is a *Craterellus*; *C. tuberculosporus* is a very rare Himalayan species close to *C. cibarius*; *C. versicolor* is the most common subalpine golden chanterelle in the Himalayas; the earliest available name for the bulk of marketed, yellow, medium-sized chanterelles in temperate and subtropical China is *C. applanatus*, not *C. yunnanensis*; *Cantharellus anzutake, C. himalayensis* and *C. natarajanii* are all synonyms of *C. applanatus*; *C. sinominor* and *C. subminor* are later synonyms of the Indian *C. elongatipes*; *C. sikkimensis* is conspecific with *C. zangii*; *C. albovenosus* is merely a white-gilled form of *C. phloginus*. Allowing third party annotations or comments directly in the nucleotide database of NCBI would constitute a much more efficient way to signal errors or omissions concerning both sequences and their associated metadata deposited in GenBank.

Keywords – *Craterellus* – holotype – INDELs – ITS – morphology – species recognition

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Introduction

For fungal groups that are difficult to identify on the basis of their morphological features, it is believed (and in most cases also proved) that the application of DNA sequences is able to delimit/recognize species much more easily and unequivocally (O'Donnell et al. 2011, Du et al. 2012, Sheedy et al. 2013, Buyck et al. 2016b, Wang et al. 2016). With or without the aid of morphological evidence, DNA data have facilitated and accelerated the description of new taxa, resulting in a dramatic increase in the numbers of new species (Yang 2011, 2020). As species circumscriptions get narrower and narrower, the quality of DNA data becomes more and more important.

Cantharellus is a genus in which species are difficult to separate on the sole basis of their morphology. Until hardly ten years ago, all of the Asian chanterelles were identified on the basis of their overall color and size (Corner 1966, 1969, 1976, Chiu 1973, Zang 1980, Eyssartier et al. 2009). This resulted in very wide species concepts in the pre-molecular era. As a consequence, many Asian *Cantharellus* were considered conspecific with American or European species (Wang et al. 2004, Shao et al. 2012). For instance, in the pre-molecular era, nearly every medium-sized, yellow *Cantharellus* was assumed to represent the European *C. cibarius*, irrespective of where it was found on the planet. This is clearly illustrated by the distribution map of *C. cibarius* on the 'discover life' website, which is based on existing historical records and preserved specimens (Fig. 1).

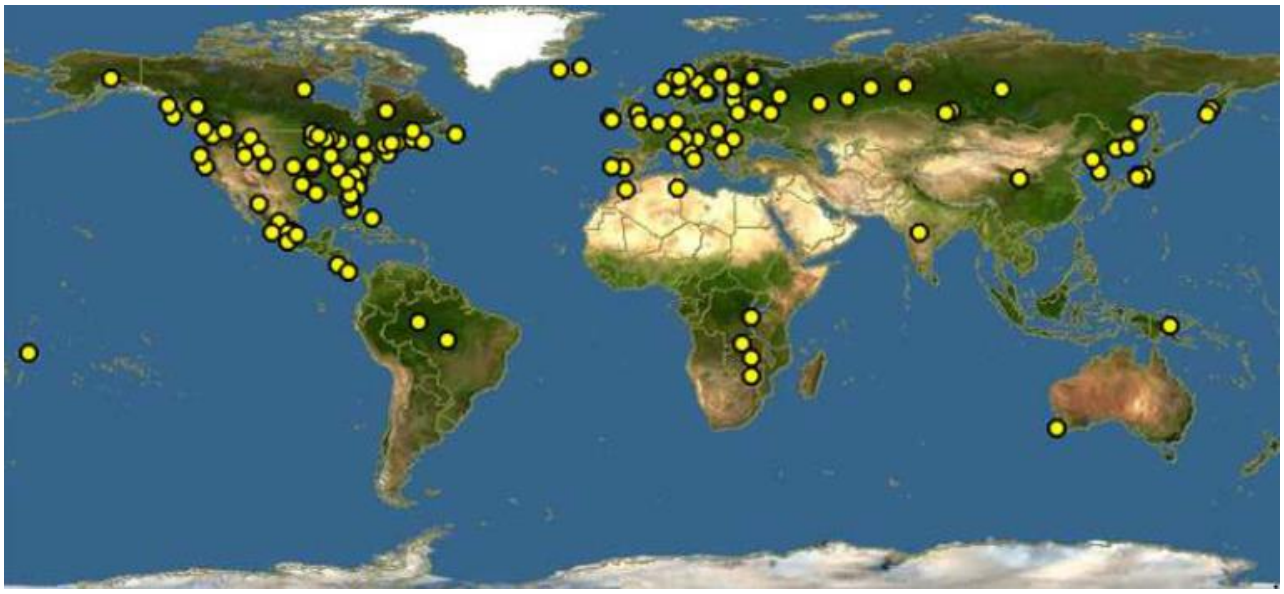


Figure 1 – Distribution map of existing records of *Cantharellus cibarius* in the world, a species with a predominantly circum-arctic distribution at higher latitudes (https://www.discoverlife.org/mp/20m?kind=Cantharellus+cibarius, Accessed on May 8, 2022).

A modern tendency in the taxonomy of *Cantharellus*, as in many other fungal groups, is to rely on DNA data to describe and identify species. As long as there is genetic difference, one may recognize a different species (e.g. Foltz et al. 2013, Antonín et al. 2017). With the generalized use of sequence data to build single gene or multilocus phylogenies to support the description of new Asian *Cantharellus*, one might think that species concepts should now be clear and well-defined. This is, however, not the case in the eastern and southern parts of Asia. Contradictory interpretations of species concepts, incomparability of DNA sequences between different species, questionable DNA sequences and puzzling or erroneous tags associated with sequences in GenBank are prevalent among the Asian species.

In this study, we made an effort to find correct names for the chanterelles in southwestern China, by carefully detecting the sequence problems with Indian *Cantharellus* species, re-checking

the holotypes of *C. yunnanensis* and *C. tuberculosporus*, and generating reliable DNA data from widely collected specimens and some holotypes to link species described from China, India, Japan and South Korea and finally separate the wheat from the chaff. The reason why we focused on the Indian species is that they are the first batch of Asian species published with DNA data but the ITS and LSU phylogenies are highly incongruent. Correct interpretation of these species is fundamental to all later research on the genus. *Cantharellus yunnanensis* and *C. tuberculosporus* were originally described from southwestern China. The correct interpretation of these two species is also of particular interest as both names are frequently used to refer to the widely commercialized 'golden chanterelles' in Yunnan. However, the recent epitypification of *C. yunnanensis* by Shao et al. (2021) seems not conform to the original description and the true identities of both species are still riddles for researchers.

Materials & Methods

Sampling of collections for sequencing

We studied and sequenced 68 specimens representing 16 species occurring in subtropical, temperate or subalpine habitats in eastern Asia, as well as 11 specimens of eight species from Europe and North America (Table 1). These species belong to subgenera *Cantharellus*, *Cinnabarini* and *Parvocantharellus*, the three dominant subgenera in the northern hemisphere (Buyck et al. 2014). Our sampling covered all the major clades described in these subgenera (Olariaga et al. 2017, Cao et al. 2021).

The holo- and paratypes of *C. tuberculosporus, C. versicolor* and *C. zangii*, the holotype of *C. albovenosus* and the epitype of *C. yunnanensis* selected by Shao et al. (2021), were sequenced to solve existing identification problems. We specifically sampled among collections made in subalpine oak forests in Tibet, China, the habitat for the holotype of *C. tuberculosporus* to understand the relation between *C. tuberculosporus* and the equally subalpine and morphologically similar *C. versicolor*.

For the phylogenetic analyses of each of the abovementioned subgenera, we further selected representatives of already known Asian, European and American species, using specimens that can minimize missing data. These sequences were retrieved from the following publications: Shao et al. (2011, 2012, 2016a, 2016b, 2021), Kumari et al. (2011, 2013), Foltz et al. (2013), Buyck et al. (2014, 2016a, 2016b, 2016c, 2016d, 2020), Das et al. (2015), Leacock et al. (2016), An et al. (2017), Olariaga et al. (2017), Ogawa et al. (2018), Lao et al. (2019), Cao et al. (2021) and Zhang et al. (2021a, 2021b, 2021c).

Morphology

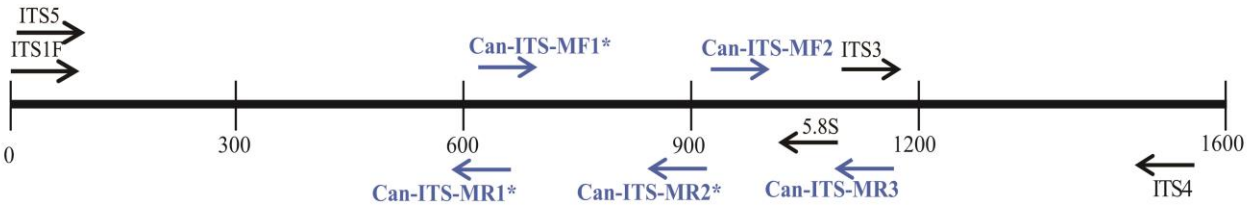
Microscopic characters were examined under a Nikon E400 microscope (Nikon, Tokyo) at a magnification of 1000 ×. Fragments of hymenium and pileipellis were briefly heated in a 5% KOH solution before observation in Congo red ammonium solution. Line drawings were made at a projected magnification of 2400 × with the aid of a drawing tube (Y-IDT, Nikon, Tokyo, Japan). Spore dimensions are based on 20 spores per individual and follow the format (a) b–***m***–c (d), with ***m*** the mean value, b–c containing at least 90% of all values and (a) and (d) the extremities. Q indicates the basidiospore length/width ratio.

DNA extraction, PCR amplifications, cloning and sequencing

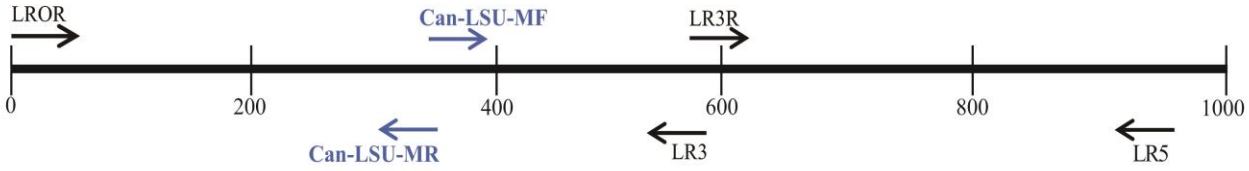
The sequencing of our collections targeted four loci (ITS, LSU, *rpb2* and *tef1*) in order to allow a comparison with previous studies in which the description of new species was supported by less loci, e.g. ITS and LSU used by Kumari et al. (2013) and Ogawa et al. (2018), *tef1* by Shao et al. (2016b) and Antonín et al. (2017) or LSU, *rpb2* and *tef1* by Cao et al. (2021) and Zhang et al. (2021a, 2022).

For DNA extraction, PCR and sequencing, we basically followed the methods of Buyck et al. (2014). General primers published by White et al. (1990), Moncalvo et al. (2000), Liu et al. (1999)

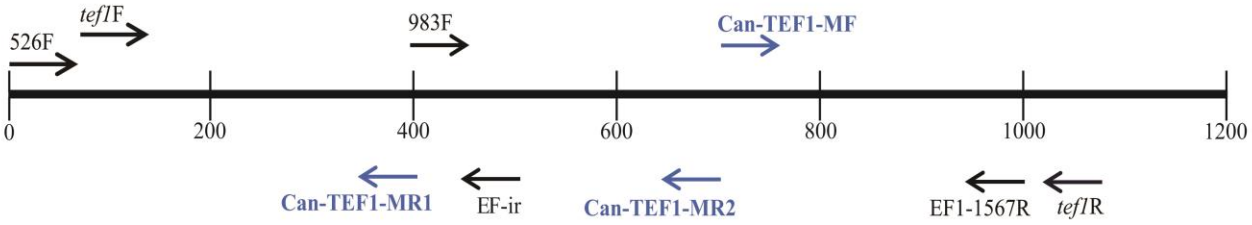
and Morehouse et al. (2003) were used to amplify the ITS, LSU, *rpb2* and *tef1* regions respectively. For problematic samples where PCR or sequencing failed, the loci were amplified using additional internal or specific primers. The internal and specific primers were designed by comparing the sequences of a certain group and finding the conserved domains. Primers for PCR are shown in Fig. 2.



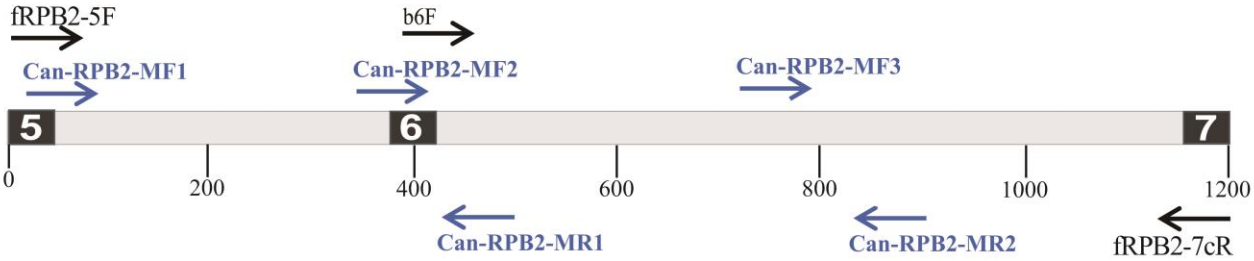
Can-ITS-MF1*: 5'- GGCCTTGTGCCAAYAACATGCC -3'
Can-ITS-MF2: 5'- CTGAAGTTATGGGCCTCGA -3'
Can-ITS-MR3: 5'- GCAACTCACACCAGTTATCGCA -3'
Can-ITS-MR1*: 5'- GGCATGTTRTTGGCACAAGGCC -3'
Can-ITS-MR2*: 5'- TCGAGGCCCATAACTTCAG -3'



Can-LSU-MF: 5'- CAAGTACCGCAAGGGAAAGATGAA -3'
Can-LSU-MR: 5'- TTCATCTTTCCCTTGCGGTACTTG -3'



Can-TEF1-MR1: 5'- ATGAAGTCACGRTGSCCRGGAGC -3'
Can-TEF1-MF: 5'- ATCAAGAARGTYGGYTACAACCC -3'
Can-TEF1-MR2: 5'- GGGTTGTARCCRACYTTCTTGAT -3'



Can-RPB2-MF1: 5'- GGCTAGTCTGTTCCGAAWGC -3'
Can-RPB2-MF2: 5'- GATTGCTAARCCTCGTCAGC -3'
Can-RPB2-MF3: 5'- ATGCCGYCCRTTRTTTATTGTCGAG -3'
Can-RPB2-MR1: 5'- GAACCRACRGATATGCAAGCCA -3'
Can-RPB2-MR2: 5'- CATGCAWATCATGACTGTYTCTTCC -3'

Figure 2 – Primers used in this study, with their positions and directions shown by arrows on a schematic map of the gene/region. Primers designed by this study are in bold blue. Other primers are given in White et al. (1990), Liu et al. (1999), Moncalvo et al. (2000) and Morehouse et al. (2003). ITS primers marked with asterisks are specific for *Cantharellus* subg. *Cantharellus*.

For sequences with INDELs, we followed the method of Flot et al. (2006) and Hughes et al. (2013) to determine heterozygosity of INDELs, i.e., INDELS were inferred when peaks abruptly went out of phase. For a simple 1–4 bp INDEL, a comparison of forward and reverse sequences allowed determination of haplotypes. For sequences with two or more INDELs, polystructures or low-quality chromatograms, it was difficult to phase the heterozygosity and we cloned the PCR products using Takara pMD^{TM}18-T cloning kit (Dalian, China) following the manufacturer's instruction. Colonies were screened for the presence of the desired products using primer pair M13F+M13R. Clones with different sizes of inserted target segments were selected by electrophoresis on 2% gel. At least two clones with the desired length of PCR product were sequenced, resulting in two or more GenBank accessions for a single sample (Table 1).

PCR amplification and Sanger sequencing of the type specimens of *C. tuberculosporus*, *C. versicolor*, *C. zangii* and a new specimen of *C. tuberculosporus* (BF1659) totally or partly failed. Therefore, lower coverage whole genome sequencing ("genome skimming"), using the next-generation sequencing by Illumina NovoSeq-5500 platform, was conducted to recover the target loci for these samples. Genomic DNAs from types of *C. versicolor*, *C. zangii* and the sample BF1659 of *C. tuberculosporus* were extracted using a CTAB protocol. The DNA from the type of *C. tuberculosporus* was extracted using Tiangen DNAsecure Plant Kit (DP320). Library preparation followed the protocol described by Zeng et al. (2018). The raw data were de novo assembled using GetOrganelle toolkit (Jin et al. 2020). The target regions were extracted from assemblies using the reference sequences of *C. enelensis*, *C. versicolor* and *C. zangii* by local BLAST.

Phylogenetic analyses

For each of the three subgenera, the four loci were combined into one dataset and the three datasets were analyzed separately. Considering that the analysis aimed at solving species recognition rather than the phylogenetic framework, the introns of *rpb2* and *tef1* were kept in the alignments. The ITS-1 region contained highly divergent sections, within which only certain subsets of the taxa or populations could be aligned. Therefore, parts of the dataset were interleaved in alternating blocks of aligned complete sequences and aligned partial sequences. The combined dataset was partitioned into eight partitions following the partitioning strategy of Buyck et al. (2014), plus two of the introns of *rpb2* and *tef1*. To avoid exclusion of regions useful for resolving terminal relationships (species rank), we used no outgroup sequences and the trees were midpoint-rooted.

Maximum Likelihood inference as implemented in RAxML ver. 7.2.6 (Stamatakis 2006) was conducted to construct the phylogenies, using a GTR Gamma model. For each analysis, a ML bootstrap analysis was performed, using 1000 fast bootstrapping replicates from random starting trees, followed by a subsequent ML search using 1000 replicates. A ML bootstrap (ML-bs) >70% was considered as the threshold for significant branch support for monophyletic taxa. Trees were viewed and exported as PDF in FigTree 1.3.1 and processed in Adobe Illustrator CS5.

Results

Sequence phasing

We obtained 353 new sequences from 79 specimens (68 from Asia, 10 from North America and one from Europe) representing 21 species: 192 ITS, 97 LSU, 60 *tef1* and 67 *rpb2* sequences. Among the 72 samples that were sequenced with Sanger sequencing method, 49 out the total of 72 have an ITS region with INDELs, i.e. several copies differing in length. For the other loci obtained from these samples, 12 out of 70 obtained LSU, 3 out of 53 obtained *tef1* and 2 out of 62 *rpb2* had INDELs.

XHW4349 (from Maguan County, Yunnan) is one of the samples that have INDELs in the ITS region. In its ITS-1 region sequenced with primer 5.8S (reverse primer), the peaks abruptly go out of phase at position 503 bp (viewed from reverse complementary direction, Fig. 3a). This

suggests that an INDEL is present among different copies. By comparing the double peaks with the ITS sequences of *C. applanatus* holotype (HQ270118) and *C. anzutake* holotype (LC085359), we found that the two base pairs of each double peak exactly coincide with the two corresponding base pairs of the two holotypes (Fig. 3a). When performing electrophoresis, two bands were observed (Fig. 3b), further supporting the presence of more than one copy with length variation. We cloned the ITS-1 region of this sample and obtained four different copies: MW415852 and MW415853, two short copies having the 100 bp deletion, MW415852, a long copy lacking the 100 bp deletion and finally MW415851, a long copy but having a GTGT insertion.

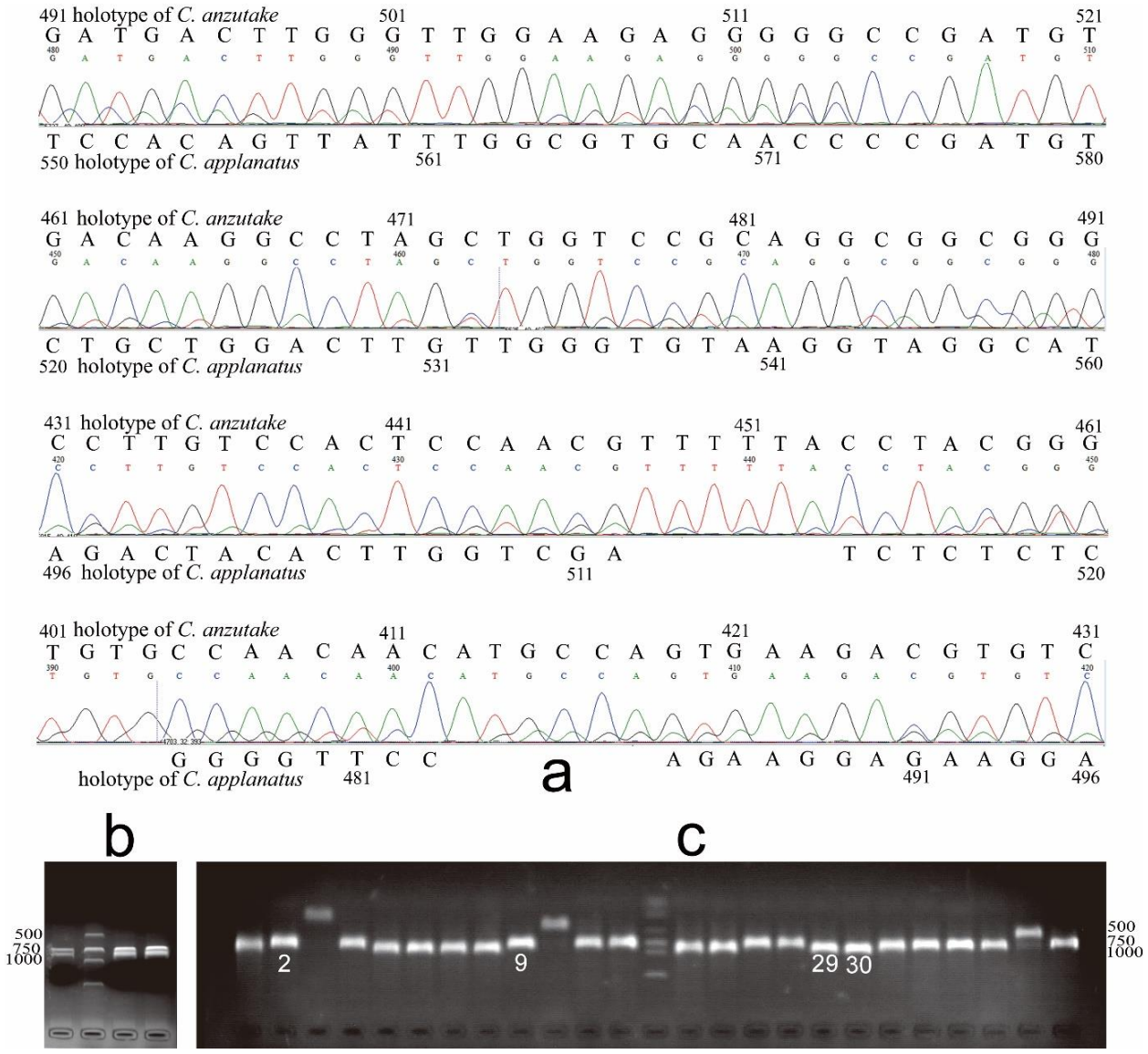


Figure 3 – a Chromatogram of ITS-1 region of XHW4349, PCR using primer pair ITS5+5.8S, sequenced with primer 5.8S and shown in reverse complementary direction. Base pairs (black letters) and numbers above the chromatogram are for the GenBank accession LC085359, ITS of the holotype of *Cantharellus anzutake*. Those beneath the chromatogram are for HQ270118, ITS of the holotype of *C. applanatus.* Note the peaks became out of phase from 504 bp (small color numbers above the reads) and the base pairs of the two holotypes sequences exactly coincide with the two base pairs of the double peaks. This clearly suggests that the long copy is highly similar to HQ270118 and short one to LC085359. b Amplification of ITS-l region (using primer pair ITS5+5.8S) of XHW4349, electrophoresed on a 2% agarose gel. Note there are two bands, indicating there are different copies with length variation. c Amplification of different clones of ITS-l region (using primer pair ITS5+5.8S) of XHW4349, electrophoresed on a 2% agarose gel. Lanes 2, 9, 29 and 30 were sequenced, resulting in four ITS sequences differing in length.

Table 1 Samples used for molecular phylogenetic analyses and species recognition in this study (Newly generated sequences are in bold. Sequences generated by next-generation sequencing are marked with *. For type specimens HT refers to holotype and ET to epitype.

Species	**Specimen (herbarium)**	**Geographical Origin**	**GenBank accession**			
			ITS	**LSU**	***tef1***	***rpb2***
C. alborufescens	1108/BB12.075 (PC)	Italy	KX907209	KX929161	KX907243	KX907232
C. alborufescens	G. Corriol (AH44783)	France	KR677492	KR677530	KX828817	KX828736
C. albovenosus	1690/VA13.152 (PC0142456) HT	South Korea	**ON197315**	**ON150910**	KY271942	**ON168704**
C. albus	SPJ615 (KUN-HKAS 107045)	China: Yunnan	–	MT782540	MT776015	MT776012
C. albus	GDGM81399	China: Guangdong	–	MZ605074	MZ613977	MZ614022
C. altipes	337/BB07.115 (PC0084082)	USA: Texas	JN944018	JN940599	GQ914943	JN993602
C. altipes	344/BB07.162 (PC0084079)	USA: Texas	–	KF294636	GQ914945	KF294713
C. amethysteus	AH44796 ET	Spain	KR677512	KR677550	KX828819	KX828738
C. amethysteus	349/BB07.284 (PC0084070)	Slovakia	JN944020	KF294639	GQ914953	KF294716
C. anzutake	C-84 (TNS-F-61925) HT	Japan	LC085359	LC085415	LC179800	–
C. appalachiensis	1084/JJ MO-Cant-3 (PC)	USA: Missourri	–	KX857090	KX857032	KX856994
C. appalachiensis	342/BB07.123 (PC0084075)	USA: Texas	–	KF294635	GQ914979	KF294711
C. applanatus	121-08 (PUN 3964) HT	India	HQ270118	HM750918	–	–
C. applanatus	XHW2994 (KUN-HKAS 73546)	China: Shandong	**MW415858**	**MW367478**	**MW368924**	**ON089586**
C. applanatus	XHW4349 (KUN-HKAS 109695)	China: Yunnan	**MW415850 MW415851 MW415852 MW415853**	**MW367474**	**MW368919 MW368920**	**ON089579**
C. applanatus	XHW4372 (KUN-HKAS 109698)	China: Yunnan	**MW415855 MW415856**	**MW367476**	**MW368922**	**ON168705**
C. applanatus	XHW4572 (KUN-HKAS 109700)	China: Yunnan	**MW415857**	**MW367477**	**MW368923**	**ON089581**
C. applanatus	XHW4355 (KUN-HKAS 109696)	China: Yunnan	**MW415859 MW415860**	**MW367479**	**MW368925**	**ON089587**
C. applanatus	XHW4356 (KUN-HKAS 109697)	China: Yunnan	**MW415861 MW415862**	**MW367480**	**MW368926**	**ON089588**
C. applanatus	XHW4555 (KUN-HKAS 109699)	China: Yunnan	**MW415854**	**MW367475**	**MW368921**	**ON089580**
C. applanatus	XHW4653 (KUN-HKAS 109820)	China: Yunnan	**ON054214**	**ON054267 ON054268**	**ON089606**	**ON089583**
C. applanatus	XHW8043 (KUN-HKAS 117674)	China: Yunnan	**ON054211 ON054212**	**ON054265**	**ON089605**	**ON089582**

Table 1 Continued.

Species	Specimen (herbarium)	Geographical Origin	GenBank accession			
			ITS	**LSU**	***tef1***	***rpb2***
C. applanatus as "*C. yunnanensis*"	Yuan13983 (IFP019491)	China	–	MW979527	MW999428	–
C. applanatus as "*C. yunnanensis*"	Yuan13985 (IFP019492)	China	–	MW979528	MW999429	–
C. applanatus as "*C. yunnanensis*"	Yuan14539 (IFP019450)	China	MW980541	MW979514	MW999422	–
C. applanatus as "*C. yunnanensis*"	Yuan14636 (IFP019451)	China	MW980542	MW979515	MW999423	–
C. applanatus as "*C. yunnanensis*"	XXD174 (KUN-HKAS 55817)	China: Yunnan	**ON054213**	**ON054266**	KU720337	–
C. applanatus as "*C. yunnanensis*"	Herrera 263C (KUN-HKAS 107313)	China: Yunnan	**ON054215**	**ON054269**	**ON089607**	**ON089584 ON089585**
C. aurantinus	M. Zhang (GDGM46278) HT	China: He'nan	–	MZ766517	MZ766560	–
C. aurantinus	Z.H. Zhang (GDGM81889)	China: Jiangsu	–	MZ766519	MZ766562	MZ766574
C. aurantinus	Z.H. Zhang (GDGM84974)	China: Jiangsu	–	MZ766521	MZ766564	MZ766572
C. austrosinensis	M. Zhang (GDGM81249) HT	China: Guangdong	–	MZ605082	MZ613983	MZ614027
C. austrosinensis	GDGM82877	China	–	MZ605088	MZ613990	MZ614033
C. austrosinensis	XHW4700 (KUN-HKAS 110470)	China: Yunnan	**ON100847 ON100848**	**ON074611**	**ON089625 ON089626**	**ON089635**
C. austrosinensis as "*C. appalachiensis*"	SCS47 (KUN-HKAS 59094)	China: Yunnan	HQ416695	HM582121	–	–
C. californicus	D. Arora (OSC122878) HT	USA: California	KX828768	KX828795	KX828820	KX828739
C. camphoratus	J. Tepp 11.08.05.av01 (UWO)	Canada: Newfoundland	KX592729	–	–	–
C. camphoratus	G.Gulden 12.09.22.av02 (UWO)	Canada: Nova Scotia	KX592737	KX592737	KX592738	–
C. chicagoensis	P.R. Leacock 8332 (F) HT	USA: Illinos	KP639200	KP639214	KP639233	–
C. chicagoensis	P.R. Leacock 8916 (F)	USA: Illinos	KP639201	KP639218	KP639230	–
C. cinnabarinus	312/BB07.001 (PC0084094)	USA: Texas	–	KF294624	GQ914985	KF294698
C. cinnabarinus	326/BB07.053 (PC0084093)	USA: Texas	–	KF294630	GQ914984	KF294705
C. cibarius	XHW2580 (KUN-HKAS 58234)	China: Jilin	**ON054209 ON054210**	KU720330	KM893847	–
C. cibarius	AFTOL-607 (not specified)	France	DQ200926	–	DQ059050	DQ366285

Table 1 Continued.

Species	Specimen (herbarium)	Geographical Origin	GenBank accession			
			ITS	**LSU**	***tef1***	***rpb2***
C. cibarius	C-142 (Shinshu Univ., Japan)	Japan	LC085397 +LC085399	–	LC085477	–
C. cibarius	XHW3576 (KUN-HKAS 76096)	Sweden	**MW415847 MW415848 MW415849**	**MW367473**	**MW368918**	**ON263464**
C. cibarius	A. Felipe & I. Olariaga (BIO-Fungi 10986) ET	Sweden	KR677501	KR677539	KX828823	KX828742
C. citrinus	1691/VA13.156 (PC0142457) HT	South Korea	–	–	MW124385	–
C. citrinus	1711/VA16.170 (PC0142468)	South Korea	–	–	MW124384	–
C. coccolobae	1065/ RC Guad11.025 (PC0142434) HT	Guadeloupe	–	KX857088	KX857020	KX856992
C. coccolobae	1064/RC Guad11.024 (LIP)	Guadeloupe	–	KX857089	KX857021	KX856993
C. corallinus	1083/JJ Mo-Canth-2 (PC0713846) HT	USA: Missouri	**ON426402 ON426403**	KX896776	KX857031	**ON260862**
C. corallinus	1086/JJ Mo-Canth-5 (PC0713849)	USA: Missouri	KX896758	**ON248120**	KX857034	**ON260863**
C. curvatus	1695/VA14.57 (PC0142461) HT	South Korea	–	–	MW124390	–
C. curvatus	XHW2590 (KUN-HKAS 58235)	China: Heilongjiang	–	KU720331	KM893840	–
C. curvatus	XHW3025 (KUN-HKAS 73570)	China: Shandong	**ON100849 ON100850**	**ON074612**	**ON089627**	**ON089636**
C. deceptivus	1074/JJ13/WI-CANT-1 (PC0142430) HT	USA: Wisconsin	KX896761	KX896779	KX85702	**ON260859**
C. deceptivus	1079/NC-CANT-5 (PC0142429)	USA: North Carolina	KX896760	KX896778	KX857030	**ON260860**
C. diminutivus	485/DS 06.033 (PC0084739)	Malaysia	–	KF294661	–	KF294740
C. enelensis	UV13.08.21.av02 (DAOM721704) HT	Canada: Newfoundland	–	KX592712	–	–
C. enelensis	C. Vilneff E5 (UWO)	Canada: Newfoundland	KX592719	KX592719	KX592720	–
C. elongatipes	184-08 (PUN 3966) HT	India	–	HM750928	–	–
C. elongatipes	XHW4447 (KUN-HKAS 110274)	China: Yunnan	**ON100841 ON100842**	**ON074609**	**ON089624**	**ON089633**
C. elongatipes	XHW4450 (KUN-HKAS 110275)	China: Yunnan	**ON100843 ON100844**	**ON074610**	–	**ON089634**
C. elongatipes	XHW2426 (KUN-HKAS 58232)	China: Guizhou	**ON100845 ON100846**	**ON114074**	–	–
C. ferruginascens	P.A. Moreau (AH44782)	France	KR677488	KR677526	KX828826	KX828747

Table 1 Continued.

Species	Specimen (herbarium)	Geographical Origin	GenBank accession			
			ITS	**LSU**	***tef1***	***rpb2***
C. ferruginascens	A.Melendez & K.Ugartetxe (Bio-Fungi 11700)	Spain	KR677486	KR677524	KX828828	KX828750
C. fibrillosus	113-07 (PUN 3957) HT	India	HQ270125	HM750917	–	–
C. fibrillosus	236-06 (PUN)	India	HQ270128	HM750922	–	–
C. flavolateritius	1078/JJ NC Canth-4 (PC0713852) HT	USA: Wisconsin	–	–	KX857029	–
C. flavolateritius	1076/JJ NC-CANT-2 (PC0713851)	USA: North Carolina	MG450675	KX896783	KX857027	–
C. flavus	C066 (C0171585F) HT	USA: Wisconsin	–	JX030437	–	–
C. flavus	321/BB07.027 (PC0084091)	USA: Texas	–	KR349274	GQ914948	**ON168706**
C. formosus	1198/BB13.015 (PC0713859)	Canada: Vancouver	**ON197316 ON197317**	**ON150911**	KX857039	**ON168707**
C. formosus	1212/BB13.163 (PC)	USA: Oregon	**ON197318 ON197319**	KM484683	**ON168700**	**ON260861**
C. friesii	481/GE07.077 (PC0084719)	France	–	KF294659	–	KF294737
C. friesii	J.Teres (AH44798)	Spain	KR677484	KR677522	KX828831	KX828752
C. friesii	1001/EC09.16 (PC0142447)	Italy	KX907208	KX857083	KX857015	KX856987
C. galbanus	M. Zhang (GDGM86249) HT	China: Hainan	–	ZM766516	MZ766569	MZ766577
C. hainanensis	NKZ2289 (FHMU) HT	China: Hainan	KY407529	KY407524	KY407536	–
C. hainanensis	XHW7576 (KUN-HKAS 109711)	China: Henan	**ON054216 ON054217**	**ON054270 ON054271**	**ON089608 ON089609**	**ON089589**
C. himalayensis	169-07 (PUN3972) HT	India	HQ270129	HM750929	–	–
C. indicus	MSR2-07 (PUN3962) HT	India	HQ270122	HM750924	–	–
C. aff. *indicus*	XHW6691 (KUN-HKAS 109709)	China: Yunnan	**MW41586 MW415865**	**MW367482**	**MW368928 MW368929**	**ON089604**
C. iuventateviridis	1309/BPL523 (PC0142425) HT	USA: Mississippi	KX896762	NG_060428	KX857047	–
C. iuventateviridis	1543/SH14.7.2012 (PC0713847)	USA: Louisiana	–	**ON150912**	KX857064	**ON168708**
C. koreanus	1689/VA13.136 (PC0142455) HT	South Korea	**ON426398 ON426399**	**ON248118**	KY271941	**ON260857**
C. koreanus	1716/VA 15.114 (BRNM 792976)	South Korea	**ON426400 ON426401**	**ON248119**	**ON260864**	**ON260858**
C. laevihymeninus	LL693 (KUN-HKAS 125910)	China: Yunnan	**OP909721 OP909722**	**OP836053**	**OP846964**	**OP846965**

Table 1 Continued.

Species	Specimen (herbarium)	Geographical Origin	GenBank accession			
			ITS	**LSU**	***tef1***	***rpb2***
C. laevihymeninus	Yuan13900 (IFP019441)	China: Yunnan	MW980543	MW979520	MW999418	MW999453
C. laevihymeninus	Yuan13902 (IFP019442)	China: Yunnan	MW980544	MW979521	MW999419	MW999454
C. lateritius	215/BB06.319 (PC0084104) HT	USA: Texas	–	**ON150913**	**ON168701**	**ON168712**
C. lateritius	332/BB07.062 (PC0084102)	USA: Texas	KX896767	KX896784	GQ914956	**ON168711**
C. lewisii	314/BB07.003 (PC0084074) HT	USA: Texas	NR_120022	NG_060394	GQ914962	KF294700
C. lewisii	1394/BB14.148 (PC0142337)	USA: Texas	MG450668	MG450676	**ON168702**	**ON168709**
C. luteolus	M. Zhang (GDGM44258)	China: Hainan	–	MZ766514	MZ766566	MZ766570
C. luteolus	M. Zhang (GDGM60393) HT	China: Hainan	–	MZ766515	MZ766568	MZ766575
C. luteovirens	X.S. Liang (GDGM81079)	China: Guangdong	–	MZ605092	MZ613994	MZ614036
C. luteovirens	X.S. Liang (GDGM80672) HT	China: Guangdong	–	MZ605090	MZ613992	MZ614035
C. macrocarpus	NKZ4050 (FHMU3304) HT	China: Hainan	MT990453	MT986061	MT990634	–
C. macrocarpus	NKZ4036 (FHMU3303)	China: Hainan	–	MT986060	MT990633	–
C. minioalbus	M. Zhang (GDGM78901) HT	China: Yunnan	–	MZ605097	MZ613998	MZ614042
C. minioalbus	M. Zhang (GDGM78916)	China: Yunnan	–	MZ605100	MZ614001	MZ614045
C. minor	313/BB07.002 (PC0084747)	USA: Texas	–	KF294625	JX192978	KF294699
C. minor	329/BB07.057 (PC0084721)	USA: Texas	–	KF294632	JX192979	KF294707
C. natarajanii	106-08 (PUN 3963) HT	India	HQ270120	HM750926	–	–
C. pallens	997/BB09.418 (PC)	Italy	KX907206	KX907216	KX907238	KX907227
C. pallens	1115/BB12.082 (PC 0142450)	Italy	KX907211	KX857092	KX857036	KX856996
C. parvoflavus	Herrera229 (XAL)	Mexico	–	MT371339	MT449708	–
C. parvoflavus	Montoya5423 (XAL) HT	Mexico	–	MT371337	MT449706	–
C. phasmatis	C057 (C0171587F)	USA: Wiscosin	JX030464	JX030431	JX030417	–
C. phasmatis	C073 (C0171588F) HT	USA: Wiscosin	–	JX030426	–	–
C. phloginus	SCS99 (KUN-HKAS 58209)	China: Yunnan	–	KF801101	KF801096	–
C. phloginus	SCS98 (KUN-HKAS 58208) HT	China: Yunnan	–	–	KF801095	–
C. phloginus	XHW4571 (KUN-HKAS 110230)	China: Yunnan	**ON114083 ON114084**	**ON114068**	**ON156022**	**ON156031**
C. phloginus	XHW4570 (KUN-HKAS 110229)	China: Yunnan	**ON114082**	**ON114067**	**ON156021**	**ON156030**
C. phloginus	XHW4476 (KUN-HKAS 110288)	China: Yunnan	**ON114079 ON114080**	**ON114065**	**ON156019**	**ON156028**
C. phloginus	XHW4568 (KUN-HKAS 110227)	China: Yunnan	**ON114089 ON114090**	**ON114072**	–	–

Table 1 Continued.

Species	Specimen (herbarium)	Geographical Origin	GenBank accession			
			ITS	**LSU**	***tef1***	***rpb2***
C. phloginus	C.J. Zhou (KUN-HKAS 121395)	China: Hebei	**ON114076 ON114077**	**ON114063**	**ON156017**	**ON156026**
C. phloginus	XHW3006 (KUN-HKAS 73555)	China: Shandong	**ON114078**	**ON114064**	**ON156018**	**ON156027**
C. phloginus	X.J. Wang (KUN-HKAS 121413)	China: Hubei	**ON114081**	**ON114066**	**ON156020**	**ON156029**
C. phloginus	XHW4475 (KUN-HKAS 110287)	China: Yunnan	**ON114085 ON114086**	**ON114069**	**ON156023**	**ON156032**
C. phloginus	XHW4567 (KUN-HKAS 110226)	China: Yunnan	**ON114087 ON114088**	**ON114070 ON114071**	–	–
C. phloginus	XHW4569 (KUN-HKAS 110228)	China: Yunnan	**ON114091 ON114092**	**ON114073**	–	–
C. phloginus	XHW3004 (KUN-HKAS 73553)	China: Shandong	**ON114075**	**ON114062**	**ON156016**	**ON156024 ON156025**
C. pseudoformosus	281-07 (PUN3883) HT	India	FJ769255	GU237071	–	–
C. romagnesianus	Romagn. 74.268 (PC0085043) HT	France	KX828783	KX828806	–	–
C. romagnesianus	J. Martin (AH44218)	Spain	KX828784	KX828807	KX828836	KX828757
C. roseocarnus	S.A. Redhead (DAOM220723) HT	Canada: British Columbia	KX828787	KX828810	KX828837	KX828758
C. roseocarnus	S.A. Redhead (DAOM220724)	Canada: British Columbia	KX828788	KX828811	KX828838	KX828759
C. roseofagetorum	D. Rodriguez (AH44789) HT	Georgia	KX828789	KX828812	KX828839	KX828760
C. roseofagetorum	D. Rodriguez (AH44786)	Georgia	KX828790	KX828813	KX828840	KX828761
C. aff. hainanensis	161-07 (PUN3958)	India	HQ270121	HM750919	–	–
C. sikkimensis	KD13-024 (CAL) HT	India	KR001903	KP938966	–	–
C. sinominor	GDGM80842 HT	China: Guizhou	–	MZ605107	MZ614006	MZ614050
Cantharellus "sp. 2"	C-88 (Shinshu Univ., Japan)	Japan	LC085381	–	LC085472	–
Cantharellus "sp. 2"	C-106 (Shinshu Univ., Japan)	Japan	LC085384	LC085418	LC085473	–
C. subminor	Yuan13917 (IFP019445) HT	China: Yunnan	MW980545	MW979522	MW999415	MW999455
C. subminor	Yuan13925 (IFP019446)	China: Yunnan	MW980546	MW979523	MW999416	MW999456
C. subminor	Yuan13926 (IFP019447)	China: Yunnan	MW980547	MW979524	MW999417	MW999457
C. subalbidus	J. Trappe (OSC81782)	USA: Oregon	KX828791	KX828814	KX828841	KX828762
C. subalbidus	1196/BB13.014 (PC0713862)	Canada: Vancouver	KX896764	KX896781	KX857037	–
C. subalbidus	J.M. Kranabetter (DAVP 28155)	Canada: British Columbia	–	–	KX592766	–
C. subalbidus	K. Wong (DAVP 28283)	Canada: British Columbia	–	–	KX592768	–
C. subvaginatus	1692/VA13.163 (PC0142458) HT	South Korea	MG450670	MG450678	–	–

Table 1 Continued.

Species	Specimen (herbarium)	Geographical Origin	GenBank accession			
			ITS	**LSU**	***tef1***	***rpb2***
C. subvaginatus	XHW2972 (KUN-HKAS 73528)	South Korea	**MW415863**	**MW367481**	**MW368927**	**ON168713**
C. tabernensis	325/BB07.042 (PC0084107)	USA: Texas	JN944014	JN940596	GQ914973	JN993598
C. tabernensis	333/BB07.064 (PC0084120)	USA: Texas	JN944012	JN940608	GQ914975	JN993600
C. tenuithrix	343/BB07.125 (PC0084084) HT	USA: Texas	JN944017	NG_060395	GQ914947	JN993596
C. tenuithrix	322/BB07.035 (PC0084087)	USA: Texas	–	KF294629	GQ914946	KF294712
C. texensis	317/BB07.018 (PC0084097) HT	USA: Texas	–	NG_064349	GQ914988	KF294701
C. texensis	341/BB07.120 (PC0084096)	USA: Texas	JN944016	JN940601	GQ914987	KF294710
C. tuberculosporus	M. Zang 514 (KUN-HKAS 28930) HT	China: Tibet	**ON311287***	**ON248967***	–	–
C. tuberculosporus	BF1659 (KUN-HKAS 94043)	China: Tibet	**ON262331** **ON262332**	**ON256659** **ON428227***	**ON462037***	**ON462040***
C. umbonatus	316-06 (PUN 3968) HT	India	HQ270116	HM750916	–	–
C. vaginatus	XHW4565 (KUN-HKAS 110224)	China: Yunnan	**ON054218**	**ON054272**	**ON089610**	**ON089590**
C. vaginatus	XHW4566 (KUN-HKAS 110225)	China: Yunnan	**ON054219** **ON054220**	**ON054273** **ON054274**	**ON089611**	**ON089591**
C. vaginatus	KH07-215 (KUN-HKAS 55730) HT	China: Yunnan	HQ416692	HM594681	–	–
C. velutinus	1321/BB14.038 (PC0142227) HT	USA: Texas	KX896774	KX896789	KX857049	–
C. velutinus	1346/BB14.078 (PC0142267)	USA: Texas	**ON197320**	**ON150914**	**ON168703**	**ON168710**
C. versicolor	XFT161 (KUN-HKAS 55762) HT	China: Yunnan	**ON054239** **ON493174***	**ON428228***	**ON462037***	**ON462041***
C. versicolor	FQY24 (KUN-HKAS 58242)	China: Yunnan	**ON054233**	**ON054283**	KM893857	–
C. versicolor	XHW6558 (KUN-HKAS 109707)	China: Sichuan	**MW415868** **MW415869** **MW415870**	**MW367483**	**MW368931**	**ON089592**
C. versicolor	XHW6575 (KUN-HKAS 109708)	China: Sichuan	**MW415871** **MW415872** **MW415873** **MW415874**	**MW367485** **MW367486**	**MW368932**	**ON089593**
C. versicolor	XHW5849 (KUN-HKAS 109705)	China: Yunnan	**MW415875** **MW415876**	**MW367487** **MW367488**	**MW368933**	**ON089594**
C. versicolor	XHW5768 (KUN-HKAS 104607)	China: Tibet	**MW415879** **MW415880**	**MW367491** **MW367492**	**MW368935**	**ON089596**

Table 1 Continued.

Species	Specimen (herbarium)	Geographical Origin	GenBank accession			
			ITS	**LSU**	***tef1***	***rpb2***
C. versicolor	XHW5572 (KUN-HKAS 109702)	China: Tibet	**MW415866 MW415867**	**MW367484**	**MW368930**	**ON263465**
C. versicolor	XHW5063 (KUN-HKAS 109701)	China: Yunnan	**MW415877 MW415878**	**MW367489 MW367490**	**MW368934**	**ON089595**
C. versicolor	XHW5842 (KUN-HKAS 109704)	China: Yunnan	**MW415881**	**MW367493 MW367494**	**MW368936**	**ON089597**
C. versicolor	XHW5890 (KUN-HKAS 109706)	China: Yunnan	**MW415882**	**MW367495**	**MW368937**	–
C. versicolor	XHW6201 (KUN-HKAS 116825)	China: Yunnan	**ON054223**	**ON256656**	–	–
C. versicolor	XHW8479 (KUN-HKAS 118099)	China: Yunnan	**ON054224**	**ON054275**	**ON089612**	–
C. versicolor	XHW8517 (KUN-HKAS 123175)	China: Yunnan	**ON054240**	**ON256657 ON256658**	–	–
C. versicolor	XHW8674 (KUN-HKAS 118284)	China: Yunnan	**ON054231**	**ON054279**	–	–
C. versicolor	XHW8974 (KUN-HKAS 123176)	China: Yunnan	**ON054237 ON054238**	**ON054284**	**ON089618**	**ON089603**
C. versicolor	XHW9296 (KUN-HKAS 123177)	China: Yunnan	**ON054225 ON054226**	**ON054276**	**ON089613**	**ON089598**
C. versicolor	XHW9326 (KUN-HKAS 123178)	China: Yunnan	**ON054227 ON054228**	**ON054277**	**ON089614**	**ON089599**
C. versicolor	XHW9337 (KUN-HKAS 123179)	China: Yunnan	**ON054229 ON054230**	**ON054278**	**ON089615**	**ON089600**
C. versicolor	XHW9394 (KUN-HKAS 123180)	China: Yunnan	**ON054232**	**ON054280**	**ON089616**	**ON089601**
C. versicolor	XHW9396 (KUN-HKAS 123181)	China: Yunnan	**ON262333 ON262334**	**ON054281 ON054282**	**ON089617**	**ON089602**
C. versicolor	XHW9433 (KUN-HKAS 123182)	China: Yunnan	**ON054234 ON054235**	**OP890705**	–	–
C. versicolor	bm-29 (KUN-HKAS 86043)	China: Yunnan	**ON054221 ON054222**	**ON387632**	–	–
C. versicolor	XHW9807 (KUN-HKAS 121198)	China: Yunnan	**ON054236**	**ON387633 ON387634**	–	–
C. versicolor	Yuan13640 (IFP019489)	China	–	MW979525	MW999427	MW999458
C. versicolor	Yuan13681 (IFP019490)	China	–	MW979526	MW999426	MW999459
C. zangii	M. Zhang (GDGM83186)	China: Yunnan	–	MZ605117	MZ614016	MZ614060

Table 1 Continued.

Species	Specimen (herbarium)	Geographical Origin	GenBank accession			
			ITS	**LSU**	***tef1***	***rpb2***
C. zangii	XFT 417 (KUN-HKAS 55791) HT	China: Yunnan	**ON100839 ON100840 ON493175***	**ON074608 ON428229***	**ON089623 ON462039***	**ON089632 ON462042***
C. zangii	XHW9753 (KUN-HKAS 119310)	China: Yunnan	**ON100837 ON100838**	**ON074607**	–	–
C. zangii	XHW8456 (KUN-HKAS 118077)	China: Yunnan	**ON100829 ON100830**	**ON074603**	**ON089619**	**ON089628**
C. zangii	XHW8458 (KUN-HKAS 118079)	China: Yunnan	**ON100831 ON100832**	**ON074604**	**ON089620**	**ON089629**
C. zangii	XHW9295 (KUN-HKAS 118876)	China: Yunnan	**ON100833 ON100834**	**ON074605**	**ON089621**	**ON089630**
C. zangii	XHW8666 (KUN-HKAS 118276)	China: Yunnan	**ON100835 ON100836**	**ON074606**	**ON089622**	**ON089631**

Phylogenetic analyses

Subgenus *Cantharellus*

Phylogenetic analysis of subgenus *Cantharellus* (Fig. 4) retrieved high support for the three sections recognized in Buyck et al. (2014), viz. sections *Cantharellus* (ML-bs 78%), *Amethystini* (ML-bs 98%) and *Sublaeves* (ML-bs 100%). Section *Cantharellus* was divided in two significantly supported clades. The crown clade that contains the type species of the genus, *C. cibariu* received maximum support (ML-bs 100%). In this core clade, *C. macrocarpus* from tropical China was placed sister with high support (ML-bs 98%) to the rest of the species. This rest-group was divided into two strongly supported subclades: the lower clade (ML-bs 95%) contained *C. tuberculosporus* and *C. cibarius* with its American satellite species (*C. elenensis* and *C. roseocanus*); the upper clade (ML-bs 91%) included *C. applanatus* and its synonyms (*C. anzutake*, *C. yunnanensis*, *C. himalayensis* and *C. natarajanii*; see discussion). The "*C. fibrillosus*" that is placed sister to the European *C. pallens* with moderate support is NOT the true *C. fibrillosus* described from India, but corresponds to the placement obtained by the wrong part of the chimeric sequence (see Discussion).

A specimen from Jilin, China (XHW2580), fell into the clade of *C. cibarius* with ML-bs 91%. Sister to the crown clade was a moderately supported clade (ML-bs 70%) composed of five strongly supported subclades two of which had Asian species. *Cantharellus versicolor* and Japanese "C. sp2" are part of a fully supported '*C. formosus*-clade'. *Cantharellus indicus* and XHW6691, from subtropical Yunnan were firmly placed as closest allies to *C. alborufescens* in the fully supported '*C. alborufescens-ferruginascens* clade'. One Indian sample of *C. lateritius* (PUN3958) represented by ITS sequence HQ270121 was grouped into a terminal clade with two samples of *C. hainanensis*, the holotype and a specimen (XHW7576) from central China (He'nan Prov.). This terminal clade was basal to the other species of sect. *Sublaeves*.

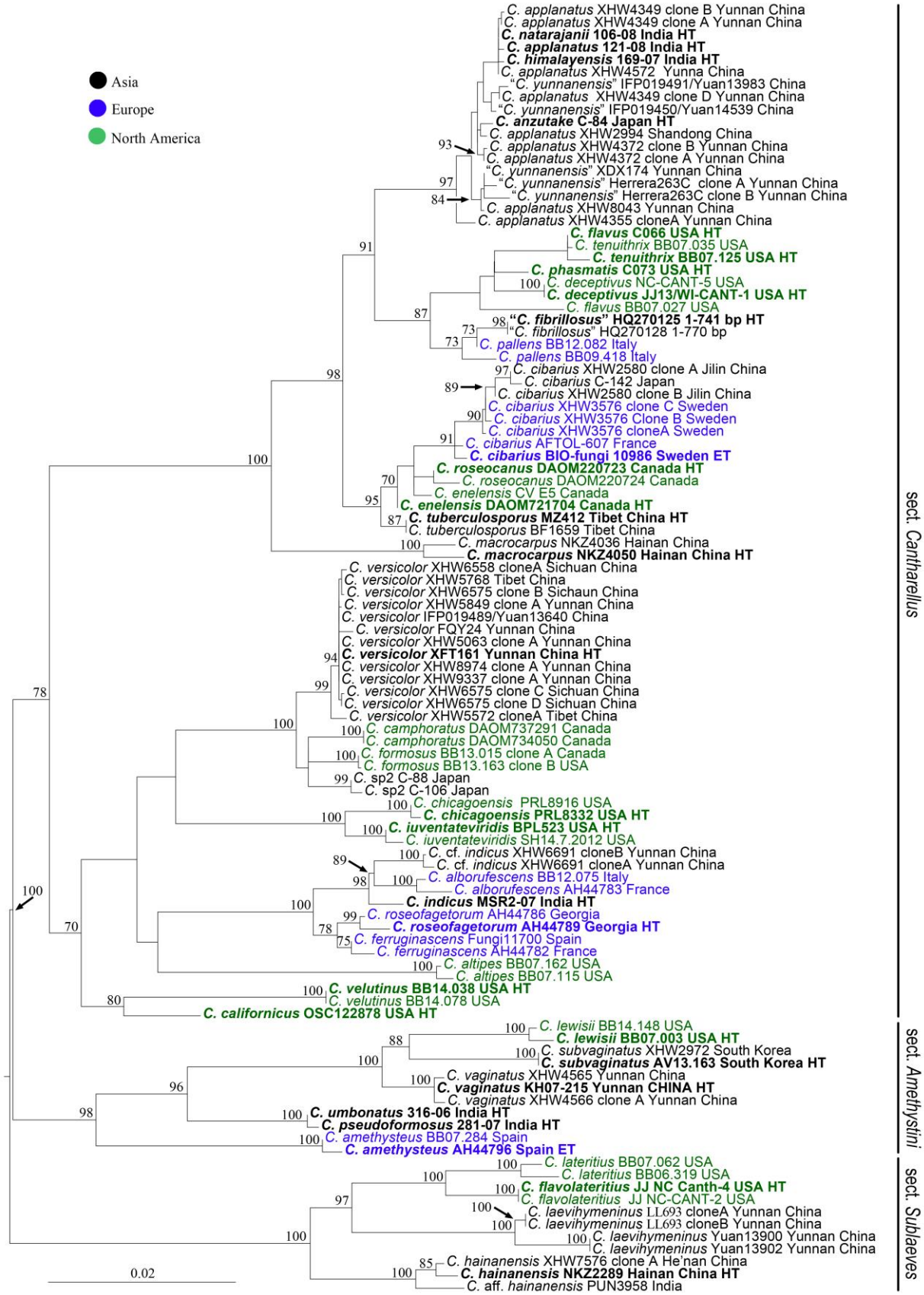


Figure 4 – Most likely tree produced by RAxML analysis of the combined ITS+LSU+ *rpb2+tef1* dataset (5600 bp) of *Cantharellus* subg. *Cantharellus.* Different clones of some samples correspond to the ITS clones in GenBank accessions. The tree was rooted with midpoint. Maximum likelihood bootstraps ≥ 70 % are shown above or by the nodes. Type specimens are in bold (HT: holotype, ET: epitype). Infrageneric classification followed Buyck et al. (2014).

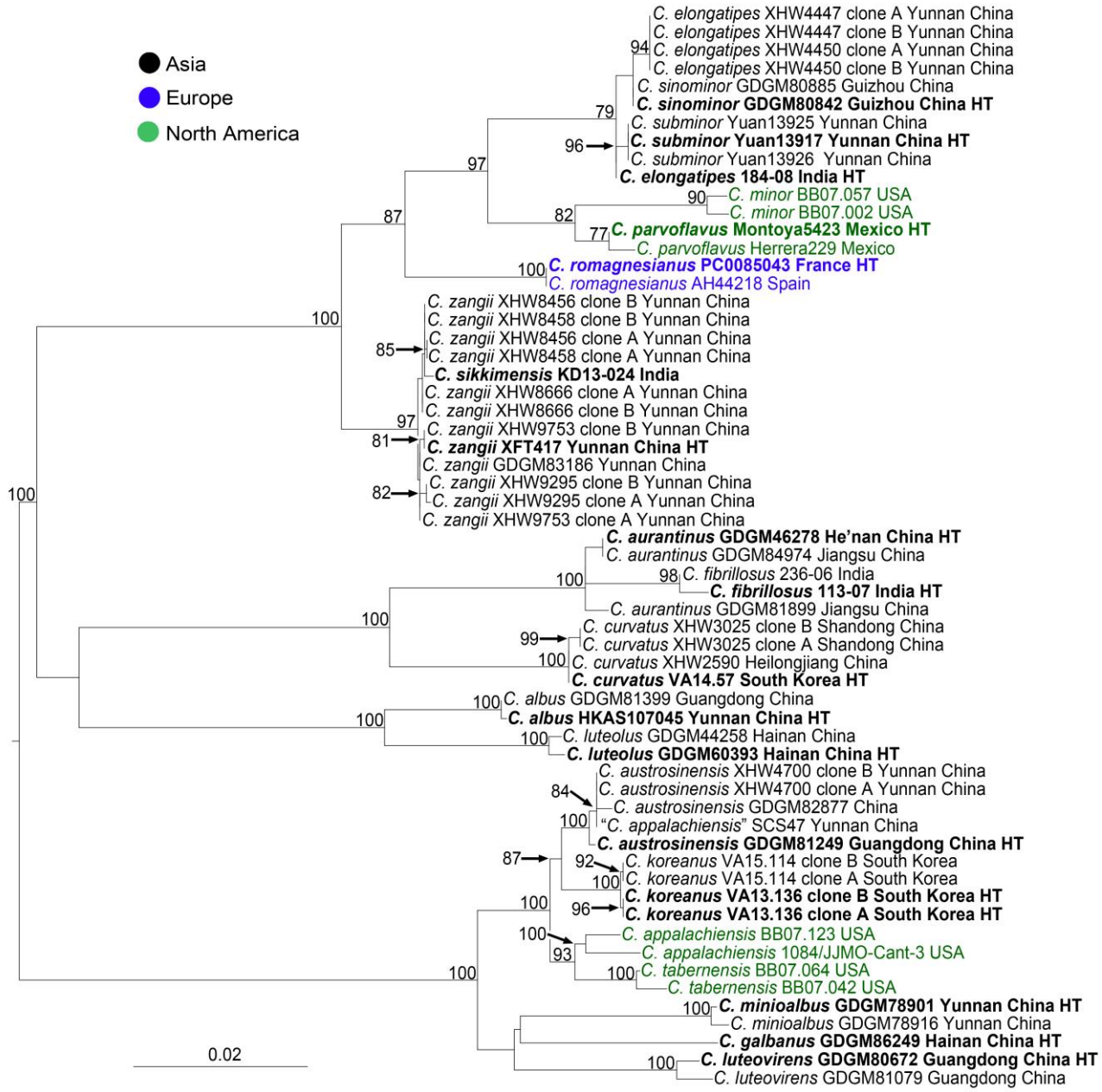


Figure 5 – Most likely tree produced by RAxML analysis of the combined ITS+LSU+ *rpb2+tef1* dataset (4776 bp) of *Cantharellus* subg. *Parvocantharellus.* The different ITS sequences we obtained by cloning PCR products or phasing for some samples were deposited as separate GenBank accessions. The tree was rooted with midpoint. Maximum likelihood bootstraps ≥ 70 % are shown above or by the nodes. Type specimens are in bold (HT: holotype).

Subgenus *Parvocantharellus*

The phylogeny of subgenus *Parvocantharellus* (Fig. 5) included fifteen Asian species. Our analysis recognized four major fully supported clades (ML-bs 100%) among northern hemisphere *Parvocantharellus*. The first and upper clade corresponds to the core clade as it contains the type species of the subgenus, *C. romagnesianus;* all of its species are small and slender, mostly yellowish and often with hollowing stipes. In this clade, two Yunnan specimens of *C. elongatipes* (XHW4447 and XHW4450), two of *C. sinominor*, three of *C. subminor* and the holotype of *C. elongatipes* (with its LSU sequence corrected to HM750928, see Discussion) formed a significantly supported terminal clade (ML-bs 79%). The second clade grouped three orange-yellowish Asian species: the true Indian *C. fibrillosus* being the closest relative to Chinese *C. aurantinus* (ML-bs 100%) and *C. curvatus*. *Cantharellus fibrillosus* was nested in *C. aurantinus* with full support. A

third, equally small and entirely Asian subclade (ML-bs 100%) grouped *C. albus* with *C. luteolus*, while the fourth and last clade contained five Asian species and their American relatives.

Subgenus *Cinnabarini*

Phylogenetic analysis of northern hemisphere representatives of the subgenus *Cinnabarini* (Fig. 6) included 11 new samples of *C. phloginus* collected from Hubei, Shandong and Yunnan Provinces in China. It allowed to place the only three Asian agaricoid chanterelles known so far. One of these, the recently described *C. albovenosus*, for which ITS, LSU and *rpb2* loci of the holotype were newly sequenced, fell into the big population of *C. phloginus* and the latter was sister to the South Korean *C. citrinus* with high support (ML-bs 99%). Both these species were again sister to the North American *C. cinnabarinus* with full support (ML-bs 100%).

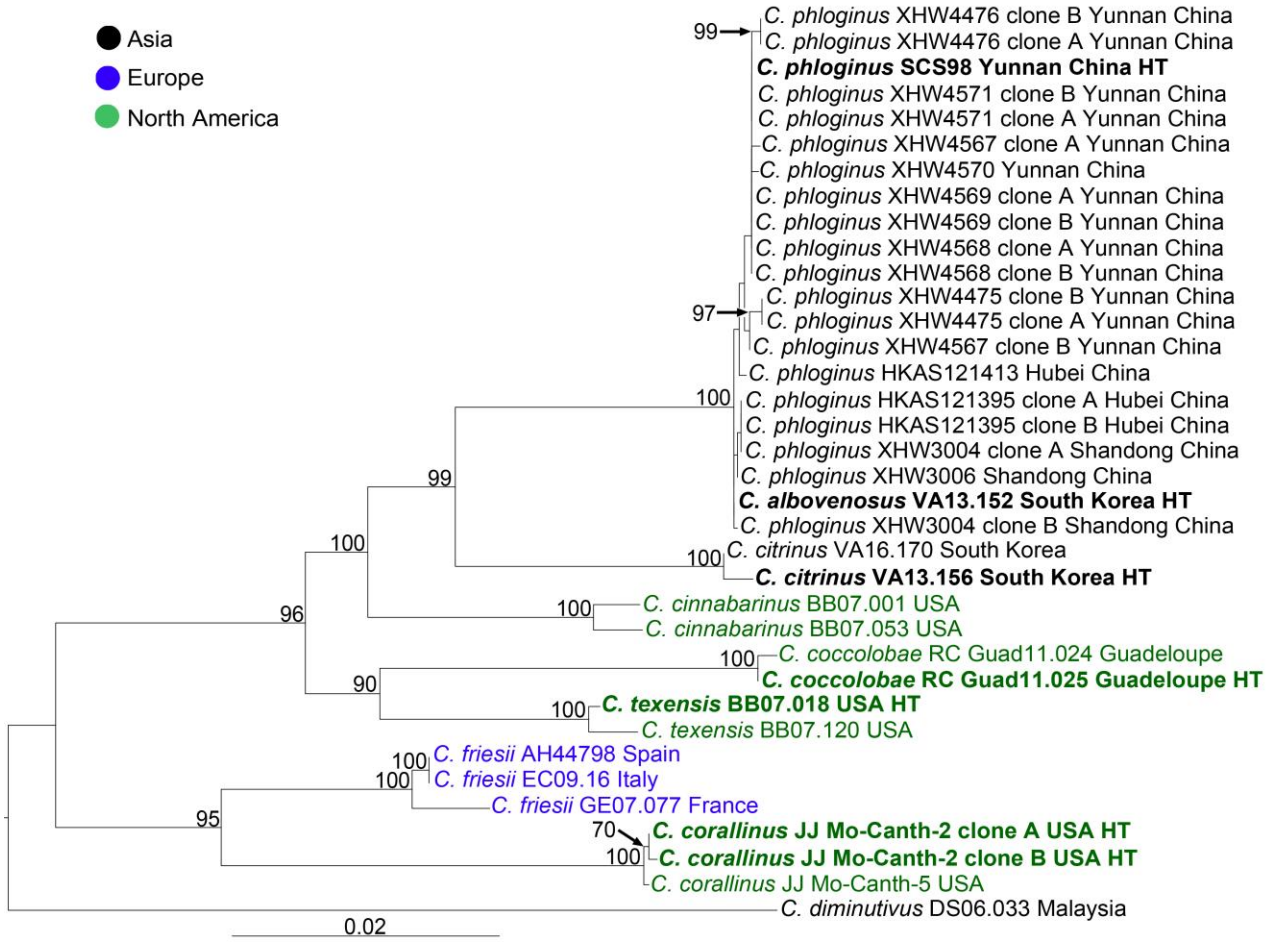


Figure 6 – Most likely tree produced by RAxML analysis of the combined ITS+LSU+*rpb2*+*tef1* dataset (4726 bp) of *Cantharellus* subg. *Cinnabarini*. The different ITS sequences we obtained by cloning PCR products or phasing for some samples were deposited as separate GenBank accessions. The tree was rooted with midpoint. Maximum likelihood bootstrap values ≥ 70 % are indicated near branch nodes. Type specimens are in bold (HT: holotype).

Type studies of *C. yunnanensis* and *C. tuberculosporus*

Cantharellus yunnanensis W.F. Chiu, Acta Microbiologica Sinica 13(2): 129 (1973)

Original diagnosis – *Pileo 1.5–2.5 cm. lato, convexo, leniter depresso, 'Capucine buff', minutissimo pubescenti, nonnihil hygrophano; margine undulato, incurvo; lamellis albidis dein "pale salmon", obtusis, dichotomis, distantibus; stipite 3–5 cm. longo, 5–10 mm. crasso,*

compresso, enormiter sulcato, sursum attenuato, albido-fibrilloso; caro alba; sporis ellipsoideis, pallidiore olivaceis, 4–5 × 2–3.5 μ.

Holotypus – China, Yunnan, Kunming, Xishan, 11 Aug. 1942, S.C. Shen, 8090 (HMAS 4090).

Type study – Basidiospores extremely few, globose to subglobose, 6–7.5 μm diam. Basidia not inflating. Pileipellis heavily infested with different molds and various contaminating spores and conidia, composed of ascending to horizontal, clamped, short-celled and thin-walled hyphal endings with large, clavate, ellipsoid to subcylindrical terminal cells measuring (10)13–19 μm wide, mostly obtuse-rounded but some rare terminal cells narrowing at the tip. Clamp connections present in all tissues.

Notes – During a visit to HMAS by BB, we had the opportunity to examine the holotype. This holotype, formerly kept at Tsinghua University where it had the herbarium number 8090, was later transferred to the Institute of Microbiology, Chinese Academy of Sciences (HMAS) where it is now filed under number 4090 (Fig. 7a). Tissues of the type are in extremely bad condition (Fig. 7b), difficult to revive for microscopic study, and heavily infested with various molds all over its surface.

The original diagnosis depicts a small mushroom that is pale-colored 'capucine buff' (a term referring to the Ridgway color code, Plate III). It has white flesh and a stipe that is approximately twice as long as the pileus diam. and is 'very strongly ("enormously" in the original diagnosis) folded-furrowed' and 'narrowing upward' (wrongly written as "tapering downwards" in the Chinese description), two features that are unusual for *Cantharellus*. The hymenophore is described as consisting of spaced, obtuse, dichotomously forking veins that are initially white but turn pale salmon with age. Moreover, we confirm here that the type is extremely fragile and brittle and needs to be handled with much care or it would fall apart in pieces, especially the stipe, suggesting it might have been at least partly hollowing. This is unlike the firmness of the fleshy fruiting bodies of typical golden chanterelles.

The basidiospore size mentioned in the original description (4–5 × 2–3.5 μm) is a mistake as these are too small for any *Cantharellus* species. The spore size given by Chiu most likely corresponds to the size of the conidia produced by one of the various contaminating molds that cover most of the surface of the fruiting bodies. Instead of finding spores with values given by Shao et al. (2021), we observed only few nearly globose basidiospores (Fig. 7c, d). We did not observe the thick-walled hyphal extremities in any tissues. Shao et al. (2021) epitypified the name *C. yunnanensis* with a typical golden chanterelle from the Kunming area, the same area where the holotype of *C. yunnanensis* was originally collected. They then applied this name to the most commonly marketed chanterelle in southwestern China which, in the entire area, is referred to as being typically yellow (chicken fat), a color that is not mentioned in the original description. This epitype is not only much larger, very fleshy and of a differet color, but has much more developed gill-like folds instead of low veins and possesses narrow hyphal terminations in the pileipellis unlike the terminations we found in the holotype of *C. yunnanensis* (compare our Figs 7e, 8a, 8c). This typification does not conform to the original diagnosis of *C. yunnanensis.* In our experience, the combination of a general habitat with strongly folded-furrowed stipe, spaced and low, forking veins, nearly globose spores and wide, thin-walled hyphal endings in the pileipellis (Figs 7e, 8a) strongly suggests that *C. yunnanensis* belongs in *Craterellus*, not in *Cantharellus* [compare with drawings of other *Craterellus* studied in Buyck et al. (2010)]. We therefore here make a new combination:

Craterellus yunnanensis (W.F. Chiu) Buyck comb. nov.

Basionym – *Cantharellus yunnanensis* W.F. Chiu, Acta Microbiologica Sinica 13(2): 129 (1973)

MycoBank number: MB 847602

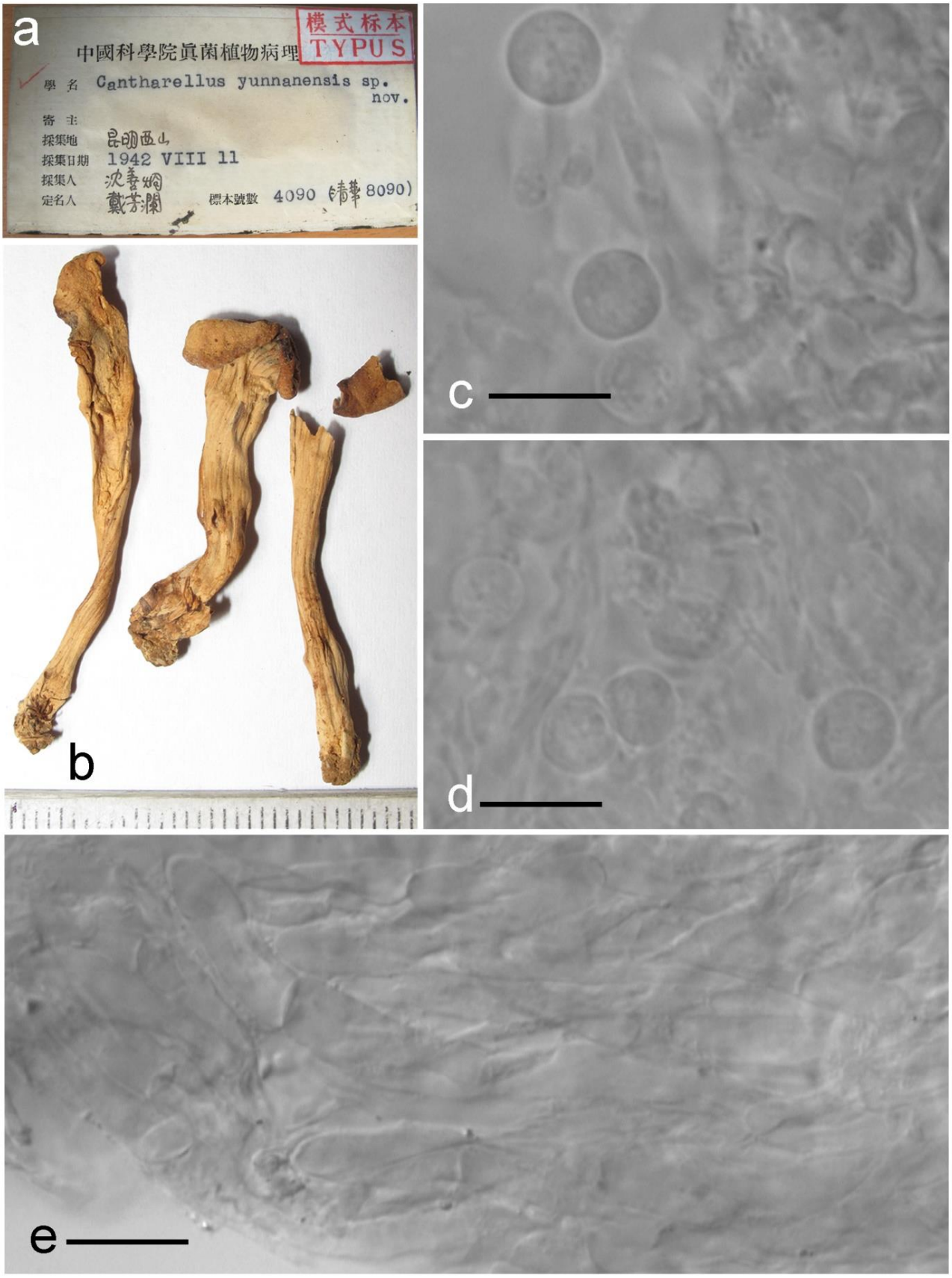


Figure 7 – Holotype of *Cantharellus yunnanensis*. a Specimen label. b Basidiocarps. c, d basidiospores enclosed in hymenium tissue. e hyphal extremities at the pileus surface. Scale bars: c, d = 10 µm, e = 20 µm. Photos by B. Buyck.

Cantharellus tuberculosporus M. Zang, Acta Microbiologica Sinica 20(1): 31 (1980)

Original diagnosis – "*Pileus 4–8.5 cm. latus, depressus dein infundibuliformis. laete flavus, aurantiofulvus vel aurantiacus, laevigatus, margine tenui recurvo. Stipes 2–4 × 1–3 cm, cylindricus. laevigatus, sursum incrassatus, concolor, basim versus attenuatus, basi mycelio albo-flavescente villoso. Lamellae decurrentes irregulariter 1–2 dichotomae anastomosantes, pallide flavae vel aurantiacae. Basidiosporae 5–6 × 7–8.6 μm., hyalinae, ellipsoideae, tuberculosae. Basidia clavata. 7–9 × 18–22 μm. Odor gratus et sapor subnullus. Hab. In sylvis praecipue Quercinis pseudosemicarpifolio. Xizang (Tibet): Mi-Lin, Ba-ga, 28, VII. 1975. Zang Mu 412. Typus! (HKAS 5412)*" [sic!]

Holotype – China, Tibet Autonomous Region, Milin County, Baga, 28 Jul. 1975, Mu Zang, 412 (HKAS 28930, KUN).

Type study – The thick-fleshed type specimen has an eccentric stipe and veined hymenophore (Fig. 9a). Basidiospores 8.5–***9.2***–10.0 (10.5) × 5.5–***5.8***–6.5 μm, Q = (1.42) –***1.46***–1.73 (1.75) [n = 40] (Fig. 9c), ellipsoid, smooth, hyaline. Basidia hardly inflating. Pileipellis a cutis, composed of yellowish brown thin to slightly thick-walled (0.5 μm) hyphae 4–10 μm wide, with cylindrical terminal cells 45–70 × 5–7 μm. Clamp connections in all tissues.

Notes – Shao (2011) studied the holotype of *C. tuberculosporus* and noticed that the herbarium box with number "HKAS 5412" was used for a recent specimen of the ascomycete *Leotia lubrica* (wrongly reported as "*Lepiota lubrica*" by Shao). The exact herbarium number for the *C. tuberculosporus* holotype is now HKAS 28930 in KUN (Fig. 9b). Our study of the holotype (Fig. 9a–c) revealed that the pileus surface is moulded and overgrown with hyaline hyphae producing nearly hyaline conidia of 4–6 × 3–4 μm. We did not find tuberculate spores but found numerous spores typical for a golden chanterelle (Fig. 9c).

According to Zang (1980), this subalpine species differed from *C. yunnanensis* in the larger fruiting bodies having a bright yellow pileus and hymenophore and distinctly tuberculate spores. Except for the mention of the tuberculate spores, *C. tuberculosporus* perfectly fits the concept of a golden chanterelle. Shao (2011) had observed that the tuberculate spores were clearly contaminating spores and that the type possessed typical *Cantharellus* spores. He therefore interpreted the commonly marketed golden chanterelle in southwestern China, whether collected from subtropical-tropical or subalpine regions, as representing *C. tuberculosporus*, and deposited 19 *tef1* sequences under that name in GenBank in 2014. When Shao et al. (2021) finally epitypified *C. yunnanensis*, they did not mention *C. tuberculosporus*, although they used one of their own *tef1* sequences (KM893834) deposited as *C. tuberculosporus* in their phylogeny. Shao et al. (2021) did not cite any other synonyms for *C. yunnanensis*, although their deposited LSU sequences were identical to some of the Indian *Cantharellus* species and their *tef1* sequences were identical to Japanese *C. anzutake*. Cao et al. (2021) accepted the epitypification by Shao et al. (2021) and used Shao's *tef1* sequences labelled as "*C. tuberculosporus*" and those of *C. anzutake* published by Ogawa et al. (2018), to synonymize both *C. tuberculosporus* and *C. anzutake* under *C. yunnanensis*. Only Yang et al. (2021) recognized *C. tuberculosporus* as a subalpine species, different from *C. cibarius* from subtropical to temperate regions, although the reasons for this were not very clear.

We carefully measured the spores of the holotype and our second collection of *C. tuberculosporus* and also the two fruiting bodies from the *C. versicolor* holotype as Shao et al. (2016b) did not provide mean values for spore size. Together with several of our own measured specimens, we could easily demonstrate that the mean values for the spore size of the *C. tuberculosporus* collections fall into the lower range of *C. versicolor* spores, but are far from the mean spore length and width of "yunnanensis" as recently epitypified (Fig. 10). Apparently, *C. tuberculosporus* is not the same as "*C. yunnanensis*" as interpreted by Shao et al. (2021), but instead shares a rather similar spore size with *C. versicolor*. When Shao et al. (2016b) published *C. versicolor*, they did not provide DNA sequences for the holotype, but published two *tef1* sequences from the paratypes. To clarify the identity of *C. versicolor,* we sequenced the holo- (XFT161) and paratype (FQY24). We obtained new sequences from the holotypes of *C. versicolor* and

C. tuberculosporus. The sequence data, however, clearly show that *C. tuberculosporus* belongs to the *C. cibarius* core clade, whereas *C. versicolor* is a typical subalpine species that belongs to the *C. formosus* clade (Fig. 4).

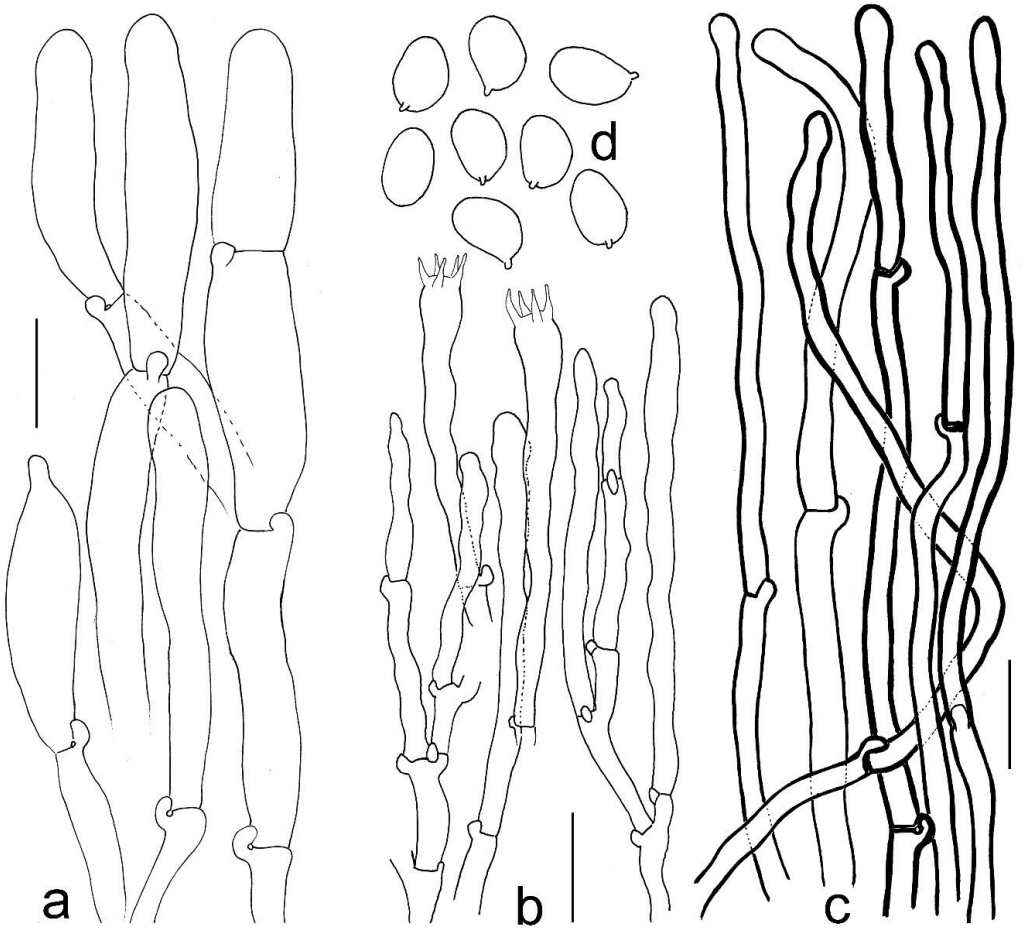


Figure 8 – a Hyphae in the pileipellis of holotype of *Cantharellus yunnanensis*. b–d Microscopic elements of a typical marketed yellow chanterelle in southwestern China (here drawn from *C. applanatus*, XHW4572): b basidia and basidioles. c hyphae in the pileipellis for comparison with 6a, d basidiospores. Scale bars: a–c = 20 µm, d = 10 µm.

Considering the holotype is in very poor condition and even genome-sequencing was not able to amplify its protein-coding genes, to make the application of *C. tuberculosporus* more precise, the well-preserved specimen KUN-HKAS 94043 is designated here as the epitype of *C. tuberculosporus.* Below we give a detailed description of the epitype:

MycoBank: 10011682 (for epitypification)

Fruiting bodies gregarious. Pileus 40–60 mm in diam., applanate convex with depressed center and wavy margin, then broadly infundibuliform with often thin margin; the extreme margin straight, in- or up-rolled, scaly at center, thick-fleshed. Hymenophore not abruptly separated from the sterile upper stipe, but rather fragmenting over a certain distance, composed of relatively well-developed, decurrent gill folds, 1–1.5 mm high, not particularly close, branched to furcate, paler than pileus; edge concolorous, even. Stipe 40–60 × 8–15 mm, tapering towards base, finely longitudinally fibrillose, nearly concolorous with hymenophore, massive. Context pale, nearly white, not changing color when injured. Smell typical cantharelloid. Taste mild.

Basidiospores (8.0) 8.5–***9.1***–10.0 (10.5) × (4.5) 5.0–***5.6***–6.0 (6.5) µm, Q = 1.46–***1.64***–1.79 (1.94), ellipsoid to cylindrical-ellipsoid, sometimes suballantoid, non-dextrinoid, thin-walled. Basidia 80–100 × 8–12 µm, 4–6-spored, pedicellate-clavate. Subhymenium well-developed,

filamentous, hyphae 4–10 µm diam, cylindrical, some subinflated. Tramal hyphae cylindrical or inflated, sometimes branched, thin-walled, non-dextrinoid, 4–15 µm wide. Pileipellis a cutis composed of cylindrical and subinflated hyphae, these 4–10 µm wide, thick-walled (0.5–1 µm thick) only in the pileipellis at center, hyaline to pale yellowish brown. Clamp connections small, abundant in all tissues.

Figure 9 – *Cantharellus tuberculosporus*. a–c holotype a Basidiocarp, with the original handwriting of M. Zang. The Chinese name below the collection data reads "Baga", the type locality. b Specimen label. Note the correct herbarium number is now HKAS 28930, not 5412. c Cantharelloid basidiospores. d and e: HKAS 94043 (BF1659). d basidiocarps growing in a mixed forest with *Pinus densata* and oak. e Collection locality (yellow star), only ca. 15 km from the type locality Baga (red triangle). Photos X. H. Wang (a–c) and B. Feng (d).

Specimens examined – China, Tibet Autonomous Region, Linzhi County, Bujiu Town, mountain behind Lamaling Temple, 29°27′36″N, 94°23′32″E, elev. 3100 m, in mixed forest with *Pinus densata* and trees of *Quercus* sect. *Heterobalanus*, 31 Jul. 2014, B. Feng, 1659 (KUN-HKAS 94043).

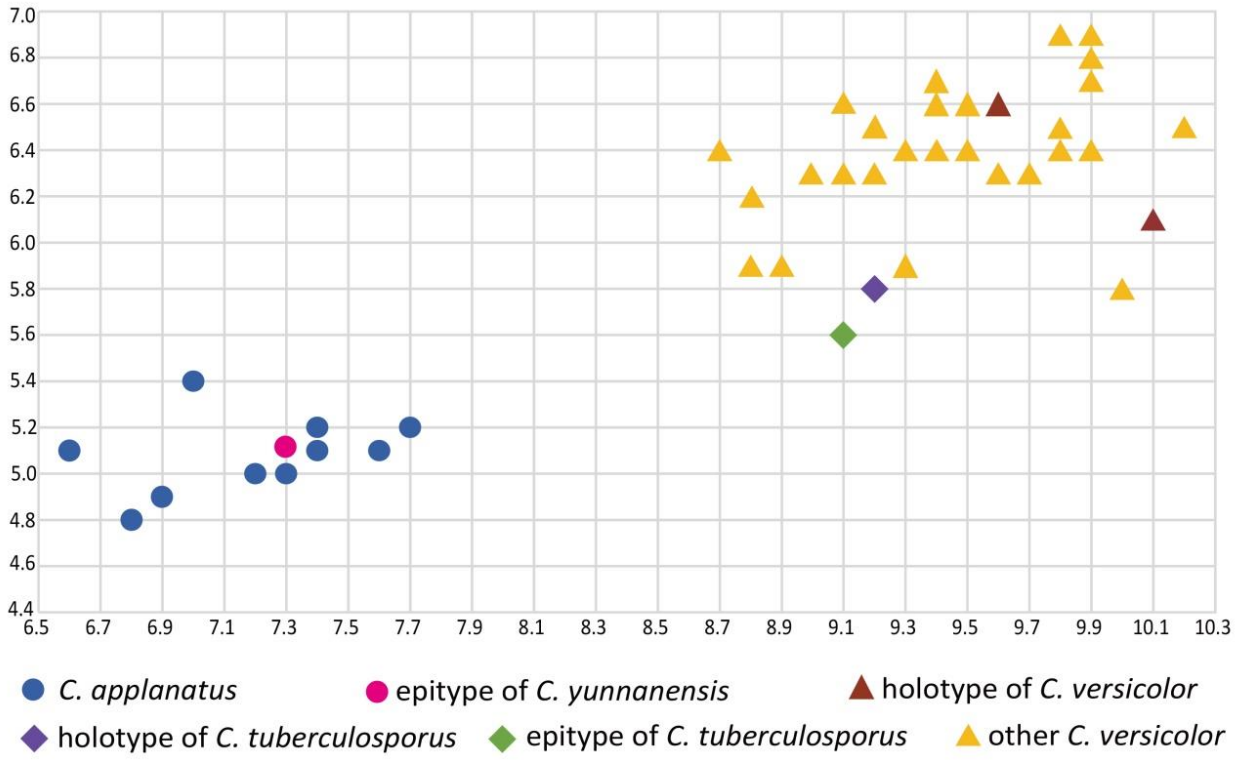


Figure 10 – Mean values for spore dimensions of different collections of *Cantharellus applanatus*, *C. tuberculosporus*, *C. versicolor* and the epitype of *C. yunnanensis*. Each symbol represents the average length and width based on 20 spores from a single fruiting body of different specimens.

Discussion

Solving the sequence problems associated with the *Cantharellus* species described from India

Kumari et al. (2011, 2013) described from India the first eight new *Cantharellus* species supported by sequence data. However, nearly all of these species are supported by strongly incongruent phylogenies generated from ITS and LSU sequence data (see Das et al. 2015, Buyck et al. 2018) and suffer from endless mistakes or inaccuracies that are associated with GenBank deposits and voucher related information. In the following paragraphs we took a tedious, in-depth look at available sequence data and morphological evidences for each of these species. Two preliminary general remarks can be made on the Indian *Cantharellus* species published by Kumari et al. (2013):

(1) none of the holotype specimens has been annotated as holotype in GenBank. The published paper is the only source to find the corresponding ITS and LSU holotype sequences. Only the holotypes have official herbarium references for PUN (Punjabi University Herbarium, Botany Department, Punjabi University, Patiala, India). Unfortunately, India is not sending any herbarium material on loan. The only way to solve the problem is to critically analyze the DNA data, cross compare their data, and compare the morphology with correct phylogeny.
(2) sequences for most of the new species have been deposited in GenBank as "*Cantharellus* sp.", followed by a collector reference ("DK" for Deepika Kumari, "MSR" for M. Sudhakara Reddy) and a year (e.g. "*Cantharellus* sp. DK2010a" for *C. applanatus*). This is the name that appears in

the definition line (which is duplicated in the first column 'description' when looking at BLAST results), while the scientific name, which appears in the second column of BLAST results, depends on what is entered under 'organism' for the submitted sequences. The importance of these clues is illustrated under *C. fibrillosus* and *C. indicus* below. Both the deposited sequences and their corresponding source modifiers contain endless mistakes, but were neither corrected nor updated since the original submission to GenBank.

Cantharellus applanatus D. Kumari et al., Mycology 4(4): 211 (2013)

The ITS and LSU sequences given in the voucher table are HQ270118 and HM750918, respectively. In both cases the scientific name, "*Cantharellus applanatus*", is correctly entered for 'organism' and the definition line mentions "*Cantharellus* sp. DK-2010a isolate 121" in GenBank. This voucher "121" corresponds to the holotype "PUN 3964 (121-08)" in the original description.

The LSU phylogeny in Kumari et al. (2013, their Fig. 2) placed *C. applanatus* in an unsupported clade together with - and undistinguishable from - the sequences for the holotypes of *C. natarajanii* and *C. elongatipes*. The LSU deposited for *C. elongatipes* was in reality from *C. himalayensis* (see under *C. himalayensis*).

In the ITS phylogeny (their Fig. 3), *C. applanatus* is also undistinguishable, not only from the holotype of *C. natarajanii* and *C. himalayensis*, but also from their collection identified as *C. cibarius* (MSR1-08) and the problematic sequence for the holotype of *C. fibrillosus* which was obtained from a different species (see under *C. fibrillosus*). BLASTn of the holotype ITS sequence showed that it was 99.87% similar with > 90% coverage to a batch of sequences of Japanese *C. anzutake*. The latter species was described based on a 100 bp deletion in the ITS1 region, compared with *C. applanatus* (Ogawa et al. 2018).

In our phylogeny of subg. *Cantharellus* (Fig. 4), both ITS and LSU placed *C. applanatus* in sect. *Cantharellus*, a phylogenetic placement that agrees with the morphological description and the accompanying illustration (their Fig. 4B). In conclusion, we acknowledge that the deposited sequences for the holotype of *C. applanatus* are correct and reliable.

Cantharellus elongatipes D. Kumari et al., Mycology 4(4): 212 (2013)

The ITS and LSU sequences deposited in GenBank for the holotype of *C. elongatipes* are HQ270115 and HM750929, respectively. Both sequence deposits mention "*Cantharellus* sp. DK2010e" in the definition line, "184" as voucher/isolate, and "*Cantharellus longipes*" [sic!] as organism in GenBank, in this case the wrong name. This voucher "184" corresponds to the holotype "PUN 3966 (184-08)" in the original description.

In the LSU phylogeny of Kumari et al. (2013), *C. elongatipes* showed very little diversification from the *C. cibarius*-group. This is confirmed by BLASTn of HM750929 which is >99% similar to Chinese "*C. yunnanensis*", Japanese *C. anzutake*, as well as to two of Kumari's own new species in the same paper, *C. applanatus* and *C. natarajanii*. BLASTn of HQ270115 gives the same result. The two sequences apparently are from a typical 'golden chanterelle' in *C.* subg. *Cantharellus* sect. *Cantharellus*.

However, their supporting Fig. 4D (with field tag "184/08", the holotype) mentions a yellowish, very small and slender chanterelle (pileus < 15 mm diam.) and the morphological description gives the same information. Such a morphology rather suggests placement in *C.* subg. *Parvocantharellus*. Surprisingly, in the ITS phylogeny of Kumari et al. (2013, their Fig. 3), *C. elongatipes* was grouped with two specimens (labelled as "*C. minor*" and "*C. appalachiensis*" respectively) belonging to *C.* subg. *Parvocantharellus*! Apparently, the deposited ITS and LSU sequences for the holotype of *C. elongatipes* in GenBank are NOT the ones obtained from the holotype and the ITS sequence used to build the ITS phylogeny is NOT the sequence in GenBank (HQ270115). The correct LSU sequence of *C. elongatipes* is HM750928, listed under *C. himalayensis* in their voucher table. The ITS of *C. elongatipes* is not traceable yet. For detailed explanation see under *C. himalayensis.*

The BLAST topscore hit of the LSU (HM750928) is on *C. sinominor*, *C. subminor* and a "*C. minor*" from Vietnam (MN331843), all with nearly identical sequences. In our phylogeny of subg. *Parvocantharellus* (Fig. 5), HM750928 grouped with *C. sinominor*, *C. subminor* and our own specimens XHW4447 and XHW4450 from southern Yunnan. *Cantharellus sinominor*, *C. subminor*, XHW4447 and XHW4450 have nearly identical *tef1* sequences. The long branch leading to *C. subminor* in Cao et al. (2021) is due to the wrong base pairs in the section 72–115 bp of the three *rpb2* sequences (MW999455, MW999456 and MW999457).

Cantharellus fibrillosus D. Kumari et al., Mycology 4(4): 213 (2013)

The ITS given in the voucher table is HQ270125, and both the entries for 'definition' and 'organism' mention "*Cantharellus* sp. MSR-2010a" for isolate "113". The LSU in their voucher table is HM750917. The definition line for LSU in GenBank reads "*Cantharellus* sp. DK-2010b" for the same isolate "113", but the name "*Cantharellus himalayensis*", given as the corresponding 'organism', is clearly a mistake. The isolate "113" in both cases corresponds to the holotype "PUN 3957 (113-07)" in the original description.

In the LSU phylogeny of Kumari et al. (2013), HM750917 for *C. fibrillosus* placed it firmly in subg. *Parvocantharellus*, in line with the results of Das et al. (2015). However, the phylogenetic analysis in Kumari et al. (2013) shows this sequence to be undistinguishable from a second sequence labelled as "*C. umbonatus* sp. nov. (236-06)". The species label "*C. umbonatus"* for this second collection is wrong as the associated voucher (236-06) corresponds in reality to a second voucher of *C. fibrillosus.* This second LSU from the sample 236-06 (HM750922) differs in just a single base pair at position 564 (C instead of T) from the holotype sequence and undoubtedly belongs to the same species. The organism label in GenBank "*Cantharellula umbonata*" is a mistake.

In the ITS phylogeny of Kumari et al. (2013), *C. fibrillosus* is undistinguishable from *C. applanatus*, their *"C. cibarius", C. himalayensis* and *C. natarajanii*, all in subg. *Cantharellus.* A critical examination of the ITS sequence HQ270125 found it is a "chimera" of two species: the first part (1–741 bp) is from *C.* aff. *pallens* of the *C. cibarius* complex and the second part (742□1361 bp) from another species whose phylogenetic position is in line with their LSU phylogeny, i.e. in subg. *Parvocantharellus*. Performing BLASTn found a sequence HQ270128 with similarity 97.14% and coverage 96%. In GenBank the organism mentioned for HQ270128 is "*Cantharellus cibarius* var. *multiramis*" with isolate number "236". This 236 apparently is from the second specimen of *C. fibrillosus* "236-06" cited in the paper. HQ270128 is also a mix-up of two species: 1–770 bp is from *C.* aff. *pallens*, while 771–1381 bp is the same as the second part of HQ270125.

In our tree of subg. *Cantharellus* using the first parts of HQ270125 and HQ270128 (Fig. 4), the two sequences formed a clade closest to *C. pallens* in subg. *Cantharellus.* In our tree of subg. *Parvocantharellus*, where we used the second parts of HQ270125 and HQ270128 and the LSU sequences HM750917 and HM750922, *C. fibrillosus* was grouped with *C. curvatus* and *C. aurantinus* (Fig. 4). in subg. *Parvocantharellus.* Zhang et al. (2021a) mis-used HM750917 of *C. fibrillosus* as the LSU for *C. himalayensis* and missed the close relationship between their new species *C. aurantinus* and *C. fibrillosus. Cantharellus fibrillosus* is clearly a member of subg. *Parvocantharellus.*

Cantharellus himalayensis D. Kumari et al., Mycology 4(4): 214 (2013)

The ITS and LSU sequences deposited in GenBank for the holotype "PUN 3972 (169-07)" are HQ270129 and HM750928, respectively. In the description/definition line this voucher was noted as "MSR 2010c isolate 169" for ITS, but as "DK-2010c isolate 169" for LSU in GenBank. Both sequences have "*Cantharellus himalayensis*" as organism.

The ITS phylogeny in Kumari et al. (2013) placed *C. himalayensis* distinctly in the *cibarius*-clade (subg. *Cantharellus* sect. *Cantharellus*). This placement agrees with the results of BLASTn of this ITS sequence and also with the general 'golden chanterelle'-habit described in the

protologue and illustrated in the accompanying field picture (their Fig. 4F). However, in the LSU phylogeny of Kumari et al. (2013, their Fig. 2) *C. himalayensis* was amongst species of subgenera *Parvocantharellus* and *Cinnabarini*, a placement confirmed by BLASTn. The only answer to this puzzle, when analyzed with the above-mentioned *C. elongatipes*, is that the LSU sequences of *L. himalayensis* and *C. elongatipes* were unfortunately switched, both in the phylogenetic LSU analysis and in the GenBank deposit. HM750928 is the LSU sequence of *C. elongatipes* and the correct LSU of *C. himalayensis* is HM750929. In our phylogeny of subg. *Cantharellus* (Fig. 4), *C. himalayensis* was in the same terminal clade as *C. applanatus, C. anzutake* and *C. natarajanii.*

Cantharellus indicus D. Kumari et al., Mycology 4(4): 214 (2013)

ITS and LSU sequence mentioned in the voucher table for this species are associated with the name "*Cantharellus cibarius* var. *longipes*" in GenBank, both as corresponding 'organism' and in the definition line. However, ITS and LSU were not obtained from the same voucher: LSU (HM750924) from "MSR2" and ITS (HQ270122) from "MSR4". These vouchers correspond to "PUN 3962 (MSR2-07)" cited as the holotype in the publication, and to MSR4-08 (a paratype collection), respectively.

The LSU holotype sequence is very similar (>99%) to those deposited in GenBank for European species in the *C. ferruginascens-C. alborufescens* species complex. Analysis of the ITS sequence, however, finds that the first section (1–702 bp) is homogeneous with the *C. ferruginascens-C. alborufescens* species complex. Following this section, the sequence (703–821 bp) is identical with the holotype of *C. pseudoformosus* (FJ769255) and HQ270119 (incorrectly labelled as "*C. minor*" by Kumari et al. 2013). From 822 bp onwards, the sequence comes back to the *C. ferruginascens-C. alborufescens* species complex. After the exclusion of 703–821 bp, in our phylogeny of subg. *Cantharellus* (Fig. 4), *C. indicus* was grouped with our sample XHW6691, in the *C. ferruginascens-C. alborufescens* species complex.

When searching NCBI's Taxonomy browser for sequences associated with *C. indicus*, one finds that this name is not associated with the above-mentioned ITS and LSU sequences, but with very different sequences: two ITS sequences (HQ270126 and HQ270127) and one LSU (HM750921), none of which is mentioned in the voucher table of Kumari et al. (2013). As in the case of *C. fibrillosus*, the reason for this erroneous association in NCBI is that the latter three sequences were submitted to GenBank with the wrong scientific name "*Cantharellus indicus*" for 'organism'. In reality, these three sequences are from specimens of *C. pseudoformosus* because they are extremely similar to the type sequences of the latter species published in Kumari et al. (2011), FJ769255 and GU237071, for ITS and LSU respectively. More details are given under *C. pseudoformosus* below.

Cantharellus natarajanii D. Kumari et al., Mycology 4(4): 216 (2013)

The ITS and LSU sequences given in the voucher table are HQ270120 and HM750926, respectively. The scientific name of the species is not mentioned in GenBank and both the description line and the entry for 'organism' mention "*Cantharellus* sp. DK-2010f" and "106" for the isolate. This "106" corresponds to the holotype "PUN 3963 (106-08)" in the original description.

The phylogenetic placement of *C. natarajanii* in the ITS and LSU phylogenies are the same as for *C. applanatus* (Kumari et al. 2013). This is logical as the morphology suggests a very similar species, and the LSU sequence is identical with that of *C. applanatus* (HM750918). A critical analysis of the ITS sequence HQ270120, however, found that the sequence is from two species: section 1–1064 bp is identical with that of *C. applanatus*, and from 1064 bp to the end the sequence is from *C. cibarius.*

A second ITS sequence [HQ270124] for *C. natarajanii* exists in GenBank, deposited as '*Cantharellus* sp. DK-2010f, isolate 35'. This second sequence is completely identical to the one obtained from the holotype and corresponds apparently to voucher 35-09. This voucher is mentioned in the voucher table, but this second ITS sequence is not.

Cantharellus pseudoformosus D. Kumari et al., Mycoscience 52: 148 (2011)

The holotype of this species is PUN3883 (281-07). LSU sequence given in the 2011 paper is GU237071. In GenBank it has organism name *C. pseudoformosus* and voucher "PUN3883". BLASTn of this sequence shows that there is a second near-identical sequence (99.76% similarity): HM750916. This sequence is reported in the voucher table of the 2013 paper as LSU sequence for *C. umbonatus.* In GenBank HM750916 is labelled as "*C. appalachiensis* with strain number "84-08". This label is a mistake, because phylogenetic analysis placed the sequence firmly in *C.* subg. *Cantharellus* sect. *Amethystini* (Fig. 4), other than in *C.* subg. *Parvocantharellus*, where *C. appalachiensis* belongs.

For the ITS sequence of *C. pseudoformosus*, the 2011 paper reports the submission of two clones FJ769255 and HM776721. The two clones are from different specimens: FJ769255 from MSR-4 (the holotype) and HM776721 from MSR-b. The authors reported that these two ITS clones were 96.87% similar to each other, which is confirmed by BLASTn. In GenBank there are two more ITS sequences, HQ270126 and HQ270127, both attributed to *C. indicus* as 'organism' but in reality, from *C. pseudoformosus*. This isolate "272" of HQ270126 corresponds to strain "272-07" in Kumari et al. (2013), one of the paratypes for *C. pseudoformosus*. The isolate "274" of HQ270127 has not been traced yet.

Cantharellus umbonatus D. Kumari et al., Mycology 4(4): 216 (2013) nom. illeg., [non-*C. umbonatus* Pers.: Fr., Syst. Mycol., 1, p. 317 (1821)]

The ITS and LSU given in the voucher table for this species are HQ270116 and HM750916, respectively. As mentioned under *C. pseudoformosus*, HM750916 is wrongly labelled in GenBank as "*C. appalachiensis*" with a wrong isolate number "84-08". This sequence is near-identical with the LSU of *C. pseudoformosus*.

The ITS sequence HQ270116 is also a mix-up, with an even more dramatic story than any case analyzed above. The section 1–632 bp is nearly identical with the holotype of *C. pseudoformosus.* Following this, the short section 633–678 bp is a piece whose correct location is between 860 bp and 861 bp. This piece was dramatically moved up 178 bp to the 5' end, which resulted in a missing block in the alignment. After this artifact, the sequence goes deviant from *C. pseudoformosus* and becomes identical with those of *C. applanatus*. It then switches back to *C. pseudoformosus* at the end (861–1386 bp).

The specimen tag in the ITS phylogeny of Kumari et al. (2013) is wrong. It should be "316-06", the holotype. The isolate number "317" in GenBank for HQ270116 is also wrong. The sample "236-06" for *C. umbonatus* in the LSU tree is the sample number of *C. fibrillosus* (see under *C. fibrillosus*).

Cantharellus umbonatus nom. illeg. is clearly a later synonym of *C. pseudoformosus*. They have near-identical sequences and grow in the same habitat, i.e with *Cedrus deodara*. As the name is illegitimate, the easiest solution is to ignore it completely.

Choosing the correct names for marketed chanterelles in southwestern China

The genus *Cantharellus* is one of the important genera of marketed edible mushrooms in China. The bulk of marketed yellowish or orange chanterelles are called "*Ji-You-Jun*" (chicken fat fungus) in the south and "*Xing-Huang-Jun*" (apricot yellow fungus) in the north (Wang et al. 2004, Bau & Bao 2016, Yang et al. 2021). Now that the interpretation and sequence problems associated with the holotypes of the earlier Indian and Chinese *Cantharellus* are solved, it is possible to choose the correct names for these marketed chanterelles in southwestern China.

Subgenus *Cantharellus*

In the past decade a total of thirteen yellowish, medium-sized *Cantharellus* species have been described with DNA data from eastern and southern Asia: *C. laevihymeninus*, *C. vaginatus* (Fig. 12c) and *C. versicolor* from southwestern China (Shao et al. 2011, 2016b, Cao et al. 2021), *C. hainanensis* (An et al. 2017) and *C. macrocarpus* (Zhang et al. 2021b) from south China,

C. magnus from Central China (Cao et al. 2021), *C. subvaginatus* from South Korea (Buyck et al. 2018), *C. anzutake* from Japan (Ogawa et al. 2018) and *C. applanatus, C. himalayensis, C. indicus, C. natarajanii,* and *C. pseudoformosus* from western India (Kumari et al. 2011, 2013). Except for *C. magnus*, all the species belong to subg. *Cantharellus.*

Cantharellus hainanensis and *C. laevihymeninus* are not problematic considering these are 'smooth chanterelles' and so is the still unsequenced *C. incrassatus* from Malaysia (Buyck 2014). Our data (Fig. 4) showed that *C. hainanensis* (Fig. 12a) is not endemic to Hainan island but extends to the central part of China (He'nan Prov.). In He'nan province, it is sold in market. One Indian sample of *C. lateritius* in Kumari et al. (2013), represented by ITS sequence HQ270121 is grouped into a terminal clade with *C. hainanensis* in our phylogenetic tree of subg. *Cantharellus* (Fig. 4). It is better to name it "*C.* aff. *hainanensis"* rather than *C. lateritius.*

In tropical Asia, two names, viz. *C. subcibarius* and *C. macrocarpus,* represent golden chanterelles. *Cantharellus subcibarius* was described by Corner from tropical forest in North Borneo (Corner 1966). It was never collected again since it was first described, although Corner (1970) mentioned a few years later a collection from Papua New Guinea under that name but with quite different microscopic features. The features of the type were recently studied by Buyck et al. (2021) and suggest strongly that *C. subcibarius* belongs in subg. *Cantharellus*. It fits the concept of a 'golden chanterelle', i.e. a medium-sized, yellowish *Cantharellus* with a hymenophore that has distinct veins or gill-folds, possesses clamp connections and has thick-walled hyphal ends at the pileus surface. Compared with *C. subcibarius, C. macrocarpus* has bigger fruiting bodies and smaller spores (Zhang et al. 2021b).

In the Himalayan subalpine region, *C. versicolor* is the most commonly sold golden chanterelle (Fig. 11a). The holo- and paratypes were all bought from markets in Shangrila, Yunnan. It was described as a species having brown scales on the pileus, long spores [(8.5) 9.0–10.0 × 5.0–6.0 μm] and thick-walled hyphae (5–14 μm diam.) in the pileipellis (Shao et al. 2016b). We confirmed this by examining more samples of this species (Fig. 10). The holotype color was described as "sandy brown" to "dark brown" (Shao et al. 2016b) due to being heavily handled, but in reality, this species is brightly colored. Fruiting bodies with yellowish or grayish brown scales are very often observed (Fig. 11b–d), but those with pure yellow or orange yellow glabrous pileus are also seen (Fig. 11e). "*C. formosus*" reported by Shao et al. (2012) from subalpine northwestern Yunnan is *C. versicolor.* The Tibetan and Sichuan specimens cited by Wei et al. (2008) under *C. cibarius* var. *squamosus* (HMAS 130555 and 96581) might be the same. It is a typical subalpine species mostly growing in *Abies* forests and rarely in forest of spruce and oak (Fig. 11d). It is present in Sikkim, India, as well (GenBank MH654991). Another subalpine golden chanterelle is *C. tuberculosporus* (Fig. 9), only known from the holo- and epitype (see Results). Considering we have quite intensively sampled in the Himalayan-Hengduan mountains, we speculate that *C. tuberculosporus* is a rare species, occurring in the transition band from subtropical *Pinus* forests to subalpine *Abies* forests.

The most challenging task is to find the correct name(s) for the bulk of marketed medium-sized golden chanterelles in temperate and subtropical regions in China (Fig. 11f–h). The identification problem of these golden chanterelles immediately becomes clear when performing BLASTn of obtained ITS sequences for most yellow *Cantharellus* bought from markets: BLASTn revealed that all were > 99.5 % similar to the deposited ITS sequences by Kumari et al. (2013) for five of their Indian species, viz. *C. applanatus,* C. *elongatipes, C. fibrillosus, C. himalayensis,* and *C. natarajanii,* and also to the ITS sequence for the holotype of *C. anzutake* from Japan and there are even more options: Chinese "*C. yunnanensis"* and *C. tuberculosporus*. How to choose a correct name among so many different possibilities? We here exclude *C. yunnanensis* as it is a *Craterellus* species (see Results). By critically analyzing the DNA data of the Indian species, we here showed that the ITS for the holotypes of *C. elongatipes* and *C. fibrillosus* were wrong and that both these species belong to subg. *Parvocantharellus* (Fig. 5). Finally, *C. tuberculosporus* and *C. versicolor* are two species occurring at high altitude. *Cantharellus versicolor* belongs to the *C. formosus*

complex and the ITS is only ca. 90% similar to the marketed yellow chanterelles. The ITS region of *C. tuberculosporus* is only 96% similar to the ITS of the marketed yellow chanterelles and is, moreover, extremely rare and not likely to be found on markets. It is not a suitable name either.

Figure 11 – a–e *Cantharellus versicolor*. a marketed golden chanterelle in Shangrila, Yunnan, China (XHW6128). b, c XHW9337 (Shangrila) and XHW5842 (Deqin), with conspicuous brownish scales on the pileus, growing in forests of *Abies georgei*. d XHW5572, growing in a mixed forest with trees of *Abies* and *Quercus* sect. *Heterobalanus* at Linzhi, Tibet. e XHW8974 (Habaxueshan, Yunnan), without scales on the pileus. f–h *C. applanatus.* f marketed golden chanterelle at Jingdong, Yunnan (XHW4572). g XHW2994, growing in a *Pinus thunbergii* forest at Laoshan, Qingdao, China. h XHW8043, growing in a *Pinus yunnanensis* forest in Lanping, Yunnan. Photos X. H. Wang.

This leaves *C. anzutake* from Japan as one of the possible options we did not yet examine closely. The description of *C. anzutake* by Ogawa et al. (2018) was supported by multi-locus data of ITS, partial LSU and *tef1*. For species recognition, these authors based their new species essentially on a single evolutionary event: a 100 base pair deletion in the ITS1 region. When comparing the ITS sequences of *C. applanatus* and *C. anzutake*, one can have, for 100% coverage, merely 5 mutations besides the 100 bp deletion out of the 1333 bp long ITS sequences. Whereas the 100 bp deletion seemed a constant feature for all ITS sequences obtained for different Japanese *C. anzutake* specimens, there were sometimes more mutations among the ITS sequences of the various Japanese specimens than between the holotypes of the Japanese and Indian species.

The ITS chromatogram of our specimen XHW4349 (see Results, Fig. 3), however demonstrates that the "anzutake" type (the short copy) can co-occur with the "applanatus" type (the long copy) in the same fruiting body. This implies that the 100 bp deletion in *C. anzutake* merely represents a length variation in the same population as *C. applanatus.* In other words, the legitimacy of a single deletion event for the recognition of *C. anzutake* as a distinct species is obsolete.

The *tef1* gene performs much better and produces more reliable alignments to distinguish among species in subg. *Cantharellus* and was therefore proposed as a 'barcode' for species within this subgenus (Buyck & Hofstetter 2011). Unfortunately, *tef1* sequences have not been generated for the Indian species. Ogawa et al. (2018) showed that *tef1* is unable to distinguish their *C. anzutake* from similar Chinese collections (the latter were mostly deposited in GenBank as '*C. tuberculosporus*' and most of these specimens were bought from markets). When aligning all 30 *tef1* sequences available on GenBank (20 from China deposited as "*C. tuberculosporus*", 10 from Japan for *C. anzutake*) with the seven sequences we produced from our own Yunnan specimens, we came to the same conclusion as Ogawa et al. (2018).

After excluding *C. anzutake*, *C. yunnanensis*, *C. tuberculosporus* and several of the Indian species as possible valid names for the marketed chanterelle in China, we propose *C. applanatus* as the best choice of the first available, correct name for the most commonly marketed golden chanterelle in China. As analyzed above, the molecular data deposited for *C. applanatus* by Kumari et al. (2013) are trustworthy, while the description and illustration (Fig. 4B in Kumari et al. 2013) of the type collection conform well to collections we studied, including very similar spore dimensions (see Fig. 10) and similar pileipellis composed of rather narrow hyphal extremities with variable wall thickness (within a single specimen from thin- to thick-walled). This is by far the safest nomenclatural and taxonomic choice for a species that covers a broad geographical distribution, from Indian Himalaya, over central and southern China, to the Republic of Korea (Buyck et al. 2020) and Japan. *Cantharellus anzutake*, *C. himalayensis*, *C. natarajanii* are all synonyms for it. Besides *C. applanatus*, other golden chanterelles such as *C. cibarius*, *C. pallens* and *C.* aff. *indicus* (XHW6691) are also present in eastern and southern Asia (Figs 4, 12b), but none of these is as common as *C. applanatus*.

Subgenus *Parvocantharellus*

Species of this subgenus, in spite of producing small and slender fruiting bodies, are also often sold in markets in southwestern China (as "*Cantharellus minor*" in Wang et al. 2004). In this subgenus, a total of fifteen species with yellow, orange to brownish fruiting bodies have been described from Asia (Corner 1966, Antonín et al. 2017, Cao et al. 2021, Zhang et al. 2021a).

Shao et al. (2011) identified some Chinese marketed samples as *C. appalachiensis* based on a comparison of the highly similar LSU sequences shared between Chinese and American samples. In our phylogeny (Fig. 5), these samples, as well as our collection XHW4700 (Fig. 12f), formed a terminal clade with *C. austrosinensis.* This terminal clade forms a sister clade of *C. koreanus.* We conclude that clude that *C. appalachiensis* is not present in China and its Asian counterparts are *C. austrosinensis* and *C. koreanus*.

Figure 12 – a *Cantharellus hainanensis* (XHW7576), bought by Wei Zhou from a market in Xinyang, He'nan, China. b *Cantharellus* cf. *indicus* (XHW6691), growing in a fagaceous forest in Binchuan, Yunnan. c *C. vaginatus* (XHW4565), sold in a market at Jingdong, Yunnan. d *C. phloginus*, sold in a market at Xishuangbanna, Yunnan. e *C. curvatus* (XHW3015), growing in a *Castanea mollissima* forest at Pingyi, Shandong. f *C. austrosinensis* (XHW4700), growing in a *Pinus yunnanensis* forest at Shilin, Yunnan. g *C. elongatipes*, growing in a fagaceous forest in Daozhen, Guizhou. h *C. zangii* (XHW8458), growing in an *Abies* forest in Deqin, Yunnan. Photos X. H. Wang.

After we corrected the LSU sequence reference of *C. elongatipes* to HM750928 and used our four-locus data to link it with other miniature species, we here conclude that *C. elongatipes* (Fig. 12g) is the earlier name for *C. sinominor* and C. *subminor*. The long branch on which *C. subminor* was sitting in Cao et al. (2021) is due to questionable base pairs in three *rpb2* sequences.

Cantharellus zangii (Fig. 12h) is a subalpine species that is collected as "Ji-You-Jun". When Tian et al. (2012) described this species, they did not provide DNA sequences. We sequenced its holotype and obtained ITS, LSU, *rpb2* and *tef1*. In our phylogeny (Fig. 5), the holotypes of *C. sikkimensis* and *C. zangii* are grouped in a terminal clade. They have near-identical ITS and LSU sequences. We here confirm that *C. sikkimensis* is a later synonym of *C. zangii*, following Zhang et al. (2021a).

Finally, we report here first Chinese collections (Figs 5, 12e) from Heilongjiang and Shandong provinces for the recently described *C. curvatus* from South Korea (Buyck et al. 2020). It seems to be an uncommon species. In the same clade as *C. curvatus* (Fig. 5), our topology shows that *C. fibrillosus* is nested within *C. aurantinus* which seems to suggest that the latter might be contaxic with the former. Considering the long branch length leading to *C. fibrillosus* and the fact that we do not have reliable data to link the two species, we leave the question of whether we are dealing here with a single or with two different species open for the moment.

Subgenus *Cinnabarini*

Chanterelles with red or small orange fruiting bodies are also quite commonly sold in China (Wang et al. 2004) (Fig. 12d). They used to be identified as *C. cinnabarinus* (Wang et al. 2004, Shao et al. 2012, Yang et al. 2021). Now the correct name for this Asian chanterelle is *C. phloginus* (Shao et al. 2016a). Compared to *C. cinnabarinus*, it is mostly quite larger in size and more variable in color. Antonín et al. (2017) described *C. albovenosus* from South Korea as a close, but morphologically distinct sister species of *C. phloginus*. It was characterized by the pure white hymenophore, composed of much lower veins, and the constant, bright orange pileus color, as opposed to the yellow-orange, more developed hymenophore and the more variable overall color of *C. phloginus*. Molecularly, the two species were supported by merely two changes in the *tef1* sequences (Antonín et al. 2017). With more samples added, the genetic gap between *C. albovenosus* and *C. phloginus* disappears (Fig. 6). In markets, specimens with either yellow-orange or white, less differentiated gills are sometimes sold together. *Cantharellus albovenosus* is merely a white-gilled form of *C. phloginus.* It has to be synonymized with the latter.

Major reasons for taxonomic problems in *Cantharellus*

At the end of this challenging adventure to find correct names for Asian chanterelles, a question we should ask ourselves is: why are there still so many problems in the taxonomy of *Cantharellus*, even in the DNA era?

One of the most serious problems is negligence of morphological evaluation, both for historical unsequenced species and species with sequence data. The study of any particular fungal group should start with a revision of what has been done before. The in-depth morphological study of all existing holotypes of the various species described earlier, accompanied by eventual sequencing trials, should have preceded the description of new taxa from the same continent. Here we are forced to conclude that many researchers prefer to ignore unsequenced older species and to describe new species as long as there is no satisfactory BLAST hit. This negligence results in a disconnection between unsequenced historical species and the more recent species descriptions supported by DNA data (Wang 2020). This problem is not specific to research on *Cantharellus*, but applies to many other fungal groups. In *Lactarius,* for example, although Wang (2007) gave a detailed morphological description of the type of *L. mininus* var. *macrosporus,* this did not stop Wang et al. (2018) describing the contaxic *L. verrucosporus* just because there were no DNA data available for the former. More cases include *L. lavandulus* (= *L. atromarginatus*) and the ascomycete *Otidea pruinosa* (= *O. subpurpurea*) (Le et al. 2007, Xu et al. 2022). Fortunately, new

generation sequencing approaches make it now possible to unveil the identity of old herbarium types, such as demonstrated here for *C. tuberculosporus*.

Even for species that have sequences, it would be wrong to conclude that morphology is of inferior importance compare to DNA data. To delimit and describe species based on DNA sequences is one thing, but being able to recognize the same species in the field is quite something else. Having sufficient and good images at disposal for the appreciation of this variability is of great importance for those who will identify species in the field. It is a pity that most publications on Asian *Cantharellus* illustrate new species usually with a single photograph that is often the size of a postage stamp. This approach does not allow readers to recognize these species in the field. Had the field photos of the Indian species published by Kumari et al. (2013) been provided with more details, it would have been possible for later researchers to follow the work. In addition, in-depth morphological analysis will not only help to recognize species in the field, it will also help to discover potential sequence errors instantly. For the Indian chanterelles, had Zhang et al. (2021) and Cao et al. (2021) noticed the slender habit of *C. elongatipes*, they might have been able to discover its wrong ITS and LSU sequences and avoid describing superfluous species. For microscopic characters, in this study, we have convincingly shown that the use of mean values for spore size will at least distinguish the golden chanterelle (*C. applanatus*) in subtropical markets from subalpine *C. versicolor* and *C. tuberculosporus*. Unfortunately, this methodology is not used by some Asian workers (Shao 2011, Cao et al. 2021, Shao et al. 2021).

A second reason why *Cantharellus* research can become problematic is when different authors select different loci for phylogenetic analysis, it makes the genetic comparison of published *Cantharellus* species impossible. The basic reason for this phenomenon is that producing high quality DNA data for *Cantharellus* is much harder than for many other fungal groups. The complete ITS regions, less than 500–800 bp long in most fungal groups, can be up to 1600 bp long in *Cantharellus*. While some researchers used only the ITS-1 region, others provided ITS-2 (e.g. An et al. 2017) or simply skipped the barcode ITS region and used other loci (Das et al. 2017, Shao et al. 2016a, 2016b, 2021, Zhang et al. 2021a, 2022). This explains why Zhang et al. (2021b) were not able to identify any of their *Cantharellus* samples correctly using a short section of ITS2. Producing comparable sequences so that researchers can integrate each other's results in their study is critical in the DNA era, just as morphological comparison between species requires study of the same set of features. For fungal groups with problematic PCR and complicated sequences, an effective way is to use specific internal primers to amplify smaller fragments of the locus separately (see Fig. 2), inspect the shorter sequences and eventually assemble them into a reliable consensus sequence.

Another problem with the DNA sequences of chanterelles is that there are numerous heterozygotous INDELs (Feibelman et al. 1994) and polystructures present in different copies in ITS and LSU and there are several introns in *rpb2* and *tef1*. For a locus in which INDELs are present among different copies, the peaks of chromatograms will be out of phase at some point (Flot et al. 2006, Hughes et al. 2013, Fig. 3). If these peaks are not correctly phased, one or more wrong nucleotide positions will be generated. Cao et al. (2021) published two low quality LSU sequences with wrong base pairs between positions 1 to 511 for *C. versicolor* (MW979525 and MW979526). These incorrect base pairs are most likely from unphased sequences as they are exactly in front of a poly G site. They are responsible for the long branch leading to *C. versicolor* in their phylogeny (their Fig. 2). The two LSU sequences of *C. laevihymeninus* (MW979520 and MW979521) also have abnormal base pairs after position 519 bp of the sequence, which is exactly after a poly G site. Three *rpb2* sequences of *C. subminor* (MW999455, MW999456 and MW999457) have wrong base pairs in the section 72–115 bp. This section is only 12 bp away from the first intron where INDELs easily occur. An additional suspicious fact in Cao et al. (2021) is that the above-mentioned low-quality sequences present identical misreadings among different specimens of the same species! A possible explanation for this remarkable coincidence is that a single bad sequence might have been copied across samples, but not really obtained from different specimens. The sequence problems resulting from INDELs are not the patent of *Cantharellus*. It is

very common in sequences published for other basidiomycetes, but in *Cantharellus* this noise is amplified. In the genus *Lactarius*, for example, the long branch of *L. viridinigrellus* (Bera et al. 2019) is apparently from unphased raw sequences as there are 26 changes even in the 5.8S region. Our sampling effort in the Himalayas and obtained DNA data convince us that *L. viridinigrellus* is a "man-made" species. Its real identity is *L. olivaceoumbrinus*, a species described from North America. The ITS sequence KR364098 of *Lactifluus volemoides* published by De Crop et al. (2017) has 47 ambiguous and degenerated base pairs in the 5.8S region. This must also be from unprocessed raw sequences. These bad sections should be excluded from any analysis as they mess up the whole alignment and create wrong taxa. Always re-inspecting the quality of sequences in an alignment with reference sequences will be helpful to discover the abnormal base pairs and avoid mistakes efficiently.

The narrower the delimitation of species, the more important the representative size of the sampling becomes. *Cantharellus* species present often problems with sequencing and possess highly flexible phenotypes, making sufficient sampling more urgent and crucial. Some taxonomic problems in chanterelles are due to limited sampling. In the *tef1* phylogeny of Shao et al. (2021), there was a gap between "*C. yunnanensis*" (now *C. applanatus*) and *C. anzutake*. Results based on our broader sampling show that this is merely a bias from limited sampling (Fig. 4). This is the same as in the *C. albovenosus*-*C. phloginus* case. Nevertheless, even very recent papers still describe new Asian chanterelles on the basis of a single or very few collections (Buyck et al. 2017, 2018, Cao et al. 2021, Zhang et al. 2021a). Although Aime et al. (2021) recommend that it is always preferable to study multiple collections of specimens when describing a new species, it is also true that many rare and often very interesting species might be missed when waiting for a sufficient number of collections before describing them. In Madagascar, for instance, the two earliest described *Cantharellus*, *C. madagascariensis* and *C. avellaneus* (Patouillard 1924), both based on a single fruiting body, are good examples of this. Whereas the former has never been found again, it took over one century to find a second collection of *C. avellaneus* and this notwithstanding intensive collecting during the past 25 years (Buyck et al. 2016e). *Cantharellus tuberculosporus* is now a similar example. One might think that it would correspond to the much more common *C. versicolor*, but now it turns out to be a very rare species that was never reported since its description. When only a single or very few collections are available to publish a rare, new species, providing high quality DNA data for multiple loci becomes even more crucial. Sufficient sampling also implies that the genetic variation among different individuals and even different copies of a particular gene region are fully mined (see Hughes et al. 2013, Chen et al. 2016). If the variation between different copies is missed, one may interpret intraspecific variation as interspecific diversification, as we demonstrated here in the case of *C. applanatus* vs. *C. anzutake.*

Labeling DNA sequences with confusing or erroneous tags is the last but not least serious problem not only in the study of *Cantharellus*, but also in many other groups (Bridge et al. 2003, Hofstetter et al. 2019). Our analysis of the sequence labels attributed to sequenced specimens by Kumari et al. (2011, 2013) clearly demonstrates how bad tags caused huge trouble. Voucher-associated problems continue to exist even in very recent papers, such as with deposited DNA data by Cao et al. (2021). DNA sequences of their new species *C. laevihymeninus* are deposited in GenBank as "*Muscinupta laevis*, a member of a completely different fungal order (Hymenochaetales [!]). Similarly, the contradictory information between their voucher table, the typifications, and the GenBank and MycoBank deposits for *C. laevihymeninus* and *C. magnus* leaves one in doubt as to which specimens are the real holotypes. The LSU sequences deposited by Cao et al. (2021) for *C. phloginus* (MW979518 and MW979519) are in reality of *C. applanatus*. Since there is no branch length for their *C. phloginus* (their Fig. 2), we can conclude that the sequences they used for phylogenetic analysis are NOT the ones they gave in the paper. In Shao et al. (2016b), the *tef1* sequences of Yu 24 and of Tian 160 are switched in their voucher table compared to the GenBank deposits. Likewise, in Zhang et al. (2021a), the *rpb2* sequence MZ766574 for *C. aurantinus* is from *C. austrosinensis* and the *rpb2* sequence used for phylogenetic analysis for this sample cannot be MZ766574.

The majority of *Cantharellus* sequences submitted to GenBank are never updated once published, and *Cantharellus* is not the only group that has either bad tags or erroneous deposits for DNA sequences. None of the DNA sequences of *Lactarius* published by Lee et al. (2019) have correct source modifiers in GenBank. From the pattern of mistakes, we suspect that when the submission files were prepared, the source modifiers mistakenly shifted between specimens (a typical problem already reported for other publications by Hofstetter et al. 2019) and readers have to rely on the voucher table in the supplementary file to retrieve the correct GenBank numbers. Worse, misapplication of DNA data will not only result in routine mis-identifications, but may also cause wrong downstream inference. In a study of Pezizales, Hansen et al. (2019) found that the *rpb2* sequences of *Gymnohydnotrya australiana* (JQ954529) and *Underwoodia* cf. *singeri* (JQ954475 and JQ954474) were switched by Bonito et al. (2013). This mismatch resulted in a wrong "Chile-Australia" species pair (*U. singeri-U. beatoni*) in the *rpb2* genealogy (Bonito et al. 2013). Kraisitudomsook et al. (2020) later used the erroneous submission from Bonito et al. (2013) to infer a wrong "*Geomorium singeri-G. australianum*" speciation event.

Conclusion

At the end of this study, we would like to cite Brinkman and Leipe (2001) to underline the importance of correct data and third-party annotation of sequences in the public database: "Paradoxical as it may sound, by far the most important factor in inferring phylogenies is not the method of phylogenetic inference but the quality of the input data. Even the most sophisticated phylogenetic inference methods are not able to correct for erroneous input data." Or, to say it with a common expression from computer sciences and mathematics: "Garbage in, garbage out [GIGO]".

The problem with the existing online "garbage" in GenBank is that it is very difficult for the taxonomic community to do something about it once it has been put online. This paper concerns the genus *Cantharellus* and this is clearly stated in the title. As a consequence, most researchers working on the genus will probably come across it and will be aware of all the above-mentioned mistakes concerning deposited sequences and/or their associated data. They should thus be able to integrate these corrections in their future publications. But what is the chance of missing reports of similar errors in sequence deposits and associated data when neither the title nor the key words mention any of the genera that are affected by these mistakes? One example of such a paper is Hofstetter et al. (2019): "The unbearable lightness of sequence-based identification". In the latter paper the authors report on an endless series of errors with sequence-associated data on species belonging to several fungal genera. The same paper also uncovered close to 80 holotype barcode sequences that were not annotated as types in GenBank. Although GenBank was informed of these findings even before the paper was finally published, no corrections or changes have been made to the implicated GenBank deposits at the time of submission of the present manuscript (four years later). In our opinion, it would be much more efficient if GenBank could insert some kind of "comment line" that can allow for third party annotation or comments on errors associated with sequence deposits and their associated data in the nucleotide database.

As a summary of this study, an overview of taxonomic changes and accepted *Cantharellus* species and their distribution in Asia is provided in Table 2. We present a chronological map to highlight the complicated relationships among the names (Fig. 13).

Table 2 Distribution of *Cantharellus* in Asia (as of June 2021). CN = China, KR = South Korea, JP = Japan, LA = Laos, IN = India, MY = Malaysia.

Species	Subgenus	Section	Country					
			CN	KR	JP	LA	IN	MY
C. omphalinoides	*Cantharellus*	*Amethystini*						×
C. pseudoformosus = *C. umbonatus nom. illeg.*	*Cantharellus*	*Amethystini*					×	

Table 2 Continued.

Species	Subgenus	Section	Country					
			CN	KR	JP	LA	IN	MY
C. subamethysteus	*Cantharellus*	*Amethystini*						×
C. subvaginatus	*Cantharellus*	*Amethystini*		×				
C. vaginatus	*Cantharellus*	*Amethystini*	×					
C. applanatus = *C. anzutake* = *C. natarajanii* = *C. natarajanii*	*Cantharellus*	*Cantharellus*	×	×	×		×	
C. cibarius	*Cantharellus*	*Cantharellus*	×		×		×	
C. indicus	*Cantharellus*	*Cantharellus*					×	
C. macrocarpus	*Cantharellus*	*Cantharellus*	×			×		
C. subcibarius	*Cantharellus*	*Cantharellus*						×
C. subcibarius var. *sordidus*	*Cantharellus*	*Cantharellus*						×
C. tuberculosporus	*Cantharellus*	*Cantharellus*	×					
C. versicolor	*Cantharellus*	*Cantharellus*	×				×	
C. hainanensis	*Cantharellus*	*Sublaeves*	×					
C. incrassatus	*Cantharellus*	*Sublaeves*						×
C. laevihymeninus	*Cantharellus*	*Sublaeves*	×					
C. subcibarius var. *rugosivensis*	*Cantharellus*	*Sublaeves*						×
C. citrinus	*Cinnabarini*		×	×				
C. chrysanthus	*Cinnabarini*		×					
C. cyphelloides	*Cinnabarini*				×			
C. diminutivus	*Cinnabarini*							×
C. phloginus	*Cinnabarini*		×					
C. phloginus f. *albovenosus*	*Cinnabarini*		×	×				
C. sinocinnabarinus	*Cinnabarini*		×					
C. magnus	*Magni*		×					
C. albus	*Parvocantharellus*	*Flavobrunnei*	×					
C. aurantinus	*Parvocantharellus*	*Flavobrunnei*	×					
C. austrosinensis	*Parvocantharellus*	*Flavobrunnei*	×					
C. convexus	*Parvocantharellus*	*Flavobrunnei*	×					
C. curvatus	*Parvocantharellus*	*Flavobrunnei*	×	×				
C. elongatipes = *C. sinominor* = *C. subminor*	*Parvocantharellus*	*Flavobrunnei*	×			×	×	
C. fibrillosus	*Parvocantharellus*	*Flavobrunnei*					×	
C. galbanus	*Parvocantharellus*	*Flavobrunnei*	×					
C. hongneungensis	*Parvocantharellus*	*Flavobrunnei*		×				
C. koreanus	*Parvocantharellus*	*Flavobrunnei*		×				
C. luteolus	*Parvocantharellus*	*Flavobrunnei*						
C. luteovirens	*Parvocantharellus*	*Flavobrunnei*	×					
C. minioalbus	*Parvocantharellus*	*Flavobrunnei*	×					
C. neopersicinus	*Parvocantharellus*	*Flavobrunnei*	×					
C. zangii = *C. sikkimensis*	*Parvocantharellus*	*Flavobrunnei*	×				×	
C. cerinoalbus	*Afrocantharellus*		×					×
C. cuticulatus	*Afrocantharellus*							×

Table 2 Continued.

Species	Subgenus	Section	Country					
			CN	KR	JP	LA	IN	MY
C. hygrophoroides	*Afrocantharellus*		×					
C. ianthinus	not determined							×
C. omphalinoides	not determined		×					×
C. pudorinus	not determined							×

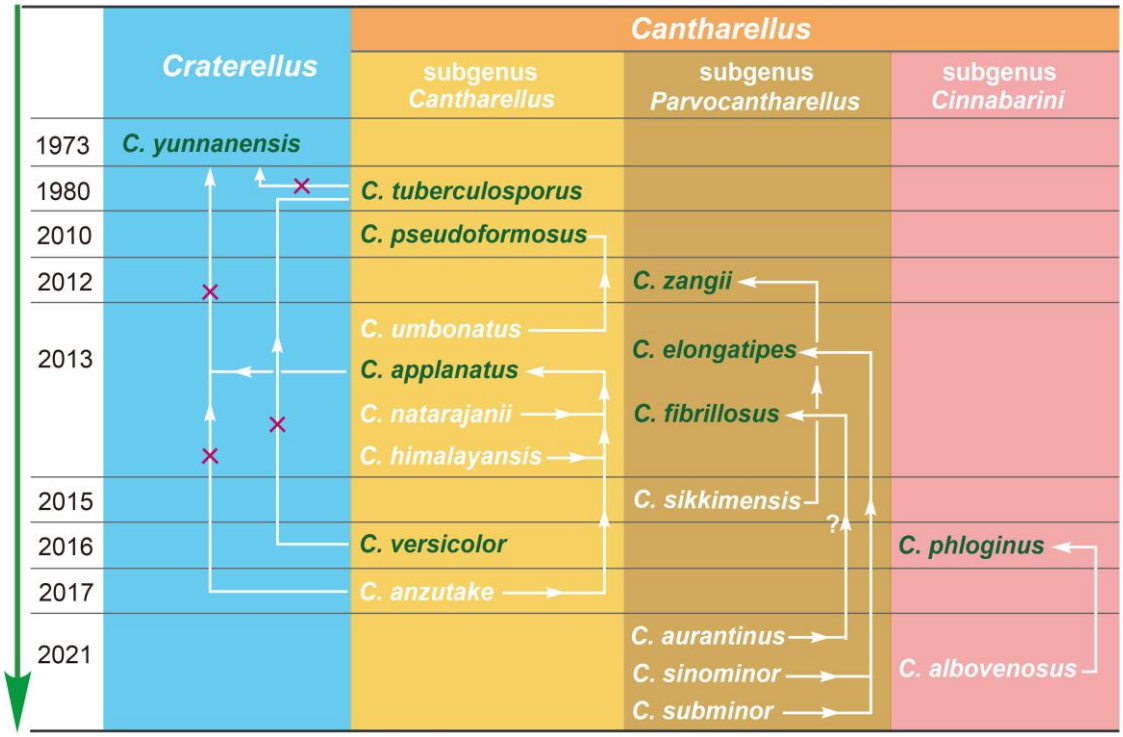


Figure 13 – Name changes of some *Cantharellus* species in Asia. *Cantharellus yunnanensis* is transferred to *Craterellus.* Names in green are acknowledged in this study.

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