available online at www.studiesinmycology.org

STUDIES IN MYCOLOGY 99: 100121 (2021).

A phylogenetic overview of the *Hydnaceae* (*Cantharellales*, *Basidiomycota*) with new taxa from China

Ting Cao[1,2], Ya-Ping Hu[3], Jia-Rui Yu[1,2], Tie-Zheng Wei[4], and Hai-Sheng Yuan[1,2*]

[1]*CAS Key Laboratory of Forest Ecology and Management, Institute of Applied Ecology, Chinese Academy of Sciences, Shenyang 110164, PR China;* [2]*University of the Chinese Academy of Sciences, Beijing 100049, PR China;* [3]*Nanjing Institute of Environmental Sciences, MEE/State Environmental Protection Scientific Observation and Research Station for Ecological Environment of Wuyi Mountains, Nanjing 210042, PR China;* [4]*State Key Laboratory of Mycology, Institute of Microbiology, Chinese Academy of Sciences, Beijing 100101, PR China*

**Correspondence*: Hai-Sheng Yuan, hsyuan@iae.ac.cn

Abstract: The family *Hydnaceae* (*Cantharellales*, *Basidiomycota*) is a group of fungi found worldwide which exhibit stichic nuclear division. The group is highly diverse in morphology, ecology, and phylogeny, and includes some edible species which are popular all over the world. Traditionally, *Hydnaceae* together with *Cantharellaceae*, *Clavulinaceae* and *Sistotremataceae* are four families in the *Cantharellales.* The four families were combined and redefined as "*Hydnaceae*", however, a comprehensive phylogeny based on multiple-marker dataset for the entire *Hydnaceae sensu stricto* is still lacking and the delimitation is also unclear. We inferred Maximum Likelihood and Bayesian phylogenies for the family *Hydnaceae* from the data of five DNA regions: the large subunit of nuclear ribosomal RNA gene (nLSU), the internal transcribed spacer regions (ITS), the mitochondrial small subunit rDNA gene (mtSSU), the second largest subunit of RNA polymerase II (*RPB2*) and the translation elongation factor 1-alpha gene (*TEF1*). We also produced three more phylogenetic trees for *Cantharellus* based on 5.8S, nLSU, mtSSU, *RPB2* and *TEF1*, *Craterellus* and *Hydnum* both based on the combined nLSU and ITS. This study has reproduced the status of *Hydnaceae* in the order *Cantharellales*, and phylogenetically confirmed seventeen genera in *Hydnaceae.* Twenty nine new taxa or synonyms are described, revealed, proposed, or reported, including eight new subgenera (*Cantharellus* subgenus *Magnus*, *Craterellus* subgenus *Cariosi*, subg. *Craterellus*, subg. *Imperforati*, subg. *Lamelles*, subg. *Longibasidiosi*, subg. *Ovoidei*, and *Hydnum* subgenus *Brevispina*); seventeen new species (*Ca. laevihymeninus*, *Ca. magnus*, *Ca. subminor*, *Cr. badiogriseus*, *Cr. croceialbus*, *Cr. macrosporus*, *Cr. squamatus*, *H. brevispinum*, *H. flabellatum*, *H. flavidocanum*, *H. longibasidium*, *H. pallidocroceum*, *H. pallidomarginatum*, *H. sphaericum*, *H. tangerinum*, *H. tenuistipitum* and *H. ventricosum*); two synonyms (*Ca. anzutake* and *Ca. tuberculosporus* as *Ca. yunnanensis*), and two newly recorded species (*H. albomagnum* and *H. minum*). The distinguishing characters of the new species and subgenera as well as their allied taxa are discussed in the notes which follow them. The delimitation and diversity in morphology, ecology, and phylogeny of *Hydnaceae* is discussed. Notes of seventeen genera which are phylogenetically accepted in *Hydnaceae* by this study and a key to the genera in *Hydnaceae* are provided.

Key words: *Cantharellales*, *Hydnaceae*, Multiple-marker phylogeny, Taxonomy.

Taxonomic novelties: New subgenera: In genus *Cantharellus*: *Cantharellus* subgenus *Magnus* T. Cao & H.S. Yuan, in genus *Craterellus*: *Craterellus* subgenus *Cariosi* T. Cao & H.S. Yuan, subg. *Craterellus*, subg. *Imperforati* T. Cao & H.S. Yuan, subg. *Lamelles* T. Cao & H.S. Yuan, subg. *Longibasidiosi* T. Cao & H.S. Yuan, subg. *Ovoidei* T. Cao & H.S. Yuan, in genus *Hydnum*: *Hydnum* subgenus *Brevispina* T. Cao & H.S. Yuan; **New species:** *Cantharellus laevihymeninus* T. Cao & H.S. Yuan, *Ca. magnus* T. Cao & H.S. Yuan, *Ca. subminor* T. Cao & H.S. Yuan, *Craterellus badiogriseus* T. Cao & H.S. Yuan, *Cr. croceialbus* T. Cao & H.S. Yuan, *Cr. macrosporus* T. Cao & H.S. Yuan, *Cr. squamatus* T. Cao & H.S. Yuan, *Hydnum brevispinum* T. Cao & H.S. Yuan, *H. flabellatum* T. Cao & H.S. Yuan, *H. flavidocanum* T. Cao & H.S. Yuan, *H. longibasidium* T. Cao & H.S. Yuan, *H. pallidocroceum* T. Cao & H.S. Yuan, *H. pallidomarginatum* T. Cao & H.S. Yuan, *H. sphaericum* T. Cao & H.S. Yuan, *H. tangerinum* T. Cao & H.S. Yuan, *H. tenuistipitum* T. Cao & H.S. Yuan, *H. ventricosum* T. Cao & H.S. Yuan; **New synonyms:** *Cantharellus anzutake* W. Ogawa, N. Endo, M. Fukuda and A. Yamada and *Ca. tuberculosporus* M. Zang as *Ca. yunnanensis* W.F. Chiu; **Species new to China:** *Hydnum albomagnum* Banker, *Hydnum minum* Yanaga & N. Maek.

https://doi.org/10.1016/j.simyco.2021.100121.

INTRODUCTION

Hydnaceae Chevall. together with *Botryobasidiaceae* Jülich, *Ceratobasidiaceae* G.W. Martin, *Tulasnellaceae* Juel is nested in *Cantharellales* (Hibbett *et al.* 2014). As initially defined, the family mainly included taxa with a hydnoid hymenophore like the type genus *Hydnum* L. (Miller 1933). In 1999, Pine *et al.* identified a distinct group in the *Homobasidiomycetes*, comprising the genera *Cantharellus* Adans. and *Craterellus* Pers. of *Cantharellaceae* J. Schröt., *Clavulina* J. Schröt. and *Multiclavula* R.H. Petersen of *Clavulinaceae* Donk as well as *Hydnum* and they share the common feature of stichic nuclear division (Pine *et al.* 1999). Several subsequent studies phylogenetically focused on the "cantharelloid clade" (Hibbett & Binder 2002, Binder *et al.* 2005, Larsson 2007) and Moncalvo *et al.* (2006) delimited the "core cantharelloid clade" which was composed of *Membranomyces* Jülich, *Sistotrema* Fr. and the five genera mentioned above. The type genus *Hydnum* of *Hydnaceae* fell in the core clade and the family "*Hydnaceae*" seemed to be inappropriate for its original narrower definition. Larsson (2007) provided the first phylogenetic evidence of the *Hydnaceae* which was delimited to embrace taxa with stichic basidia. Hibbett *et al.* (2014) proposed that *Cantharellaceae*, *Clavulinaceae* and *Sistotremataceae* were synonyms of the family *Hydnaceae*. The new combined *Hydnaceae* comprised nine genera and was characterised by having stichic basidia and septa with perforate parenthesomes (Hibbett *et al.* 2014). Lawrey *et al.* (2016) did the first phylogeny analysis of *Hydnaceae* based on the nLSU dataset and proposed a new genus in the family, and the result supported the concept of the *Hydnaceae* of Hibbett *et al.* (2014).

Peer review under responsibility of Westerdijk Fungal Biodiversity Institute.

Hydnaceae is a highly diverse family in terms of morphology, ecology, and phylogeny. Morphologically, the basidiocarps of species in the family can be cantharelloid (*e.g. Cantharellus* and *Craterellus*) (Wilson *et al.* 2012, Henkel *et al.* 2014), clavarioid (*e.g. Clavulina* and *Multiclavula*) (Petersen 1967, Thacker & Henkel 2004, Yuan *et al.* 2020) or corticioid (*e.g. Sistotrema* and *Membranomyces*) (Jülich 1975, Kotiranta & Larsson 2013); the hymenophores range from hydnoid (*e.g. Hydnum*) (Niskanen *et al.* 2018), poroid (*e.g. Sistotrema*) (Zhou & Qin 2013), smooth (*e.g. Cantharellus*) (Buyck 2014) to veined (*e.g. Craterellus*) (Dahlman *et al.* 2000, Redhead *et al.* 2002, Contu *et al.* 2009); the number of sterigmata of basidia can be two (*e.g. Clavulina* and *Membranomyces*) (Petersen 1967, Kotiranta & Saarenoksa 1993), two to six (*e.g. Cantharellus*) (Buyck *et al.* 2014) or eight (*e.g. Sistotrema* and *Sistotremella*) (Eriksson *et al.* 1984). Ecologically, *Cantharellus*-*Craterellus*, *Hydnum*-*Sistotrema sensu stricto* and *Clavulina*-*Membranomyces* are three distinct ectomycorrhizal (ECM) lineages in the family while most species of *Sistotrema* and *Sistotremella* are saprotrophic (Eriksson *et al.* 1984, Boidin & Gilles 1994, Nilsson *et al.* 2006, Hibbett *et al.* 2014). Besides, some genera with lichenicolous or lichenised nutritional modes (*e.g., Multiclavula* and *Burgoa*) are also embedded in *Hydnaceae* (Lawrey *et al.* 2016, Masumoto & Degawa 2020a). Phylogenetically, most genera in *Hydnaceae* are monophyletic whereas *Sistotrema* is highly polyphyletic (Moncalvo *et al.* 2006, Nilsson *et al.* 2006, Larsson 2007, Veldre *et al.* 2013, Hibbett *et al.* 2014). In additon, culinary mushrooms occur in *Cantharellus*, *Clavulina*, *Craterellus* and *Hydnum* (Boa 2004, Dai *et al.* 2010); toxic mushrooms have not yet been reported from family *Hydnaceae.*

In the recent decade, molecular studies of new species and lineages in the *Hydnaceae* have been prolific from around the world (Buyck *et al.* 2014, Diederich *et al.* 2014, Henkel *et al.* 2014, Lawrey *et al.* 2016, An *et al.* 2017, Gruhn *et al.* 2017, Hembrom *et al.* 2017, Niskanen *et al.* 2018, Swenie *et al.* 2018, Kaur *et al.* 2019, Pérez-Pazos *et al.* 2019, Wu *et al.* 2019, Jian *et al.* 2020, Lawrey *et al.* 2020, Masumoto & Degawa 2020a, b, Yuan *et al.* 2020, Zhang *et al.* 2020). However, since Hibbett *et al.* (2014) redivided the *Cantharellales*, there have been only a few phylogenies involving the family (Lawrey *et al.* 2016, 2020, Masumoto & Degawa 2020a), based on ITS or nLSU dataset and often including partial genera in *Hydnaceae*. Although *Hydnaceae* has been estimated to originate at 259 Mya and the outline shows it including 21 genera (He *et al.* 2019), a comprehensive phylogeny based on a multiple-marker dataset for the entire *Hydnaceae* is still lacking and the delimitation as well as diversity of genera is also unclear.

Increasing numbers of studies of *Hydnaceae* are emerging in China (Tian *et al.* 2012, Shao *et al.* 2011, 2014, 2016a, b, Feng *et. al* 2016, He *et al.* 2016, An *et al.* 2017, Zhong *et al.* 2018, Wu *et al.* 2019, Jian *et al.* 2020, Yuan *et al.* 2020). During an investigation of specimens in *Hydnaceae* from China, many specimens were collected. The morphological features and multiple-marker molecular analyses showed that fifty samples are undescribed taxa which belong to the genera *Cantharellus*, *Craterellus* and *Hydnum*. In this study, we describe twenty-seven new taxa, merge two synonyms based on morphological characteristics and phylogenetic analyses, and infer the first relatively comprehensive multilocus phylogeny for the family *Hydnaceae* based on nLSU + ITS + mtSSU + *RPB2* + *TEF1* combined dataset.

The aims of this study are (1) To describe the new taxa of *Hydnaceae* from China, confirm or propose infrageneric subdivision within the genera *Cantharellus*, *Craterellus* and *Hydnum* based on morphological and phylogenetic analyses; (2) To confirm the phylogenetic position of *Hydnaceae* within the *Cantharellales* and (3) To provide more accurate delimitation of *Hydnaceae* at the genus level and clarify the generic diversity in the family.

MATERIALS AND METHODS

Specimens, isolates and identification

The studied specimens were collected from Hunan, Liaoning, Yunnan Province and Xinjiang Autonomous Region in China and deposited at the herbarium of the Institute of Applied Ecology, Chinese Academy of Sciences (IFP). Macroscopic descriptions of collected specimens were based on fresh basidiocarps. Microscopic procedures followed Shao *et al.* (2014). Dried material was mounted in 5 % aqueous KOH, and Melzer's reagent to test for any amyloid and/or dextrinoid reactions (Melzer's reagent: 1.5 g KI (potassium iodide), 0.5 g I (crystalline iodine), 22 g chloral hydrate, distilled water 20 mL). The following abbreviations are used in the text: KOH = 5 % potassium hydroxide; L_m = mean spore length (arithmetic average of all spores); W_m = mean spore width (arithmetic average of all spores); Q = variation in the ratios of L_m/W_m between specimens studied, and n = total number of spores measured from a given number of specimens. Sections were studied at magnifications up to ×1 000 using a Nikon Eclipse E600 microscope (Tokyo, Japan) with phase-contrast illumination, and dimensions were estimated with an accuracy of 0.1 µm. Microscopic drawings were made with the aid of a drawing tube. Spore measurements excluded the apiculus, and 5 % of the measurements at each end of the range are given in parentheses. The spore measurements were made with a Nikon SMZ 645 compound microscope. Colour codes are from Kornerup & Wanscher (1981).

DNA extraction, PCR, and sequencing

Genomic DNA was extracted from dried herbarium specimens with a Thermo Scientific Phire Plant Direct PCR kit (Thermo Fisher Scientific, Waltham, Massachusetts, USA) according to the manufacturer's instructions which was also used for the polymerase chain reaction (PCR) (Chen *et al.* 2016). Nuclear ribosomal RNA markers were used to determine the phylogenetic position of the new species. The internal transcribed spacer (ITS) was amplified with the primers ITS1F/ITS4 (White *et al.* 1990) and LROR/LR5 (Vilgalys & Hester 1990) for partial nLSU; MS1/MS2 (Matheny 2005) for mtSSU; rpb2-5FCanth/rpb2-7cRCanth (Buyck *et al.* 2014) for *RPB2* of *Cantharellus* and fRPB2-5F/bRPB2-7.1R (Matheny *et al.* 2007) for *Craterellus* and *Hydnum*; Tef1R/Tef1RF (Morehouse *et al.* 2003) for *TEF1* of *Cantharellus* and *Craterellus*, and HEF1F/HEF1R for *Hydnum* (Feng *et al.* 2016).

PCR reactions were performed in 30 µL reaction mixtures containing 15 µL of 2 × Phire® Plant PCR buffer, 0.6 µL Phire® Hot Start II DNA Polymerase, 1.5 µL of each PCR primer (10 µM), 10.5 µL double deionised H_2O (ddH_2O), and 0.9 µL template DNA. PCR amplification was confirmed on 1 % agarose

Table 1. Specimens and sequences used in this study.

Species	**GenBank No.**					**Specimen/culture voucher**	**Country**
	nLSU	**ITS**	**mtSSU**	***RPB2***	***TEF1***		
Cantharellales							
Hydnaceae							
Bergerella atrofusca Diederich & Lawrey	-	MN902070	-	-	-	Berger 34240 (T)	Austria
Bryoclavula phycophila H. Masumoto & Y. Degawa	LC508118	NR169921	-	-	-	TNS F-79667 (T)	Japan
	LC544110	LC544109	-	-	-	S-287-FB3	Japan
Bulbilla applanata Diederich, Flakus & Etayo	-	KC336078	-	-	-	Flakus 16422 (T)	Bolivia
	-	KC336079	-	-	-	Flakus 16424	Bolivia
Burgella flavoparmeliae Diederich & Lawrey *(T)*	DQ915469	-	-	-	-	JL192-01 (T)	USA
B. lutea Diederich, Capdet, A.I. Romero & Etayo	KC336075	KC336076	-	-	-	Etayo 27623 (T)	Bolivia
Burgellopsis nivea Diederich & Lawrey	KC336077	-	-	-	-	ATCC MYA-4209 (T)	UK
Burgoa angulosa Diederich, Lawrey & Etayo	DQ915471	-	DQ915480	-	-	JL146-00 (T)	Spain
B. verzuoliana Goid. *(T)*	NG058614	NR145334	-	-	-	CBS 131.38 (T)	Japan
Cantharellus addaiensis Henn.	KF294667	-	KF294592	KF294745	JX192992	BB 98.033 (neotype)	Tanzania
	KF294621	-	KF294550	KF294695	JX192976	BB 98.057	Tanzania
Ca. afrocibarius Buyck & V. Hofstetter	KF294668	-	KF294593	KF294746	JX192993	BB 96.235 (T)	Zambia
	KF294669	-	KF294594	KF294747	JX192994	BB 96.236	Zambia
Ca. albidolutescens Buyck, Eyssart. & V. Hofst.	KF294646	KF981365	KF294577	KF294723	JX192982	BB 08.070 (T)	Madagascar
	KF294645	-	KF294576	KF294722	KF294752	BB 08.057	Madagascar
Ca. alborufescens (Malençon) Papetti & S. Alberti	KR677531	KR677493	-	KX828735	KX828816	AH44223	Spain
	KX929161	KX907209	-	KX907232	KX907243	BB 12.075	Switzerland
Ca. albovenosus Buyck, Antonín & Ryoo	-	-	-	-	MW124387	PC0142470	Korea
	-	-	-	-	KY271942	1690/V.Antonin 13.152 (T)	Korea
Ca. albus S.P. Jian & B. Feng	MT782540	-	-	MT776012	MT776015	KUN-HKAS:107045 (T)	China
	MT782542	-	-	MT776014	MT776017	KUN-HKAS:107047	China
Ca. altipes Buyck & V. Hofst.	KF294636	-	KF294567	KF294713	GQ914945	BB 07.162	USA
	KF294627	-	KF294556	KF294702	GQ914939	BB 07.019 (T)	USA

(*continued on next page*)

Table 1. (Continued).

Species	**GenBank No.**					**Specimen/culture voucher**	**Country**
	nLSU	**ITS**	**mtSSU**	***RPB2***	***TEF1***		
Ca. ambohitantelyensis Buyck & V. Hofst.	KF294656	KF981366	KF294582	KF294733	JX192989	BB 08.336 (T)	Madagascar
Ca. amethysteus (Quel.) Sacc.	KF294639	JN944020	KF294570	KF294716	GQ914953	BB 07.284	Slovakia
	KR677550	KR677512	-	KX828738	KX828819	AH44796 (neotype)	Spain
Ca. anzutake W. Ogawa, N. Endo, M. Fukuda and A. Yamada	LC085415	LC085359	-	-	LC179800	TNS-F-61925 (T)	Japan
Ca. appalachiensis R.H. Petersen	KF294635	-	KF294565	KF294711	GQ914979	BB 07.123	USA
	DQ898690	-	DQ898646	DQ898748	-	GRSM77088	USA
Ca. brunneopallidus Buyck, Randrianj. & V. Hofst.	MK422941	-	MT002300	MT004809	MK422926	BB 11.105 (T)	Madagascar
	MK422940	-	MT002301	MT004810	MK422925	BB 11.116	Madagascar
Ca. californicus D. Arora & J.S. Dunham	KX828795	KX828768	-	KX828739	KX828820	OSC 122878 (T)	USA
Ca. cascadensis J.S. Dunham, O'Dell & R. Molina	AY041160	AY041181	DQ898676	-	-	OSC 75908	USA
Ca. chicagoensis Leacock, J. Riddell, Rui Zhang & G.M. Muell.	KP639218	KP639201	-	-	KP639230	PRL8916	USA
	KP639214	KP639200	-	-	KP639233	PRL8332	USA
Ca. cerinoalbus Eyssart. & Walleyn	KF294663	-	KF294590	KF294741	-	AV 06.051 (T)	Malaysia
Ca. cibarius Fr.	KF294658	KX907204	KF294585	KF294736	GQ914949	GE 07.025	France
	KR677539	KR677501	-	KX828742	KX828823	BIO-Fungi 10986 (T)	Sweden
Ca. cinnabarinus (Schwein.) Schwein.	KF294630	-	KF294559	KF294705	GQ914984	BB 07.053	USA
	KF294624	-	KF294552	KF294698	GQ914985	BB 07.001 (T)	USA
Ca. citrinus Buyck, R. Ryoo & Antonín	-	-	-	-	MW124385	BRNM825748 (T)	Korea
	-	-	-	-	MW124388	PC0142472	Korea
Ca. congolensis Beeli	KF294609	-	KF294542	-	JX193015	BB 98.039	Tanzania
	KF294673	-	KF294599	-	JX192996	BB 98.058	Tanzania
Ca. conspicuus Eyssart., Buyck & Verbeken	-	-	KF294598	KF294751	-	GE 99.560 (T)	Zimbabwe
Ca. curvatus Buyck, R. Ryoo & Antonín	-	-	-	-	MW124390	BRNM825749 (T)	Korea
Ca. cyphelloides Suhara & S. Kurogi	NG059027	NR154853	-	-	-	TNS:F-61721 (T)	Japan
Ca. decolorans Eyssart. & Buyck	KF294654	NR154788	-	KF294731	GQ914968	469/BB 08.278	Madagascar
Ca. densifolius Heinem.	KF294616	-	-	KF294690	JX193014	BB 98.013	Tanzania
Ca. ferruginascens P.D. Orton	KR677524	KR677486	-	KX828750	KX828829	BIO-Fungi 11700	Spain
	KF294638	-	KF294569	KF294715	GQ914952	BB 07.283	Slovakia

Table 1. (Continued).

Species	**GenBank No.**					**Specimen/culture voucher**	**Country**
	nLSU	**ITS**	**mtSSU**	***RPB2***	***TEF1***		
Ca. flavolateritius Buyck & V. Hofst.	KX896783	MG450675	-	-	KX857027	VH 1076	USA
	-	-	-	-	KX857029	VH 1078 (T)	USA
Ca. gracilis Buyck & V. Hofst.	KF294612	-	-	KF294686	JX192970	BB 98.234 (T)	Tanzania
Ca. guyanensis Mont.	KX857095	-	KX857121	KX856999	KX857061	1517/MR	Guyana
	KX857094	-	KX857120	KX856998	KX857060	1501/MRG07	Guyana
Ca. hainanensis N.K. Zeng, Zhi Q. Liang & S. Jiang	KY407524	-	-	-	KY407536	FHMU 1931 (T)	China
Ca. humidicolus Buyck & V. Hofst.	KF294666	-	-	KF294744	JX193005	BB 98.036 (T)	Tanzania
Ca. hygrophorus Shao, Buyck & Yu	KJ004002	-	-	-	KJ004003	HKAS80614 (T)	China
Ca. ibityensis Buyck, Randrianj. & V. Hofst.	KF294651	-	-	KF294728	JX192985	BB 08.203	Madagascar
	KF294650	KF981368	-	KF294727	GQ914980	BB 08.196 (T)	Madagascar
Ca. lateritius (Berk.) Singer	KF294628	-	KF294557	KF294703	GQ914957	BB 07.025 (T)	USA
	KF294633	-	KF294562	KF294708	GQ914959	BB 07.058	USA
Ca. laevihymeninus	**MW979520**	**MW980543**	**MW980526**	**MW999453**	**MW999418**	**Yuan 13900**	**China**
	MW979521	**MW980544**	**MW980527**	**MW999454**	**MW999419**	**Yuan 13902**	**China**
Ca. lewisii Buyck & V. Hofst.	JN940597	JN944021	KF294554	KF294700	GQ914962	BB 07.003 (T)	USA
	KF294623	-	KF294551	KF294697	GQ914961	BB 02.197	USA
Ca. magnus	**MW979516**	**-**	**MW980524**	**MW999451**	**MW999421**	**Wei 10319**	**China**
	MW979517	**-**	**MW980525**	**MW999452**	**MW999420**	**Wei 10244**	**China**
Ca. minor Peck	KF294632	-	KF294561	KF294707	JX192979	BB 07.057	USA
	KF294625	-	KF294553	KF294699	JX192978	BB 07.002	USA
Ca. miomboensis Buyck & V. Hofst.	KF294613	-	KF294544	KF294687	JX192971	BB 98.021 (T)	Tanzania
Ca. nigrescens Buyck, Randrianj. & V. Hofst.	KF294608	-	KF294541	KF294683	GQ914982	BB 06.197 (T)	Madagascar
Ca. pallens Pilát	KX907215	KX929162	-	KX929160	KX857014	BB 09.409	Italy
Ca. parvisporus (Eyssart. & Buyck) Buyck & V. Hofst.	KF294614	-	-	KF294688	JX192972	BB 98.020	Tanzania
Ca. parvisporus Eyssart. & Buyck	KF294611	-	-	KF294685	GQ914966	BB 98.037	Tanzania
Ca. phloginus S.C. Shao & P.G. Liu	KF801100	-	-	-	KF801095	SSC98 (T)	China
	KF801101	-	-	-	KF801096	SSC99	China

(*continued on next page*)

Table 1. (Continued).

Species	**GenBank No.**					**Specimen/culture voucher**	**Country**
	nLSU	**ITS**	**mtSSU**	***RPB2***	***TEF1***		
Ca. phloginus	**MW979518**	-	-	-	**MW999424**	**Yuan 14468**	**China**
	MW979519	-	-	-	**MW999425**	**Yuan 14490**	**China**
Ca. platyphyllus Heinem.	KF294620	-	KF294549	KF294694	JX192975	BB 98.126 (T)	Tanzania
	KF294617	-	KF294546	KF294691	GQ914969	BB 98.012	Tanzania
Ca. platyphyllus subsp. *Bojeriensis* Eyssart. & Buyck	KF294648	-	KF294579	KF294725	JX192984	BB 08.160	Madagascar
Ca. romagnesianus Eyssart. & Buyck	KX828806	KX828783	-	-	-	PC0085043 (T)	France
	KX828807	KX828784	-	KX828757	KX828836	AH44218	Spain
Ca. roseocanus (Redhead, Norvell & Danell) Redhead, Norvell & Moncalvo	KX828810	KX828787	-	KX828758	KX828837	DAOM220723	Canada
Ca. sebosus Buyck, Randrianj. & V. Hofst.	KF294652	NR154789	KF294581	KF294729	JX192986	BB 08.234 (T)	Madagascar
	KF294649	KF981371	KF294580	KF294726	GQ914981	BB 08.162	Madagascar
Ca. splendens Buyck	KF294671	-	KF294596	KF294749	-	BB 96.199	Zambia
	KF294670	-	KF294595	KF294748	-	BB 96.306	Zambia
Ca. subalbidus A.H. Sm. & Morse	AY041149	AY041179	DQ898680	-	-	OSC 75937	USA
	KX828814	KX828791	-	KX828762	KX828841	OSC 81782	USA
Ca. subamethysteus Eyssart. & D. Stubbe	KF294664	-	KF294591	KF294742	-	DS 06.218 (T)	Malaysia
Ca. subincarnatus Eyssart. & Buyck	KF294601	-	KF294536	KF294675	JX192962	BB 06.080 (T)	Madagascar
	KF294602	KF981372	KF294537	KF294676	JX192963	BB 06.096	Madagascar
Ca. subminor	**MW979522**	**MW980545**	**MW980528**	**MW999455**	**MW999415**	**Yuan 13917**	**China**
	MW979523	**MW980546**	**MW980529**	**MW999456**	**MW999416**	**Yuan 13925**	**China**
	MW979524	**MW980547**	**MW980530**	**MW999457**	**MW999417**	**Yuan 13926**	**China**
Ca. subpruinosus Eyssart. & Buyck	KF294660	-	KF294587	KF294739	-	GE07.080	France
Ca. symoensii Heinem.	KF294619	-	KF294548	KF294693	JX192974	BB 98.113 (epitype)	Tanzania
	KF294618	-	KF294547	KF294692	GQ914970	BB 98.011	Tanzania
Ca. tabernensis Feib. & Cibula	JN940608	JN944012	-	JN993600	GQ914975	BB 07.064	USA
	JN940609	JN944013	-	JN993599	GQ914977	BB 07.040	USA
Ca. tanzanicus Buyck & V. Hofst.	KF294622	-	-	KF294696	JX192977	BB 98.040 (T)	Tanzania
Ca. tenuithrix Buyck & V. Hofstetter	JN940600	JN944017	KF294566	KF294712	GU914947	BB 07.125 (T)	USA
	KF294629	-	KF294558	KF294704	GU914976	BB 07.035 (T)	USA

Table 1. (Continued).

Species	GenBank No.					Specimen/culture voucher	Country
	nLSU	ITS	mtSSU	*RPB2*	*TEF1*		
Ca. texensis Buyck & V. Hofst	JN940601	-	KF294564	KF294710	GQ914987	BB 07.120	USA
	KF294626	-	KF294555	KF294701	GQ914988	BB 07.018 (T)	USA
Ca. tomentosoides Buyck & V. Hofst.	MK422937	-	MT002295	MT004804	MG450685	BB16.007 (T)	Central African Republic
Ca. tomentosus Eyssart. & Buyck	KF294672	-	KF294597	KF294750	JX192995	BB 98.060 (T)	Tanzania
	KF294610	-	KF294543	KF294684	GQ914965	BB 98.038	Tanzania
Ca. tuberculosporus M. Zang	KU720305	-	-	-	KM893837	SSC 6	China
	KU720306	-	-	-	KM893835	SSC 2	China
Ca. vaginatus S.C. Shao, X.F. Tian & P.G. Liu	HM594681	HQ416692	-	-	-	HKAS55730 (T)	China
Ca. versicolor S.C. Shao & P.G. Liu	-	-	-	-	KM893857	HKAS55762 (T)	China
	MW979525	-	**MW980531**	**MW999458**	**MW999427**	**Yuan 13640**	**China**
	MW979526	-	**MW980532**	**MW999459**	**MW999426**	**Yuan 13681**	**China**
Ca. yunnanensis W.F. Chiu	KU720333	-	-	-	KU720337	XieXD174	China
	MW979527	-	-	-	**MW999428**	**Yuan 13983**	**China**
	MW979528	-	-	-	**MW999429**	**Yuan 13985**	**China**
***Ca. yunnanensis* “as *Cantharellus anzutake*”**	**MW979514**	**MW980541**	-	-	**MW999422**	**Yuan 14539**	**China**
	MW979515	**MW980542**	-	-	**MW999423**	**Yuan 14636**	**China**
Clavulina cerebriformis Uehling, Aime & T.W. Henkel	JN228222	NR121504	-	JN228233	-	MCA4022 (T)	Guyana
Clavulina cf. cristata	JN228225	JN228225	-	JN228240	-	MES426	China
Cl. cinereoglebosa Uehling, Aime & T.W. Henkel	JN228232	JN228218	-	JN228246	-	TH8561 (T)	Guyana
Cl. cristata (Holmsk.) J. Schröt.	JN228227	JN228227	-	JN228241	-	JKU8	USA
Clavulina sp.	AY745694	DQ202266	-	DQ366286	DQ028589	MB03-034	USA
Craterellus albidus Fr.	MT921161	-	-	-	-	HGASMF01-3581 (T)	China
	MT921162	-	-	-	-	HGASMF01-10046	China
Cr. albostrigosus C.K. Pradeep & K.B. Vrinda	MG593194	-	-	-	-	TBGT16577 (T)	India
Cr. atratoides T.W. Henkel, Aime & A.W. Wilson	JQ915129	JQ915103	-	-	-	TH8473	Guyana
	NG042660	JQ915111	-	-	-	TH9232 (T)	Guyana

(*continued on next page*)

Table 1. (Continued).

Species	GenBank No.					Specimen/culture voucher	Country
	nLSU	ITS	mtSSU	*RPB2*	*TEF1*		
Cr. atratus (Corner) Yomyart, Watling, Phosri, Piap. & Sihan.	JQ915118	JQ915092	-	-	-	MCA1070	Guyana
	JQ915126	JQ915100	-	-	-	MCA990	Guyana
Cr. atrobrunneolus T. Cao & H.S. Yuan	MN894058	MN902353	-	-	-	Yuan 13878	China
Cr. badiogriseus	**MW979532**	**MW980548**	-	-	**MW999432**	**Yuan 14776**	**China**
	MW979533	**MW980549**	-	-	**MW999433**	**Yuan 14779**	**China**
Cr. caeruleofuscus A.H. Sm.	-	GU590930	-	-	-	ADW00122	USA
	-	MH558300	-	-	-	MH17001	USA
Cr. carolinensis R.H. Petersen	-	KY654712	-	-	-	FLAS-F-59997	USA
Cr. cinereofimbriatus T.W. Henkel & A.W. Wilson	JQ915130	JQ915104	-	-	-	TH8999	Guyana
	JQ915131	JQ915105	-	-	-	TH9075 (T)	Guyana
Cr. cinereus (Pers.) Pers.	JF412278	-	-	-	-	isolate 107-08 (T)	India
Cr. cornucopioides (L.) Pers.	-	UDB000053	-	-	-	KF01-46	Denmark
	-	KT693262	-	-	-	groc_11399	USA
Cr. croceialbus	**MW979529**	**MW980572**	-	**MW999460**	**MW999430**	**Yuan 14623**	**China**
	MW979530	**MW980573**	-	**MW999461**	**MW999431**	**Yuan 14647**	**China**
Cr. excelsus T.W. Henkel & Aime	JQ915127	JQ915101	-	-	-	TH7515	Guyana
	JQ915128	JQ915102	-	-	-	TH8235 (T)	Guyana
Cr. fallax A.H. Sm.	AY700188	DQ205680	-	-	-	AFTOL-ID 286	USA
	-	GU590924	-	-	-	MGW652	USA
Cr. hesleri R.H. Petersen	-	GU590931	-	-	-	RHP55560	USA
Cr. ignicolor (R.H. Petersen) Dahlman, Danell & Spatafora	AF105314	-	-	-	-	UPSF 11794	USA
Cr. indicus D. Kumari, Ram. Upadhyay & Mod.S. Reddy	NG060387	NR119831	-	-	-	PUN 3884 (T)	India
	-	HQ450769	-	-	-	MSR6	India
Cr. inusitatus C.K. Pradeep & K.B. Vrinda	MG593195	-	-	-	-	taxon:2056430	India
Cr. luteus T.H. Li & X.R. Zhong	MG701171	MG727896	-	-	-	GDGM48105 (T)	China
	MG727898	MG727897	-	-	-	GDGM46432	China
Cr. lutescens (Fr.) Fr.	-	AY082606	-	-	-	taxon:104198	Ireland
	-	GU373513	-	-	-	H 6005875	Finland

Table 1. (Continued).

Species	GenBank No.					Specimen/culture voucher	Country
	nLSU	ITS	mtSSU	*RPB2*	*TEF1*		
Cr. macrosporus	**MW979531**	**MW980574**	-	-	-	**Yuan 14782**	**China**
Cr. melanoxeros (Desm.) Pérez-De-Greg.	JQ976983	-	-	-	-	SS576	Sweden
Cr. odoratus (Schwein.) Fr.	AF105306	-	-	-	-	UPSF 11794	USA
Cr. olivaceoluteus T.W. Henkel, Aime & A.W. Wilson	JQ915124	JQ915098	-	-	-	MCA3186	Guyana
	JQ915135	JQ915109	-	-	-	TH9205 (T)	Guyana
Cr. parvogriseus U. Singh, K. Das & Buyck	MF421098	MF421099	-	-	-	CAL 1533 (T)	India
Cr. pleurotoides (T.W. Henkel, Aime & S.L. Mill.) A.W. Wilson	JQ915123	JQ915097	-	-	-	MCA3124	Guyana
	JQ915136	JQ915110	-	-	-	TH9220	Guyana
Cr. shoreae Hembrom, K. Das, A. Parihar & Buyck	KY290585	-	-	-	-	CAL 1396 (T)	India
Cr. squamatus	**MW979534**	**MW980571**	-	**MW999462**	**MW999434**	**Yuan 14520**	**China**
	MW979535	**MW980570**	-	**MW999463**	**MW999435**	**Yuan 14721**	**China**
Cr. strigosus T.W. Henkel, Aime & A.W. Wilson	JQ915120	JQ915094	-	-	-	MCA1750	Guyana
	JQ915134	JQ915108	-	-	-	TH9204 (T)	Guyana
Cr. tubaeformis (Fr.) Quél.	DQ898741	-	DQ898651	DQ898749	-	TM 0268	Canada
	KF294640	-	KF294571	KF294717	GQ914989	BB 07.293	Slovakia
Hydnum albertense Niskanen & Liimat.	-	KX388664	-	-	-	H T. Niskanen 11-354 (T)	Canada
Hy. albomagnum Banker	AY700199	DQ218305	-	DQ234553	DQ234568	AFTOL-ID 471	USA
	-	MH379943	-	-	-	RAS231 (epitype)	USA
	MW979536	**MW980550**	-	-	-	**Wei 10194**	**China**
	MW979537	**MW980551**	-	-	-	**Wei 10247**	**China**
Hy. berkeleyanum K. Das, Hembrom, A. Baghela & Vizzini	NG070500	NR158533	-	-	-	CAL 1656 (T)	India
	KU612667	KU612525	-	-	-	HKAS77834	China
	MW979538	**MW980552**	**-**	**-**	**-**	**Wei 10375**	**China**
Hy. boreorepandum Niskanen, Liimat. & Niemelä	-	KX388658	-	-	-	HTN 1679	Finland
	-	KX388657	-	-	-	H 6003711 (T)	Finland

(*continued on next page*)

Table 1. (Continued).

Species	**GenBank No.**					**Specimen/culture voucher**	**Country**
	nLSU	**ITS**	**mtSSU**	***RPB2***	***TEF1***		
Hy. brevispinum	**MW979559**	**MW980578**	-	-	-	**Wei 10214**	**China**
	MW979560	**MW980579**	-	-	-	**Wei 10258**	**China**
Hy. canadense Niskanen & Liimat.	-	KX388681	-	-	-	HTN 09-006 (T)	Canada
Hy. cremeoalbum Liimat. & Niskanen	-	AB906674	-	-	-	TUMH 40462	Japan
	-	AB906678	-	-	-	TUMH 60740 (T)	Japan
	KU612676	KU612619	-	-	-	HKAS92345	China
Hy. cuspidatum Swenie & Matheny	-	MH379944	-	-	-	RAS 246 (T)	USA
	-	MH379936	-	-	-	RAS 205	USA
Hy. ellipsosporum Ostrow & Beenken	-	AY817138	-	-	-	Os5579 (T)	Germany
	-	KX388671	-	-	-	HTN 12-036	Finland
	KX086217	KX086215	-	-	-	FD3281	Switzerland
Hy. ferruginescens Swenie & Matheny	-	MH379905	-	-	-	MH16005 (T)	USA
	-	MH379942	-	-	-	RAS229	USA
Hy. flabellatum	**MW979556**	**MW980575**	-	-	-	**Yuan 14708**	**China**
Hy. flavidocanum	**MW979545**	**MW980559**	**MW980535**	**MW999466**	**MW999440**	**Yuan 13903a**	**China**
	MW979546	**MW980560**	**MW980536**	**MW999467**	**MW999441**	**Yuan 13900a**	**China**
Hy. ibericum Olariaga, Liimat. & Niskanen	-	HE611086	-	-	-	BIO:Fungi:12330 (T)	Spain
	-	AJ547879	-	-	-	MA-fungi 3457	Spain
Hy. jussii Niskanen, Liimat. & Kytöv	-	KX388665	-	-	-	H 6003709 (T)	Finland
	MW979539	**MW980553**	-	-	**MW999436**	**Yuan 14008**	**China**
	MW979540	**MW980554**	-	-	**MW999437**	**Yuan 14009**	**China**
Hy. longibasidium	**MW979541**	**MW980556**	**MW980533**	**MW999464**	**MW999438**	**Wei 10383**	**China**
	MW979542	**MW980555**	**MW980534**	**MW999465**	**MW999439**	**Wei 10367**	**China**
Hy. magnorufescens Vizzini, Picillo & Contu	KU612669	KU612549	-	-	-	voucher 161209	Slovenia
	-	KC293545	-	-	-	TO HG2818 (T)	Italy
Hy. melitosarx Ruots., Huhtinen, Olariaga, Niskanen, Liimat. & Ammirati	-	KX388683	-	-	-	H 7043937 (T)	USA
	-	KX388685	-	-	-	K 176869	UK
Hy. melleopallidum Kranab., Liimat. & Niskanen	-	FJ845406	-	-	-	SMI356 (T)	Canada

Table 1. (Continued).

Species	GenBank No.					Specimen/culture voucher	Country
	nLSU	ITS	mtSSU	*RPB2*	*TEF1*		
Hy. minum Yanaga & N. Maek.	-	AB906675	-	-	-	TUMH60737 (T)	Japan
	KY407528	KY407533	-	-	-	N.K.Zeng2819	China
	MW979543	**MW980557**	-	-	-	**Wei 10252**	**China**
	MW979544	**MW980558**	-	-	-	**Wei 10260**	**China**
Hy. mulsicolor Liimat. & Niskanen	-	AJ547885	-	-	-	LJU GIS 1336 (T)	Slovenia
	-	JX093560	-	-	-	REB 341	USA
Hy. neorepandum Niskanen & Liimat.	-	KX388659	-	-	-	HTN10-095 (T)	Canada
	-	KX388660	-	-	-	HTN 10-086	Canada
Hy. olympicum Niskanen, Liimat. & Ammirati	-	KX388661	-	-	-	09-134 (T)	USA
	-	MT955159	-	-	-	SAT-10-208-05	USA
Hy. oregonense Norvell, Liimat. & Niskanen	-	KF879509	-	-	-	HVM61	USA
	-	AJ534972	-	-	-	PNW-MS g2010502h1-09 (T)	USA
Hy. ovoideisporum Olariaga, Grebenc, Salcedo & M.P. Martín	-	KU612536	-	-	-	voucher 71106	Slovenia
	-	NR119818	-	-	-	BIO Fungi 12683 (T)	Spain
Hy. pallidocroceum	**MW979554**	**MW980568**	-	-	**MW999449**	**Yuan 14023**	**China**
	MW979555	**MW980569**	-	-	**MW999450**	**Yuan 14017**	**China**
Hy. pallidomarginatum	**MW979552**	**MW980566**	**MW980539**	**MW999473**	**MW999447**	**Yuan 13928a**	**China**
	MW979553	**MW980567**	**MW980540**	**MW999474**	**MW999448**	**Yuan 13940a**	**China**
Hy. quebecense Niskanen & Liimat.	-	KX388662	-	-	-	HTN 10-064 (T)	Canada
	-	MH379881	-	-	-	CN9	USA
Hy. repandum L.	-	NR164553	-	-	-	H6003710 (T)	Finland
Hy. repando-orientale Liimat. & Niskanen	-	AB906683	-	-	-	TUMH60745 (HT)	Japan
	-	AB906684	-	-	-	TUMH60743	Japan
Hy. rufescens Pers.	-	KX388688	-	-	-	H 6003708 (epitype)	Finland
	-	KX388656	-	-	-	HTN 7839	Estonia
Hy. slovenicum Liimat. & Niskanen	-	AJ547870	-	-	-	LJU GIS 1338 (T)	Slovenia
	-	AJ547884	-	-	-	LJU GIS 1340	Slovenia

(*continued on next page*)

Table 1. (Continued).

Species	GenBank No.					Specimen/culture voucher	Country
	nLSU	ITS	mtSSU	*RPB2*	*TEF1*		
Hydnum sp.	KU612668	KU612607	-	-	-	HKAS82411	Taiwan-Island
	KU612644	KU612597	-	-	-	HKAS61337	China
	-	KC679834	-	-	-	wi8T4spel	Taiwan-Island
	-	KC679833	-	-	-	wi1A4spel	Taiwan-Island
Hydnum sp.2	KU612661	KU612543	-	-	-	HKAS92340	China
Hydnum sp.3	KU612665	KU612531	-	-	KU612776	HKAS61795	Canada
Hydnum sp.6	-	KU612547	-	-	KU612773	HKAS45769	China
Hydnum sp.7	-	KU612584	-	-	-	HKAS51070	China
Hydnum sp.8	KU612654	KU612596	-	-	-	HKAS55410	China
Hydnum sp.10	KU612681	KU612567	-	-	-	HKAS93261	China
Hydnum sp.13	KU612673	KU612617	-	-	-	HKAS57714	China
	KU612675	KU612616	-	-	-	HKAS58838	China
Hydnum sp.15	-	KU612613	-	-	-	HKAS55325	China
	-	KU612614	-	-	-	HKAS92336	China
Hydnum sp.16	-	KU612609	-	-	-	HKAS52807	China
	KU612672	KU612610	-	-	-	HKAS92350	China
Hy. sphaericum	**MW979549**	**MW980563**	-	**MW999470**	**MW999444**	**Wei 10243**	**China**
	MW979550	**MW980564**	-	**MW999471**	**MW999445**	**Wei 10300**	**China**
	MW979551	**MW980565**	-	**MW999472**	**MW999446**	**Wei 10262**	**China**
Hy. subconnatum Swenie & Matheny	-	MH379930	-	-	-	RAS235 (T)	USA
	-	MH379916	-	-	-	RAS169	USA
Hy. subcremeoalbum Tedersoo, Liimat. & Niskanen	-	UDB013289	-	-	-	TU110688 (T)	Papua New Guinea
Hy. submulsicolor Niskanen & Liimat.	-	KX388682	-	-	-	HTN 10-132 (T)	Canada
Hy. subolympicum Liimat. & Niskanen	KU612653	KU612599	-	-	-	F1188765	USA
	-	MH174257	-	-	-	DAOM744368 (T)	Canada
Hy. subovoideisporum Niskanen & Liimat.	-	NR158494	-	-	-	H 6003707 (T)	Finland
Hy. subrufescens Niskanen & Liimat.	-	KX388649	-	-	-	HTN 10-154 (T)	Canada
	KU612663	KU612535	-	-	-	F1188749	USA

Table 1. (Continued).

Species	GenBank No.					Specimen/culture voucher	Country
	nLSU	ITS	mtSSU	*RPB2*	*TEF1*		
Hy. subtilior Swenie & Matheny	-	MH379918	-	-	-	RAS180	USA
	-	NR164029	-	-	-	TENN073034 (T)	USA
Hy. tangerinum	**MW979561**	**MW980580**	-	-	-	**Wei 10245**	**China**
	MW979562	**MW980581**	-	-	-	**Wei 10249**	**China**
	MW979563	**MW980582**	-	-	-	**Wei 10250**	**China**
Hy. tenuistipitum	**MW979557**	**MW980576**	-	-	-	**Wei 10410**	**China**
	MW979558	**MW980577**	-	-	-	**Wei 10417**	**China**
Hy. treui Tedersoo, Liimat. & Niskanen	-	UDB013043	-	-	-	TU110403 (T)	Papua New Guinea
Hy. umbilicatum Peck	-	MH379883	-	-	-	10640TJB (epitype)	USA
Hy. vagabundum Swenie, Ovrebo & Matheny	-	MH379909	-	-	-	CLO4985 (T)	USA
	-	MH379949	-	-	-	10782TJB	USA
Hy. ventricosum	**MW979547**	**MW980561**	**MW980537**	**MW999468**	**MW999442**	**Yuan 14536**	**China**
	MW979548	**MW980562**	**MW980538**	**MW999469**	**MW999443**	**Yuan 14601**	**China**
Hy. vesterholtii Olariaga, Grebenc, Salcedo & M.P. Martín	-	HE611084	-	-	-	BIO Fungi 12904 (T)	Spain
	-	HE611085	-	-	-	BIO:Fungi:10452	Spain
Hy. washingtonianum Ellis & Everh.	-	MF954990	-	-	-	UBC F-32538	Canada
	-	MH379846	-	-	-	strain 214 (isotype)	USA
Hy. zongolicense Garibay	-	KC152121	-	-	-	GO-2010-142a (T)	Mexico
Membranomyces delectabilis (H.S. Jacks.) Kotir. & Saaren.	AY586688	AY463442	-	-	-	KHL11147	Sweden
Minimedusa obcoronata (B. Sutton, Kuthub. & Muid) Diederich, Lawrey & Heylen	GQ303309	GQ303278	-	-	-	CBS 120605	Thailand
Mi. polyspora (Hotson) Weresub & P.M. LeClair	MH866167	MH854646	-	-	-	CBS 113.16 (T)	USA
	MG833798	MG833806	-	-	-	SH-Ecto-3	China
Multiclavula corynoides (Peck) R.H. Petersen	U66440	U66440	-	-	-	Lutzoni 930804-2	USA
Mu. mucida (Pers.) R.H. Petersen	EU909345	EU909345	-	-	-	TUB 011734	Germany
Mu. petricola H. Masumoto & Y. Degawa	LC516465	LC516464	-	-	-	356 ex-type (T)	Japan

(*continued on next page*)

Table 1. (Continued).

Species	GenBank No.					Specimen/culture voucher	Country
	nLSU	ITS	mtSSU	*RPB2*	*TEF1*		
Mu. vernalis (Schwein.) R.H. Petersen	U66439	U66439	-	-	-	Lutzoni 930806-1	USA
Neoburgoa freyi Diederich, E. Zimm. & Lawrey	KX423756	KX423756	-	-	-	LF1256 (T)	Switzerland
	KX423755	KX423754	-	-	-	JL596-16	Switzerland
Pseudocraterellus sinuosus (Fr.) Corner	-	GU590932	-	-	-	TENN062865	Sweden
Pseudocraterellus sp.	-	KM576333	-	-	-	LM5294	Austria
	-	MF352690	-	-	-	SK1161	UK
Rogersiomyces malaysianus (K. Matsush. & Matsush.) Zmitr.	KU820986	KT779285	-	-	-	LE-BIN 3507-10	Vietnam
	KT779286	KT779284	-	-	-	LE-BIN 3507	Vietnam
Sistotrema brinkmannii (Bres.) J. Erikss.	DQ898709	-	DQ898655	DQ898755	-	FCUG 2217	USA
S. confluens Pers.	AY647214	DQ267125	-	DQ381837	-	FCUG298	USA
	AY586712	AY463466	-	-	-	PV174	Czechia
S. eximum (H.S. Jacks.) Ryvarden & Solheim	DQ898695	-	DQ898660	DQ898762	-	FCUG 2342	USA
S. muscicola Pers.	AJ606041	AJ606041	-	-	-	taxon:154757	Finland
	AJ606040	AJ606040	-	-	-	KHL 11721	Finland
S. oblongisporum M.P. Christ. & Hauerslev	DQ898728	-	DQ898732	DQ898767	-	GEL2125	USA
S. octosporum (J. Schröt. ex Höhn. & Litsch.) Hallenb.	DQ898698	-	DQ898663	DQ898764	-	FCUG 2822	USA
S. subconfluens L.W. Zhou	JX076810	JX076812	-	-	-	Dai 12577 (T)	China
Sistotremella perpusilla Hjortstam	MH875516	MH864061	-	-	-	CBS 126048	USA
Tulasnellaceae							
Tulasnella asymmetrica Warcup & P.H.B. Talbot	DQ520101	DQ520101	-	-	-	AFTOL-ID 1678	Germany
T. irregularis Warcup & P.H.B. Talbot	NG057720	NR160166	-	-	-	CBS 574.83 (T)	Australia
T. pruinosa Bourdot & Galzin	AF518662	DQ457642	-	DQ381839	DQ061274	DAOM 17641	USA
Tulasnella sp.	DQ898731	-	DQ898736	DQ898771	-	GEL5130	Canada
T. violea (Quél.) Bourdot & Galzin	-	-	DQ898735	DQ898768	-	GEL2561	Canada
	DQ520097	DQ520097	-	DQ521418	-	AFTOL-ID 1879	Germany

Table 1. (Continued).

Species	GenBank No.					Specimen/culture voucher	Country
	nLSU	ITS	mtSSU	*RPB2*	*TEF1*		
Ceratobasidiaceae							
Ceratobasidium globisporum Warcup & P.H.B. Talbot	MH873365	DQ278942	-	DQ301723	DQ301644	CBS 569.83	Australia
Ceratobasidium sp.	AY293171	-	AY293223	-	-	GEL 5602	USA
	AF354083	AF354083	KJ380768	-	-	CAG6	USA
Ceratorhiza hydrophila (Sacc. & P. Syd.) Z.H. Xu, T.C. Harr., M.L. Gleason & Batzer	MT381951	MT381956	-	MT381954	MT381955	E14504F	Ecuador
Rhizoctonia endophytica H.K. Saksena & Vaartaja	KP171655	KP171640	-	KP171658	-	DAOM 138188	Canada
Rh. solani J.G. Kühn	MN078809	MK481078	-	-	MN078941	BRS17	India
Thanatephorus cucumeris (A.B. Frank) Donk	MH873283	DQ278946	-	DQ301727	DQ301660	CBS 700.82	Panama
	AF518655	-	AF518697	-	-	IMI-34886	USA
Uthatobasidium fusisporum (J. Schröt.) Donk	-	DQ398957	-	DQ381842	-	AFTOL-ID 611	USA
Uthatobasidium sp.	AF518664	-	AF518698	-	-	HHB-102155	USA
Botryobasidiaceae							
Botryobasidium obtusisporum J. Erikss.	DQ898729	-	DQ898733	DQ898769	-	GEL3030	Canada
Bo. simile Hol.-Jech.	DQ898730	KP171641	DQ898734	DQ898770	-	GEL2348	Canada
Bo. subcoronatum (Höhn. & Litsch.) Donk	AY647212	DQ200924	-	DQ366284	-	AFTOL-ID 614	USA
Haplotrichum conspersum (Link) Hol.-Jech.	DQ521414	DQ911612	-	-	DQ521420	AFTOL-ID 1766	USA
Oliveoniaceae							
Oliveonia sp.	MT235618	MT235650	-	-	-	TH 2018074	Finland
	MT235617	MT235649	-	-	-	TH 2018179	Finland
	MT235615	MT235647	-	-	-	VS 9048	Russia
	MT235614	MT235645	-	-	-	VS 9053	Russia
Tremellomycetes							
Holtermanniaceae							
Holtermannia corniformis Kobayasi	NG057658	NR154050	-	KF036899	KF037162	CBS 6979 (T)	Japan

(*continued on next page*)

Table 1. (Continued).

Species	GenBank No.					Specimen/culture voucher	Country
	nLSU	ITS	mtSSU	*RPB2*	*TEF1*		
Holtermanniella festucosa (Golubev & J.P. Samp.) Libkind, Wuczk., Turchetti & Boekhout	KY107040	KY102693	-	KF036779	KF037052	CBS10162 (T)	Russia
Ho. nyarrowii (Thomas-Hall & K. Watson) Libkind, Wuczk., Turchetti & Boekhout	NG058306	NR155182	-	KF036803	KF037075	CBS 8804 (T)	Antarctica
Ho. wattica (Guffogg, Thomas-Hall, P. Holloway & K. Watson) Libkind, Wuczk., Turchetti & Boekhout	NG058307	NR138371	-	KF036828	KF037099	CBS 9496 (T)	Antarctica
Trichosporon insectorum Fuent., S.O. Suh, Landell, Faganello, A. Schrank, Vainstein, M. Blackw. & P. Valente	KY109953	KF036603	-	KF036972	KF037232	CBS 10422 (T)	Panama
Tr. lactis Lopandić, Sugita, Middelhoven, Herzberg & Prillinger	NG058421	NR073334	-	KF036975	KR046413	CBS 9051 (T)	Austria
Dacrymycetales							
Dacrymyces australis Lloyd	-	DQ205684	-	DQ381845	DQ028587	FPL8953	USA

[1] Newly generated sequences in this study are in bold. The number of the *Hydnum* sp. follows Feng *et al.* (2016).

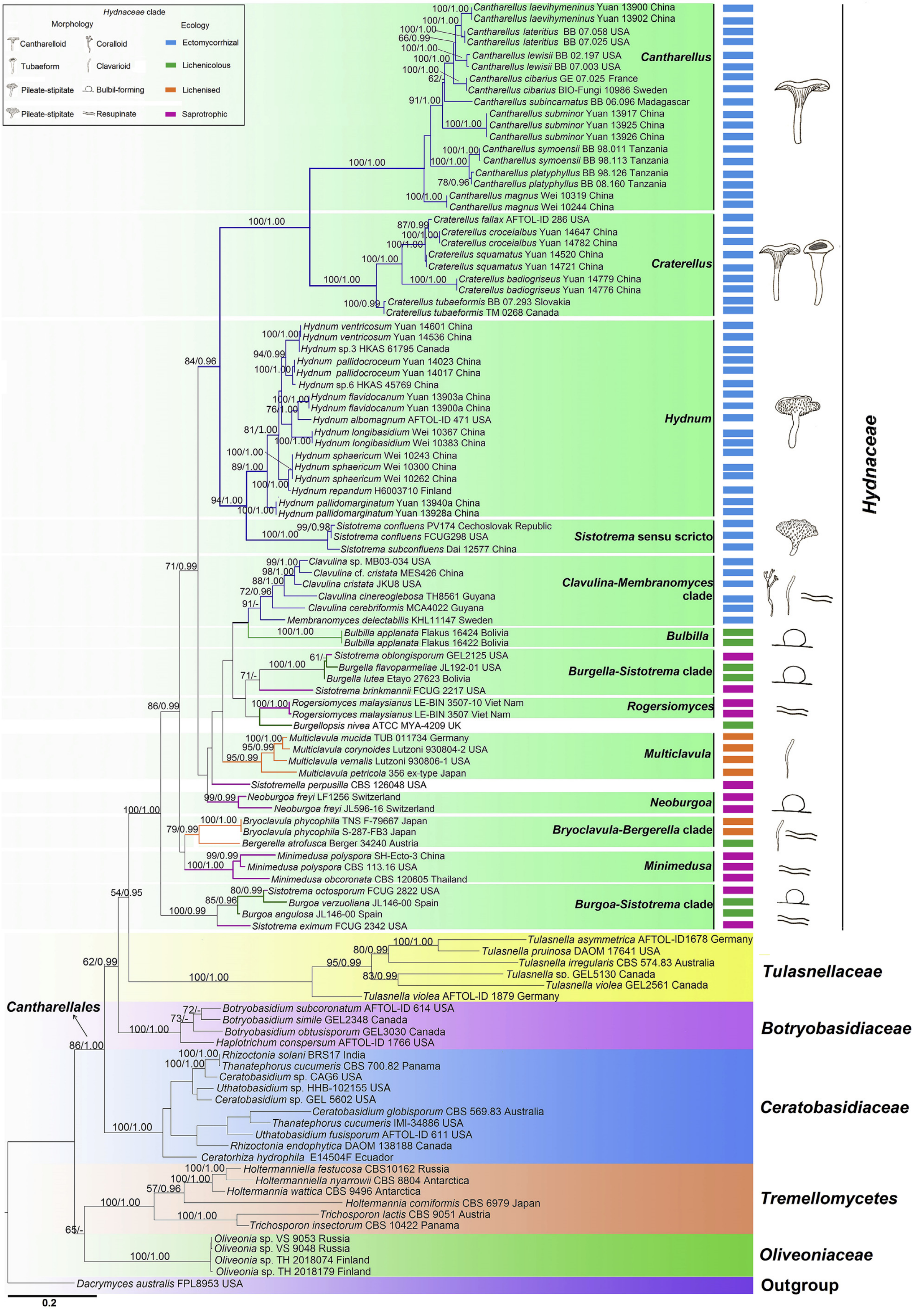

Fig. 1. Maximum Likelihood tree based on the combined nLSU + ITS + mtSSU + *RPB2* + *TEF1* sequence dataset illustrating the phylogeny of *Cantharellales*. The taxa in *Hydnaceae* have a green background; the blue branches represent the ECM taxa; the green represents the lichenicolous taxa; the orange represents the lichenised taxa and the pink represents the saprotrophic taxa; the shape of the basidiocarps is represented by line diagrams to the right of the tree. Branches are labelled with Maximum Likelihood bootstrap higher than 50 % and Bayesian Posterior Probabilities > 0.95.

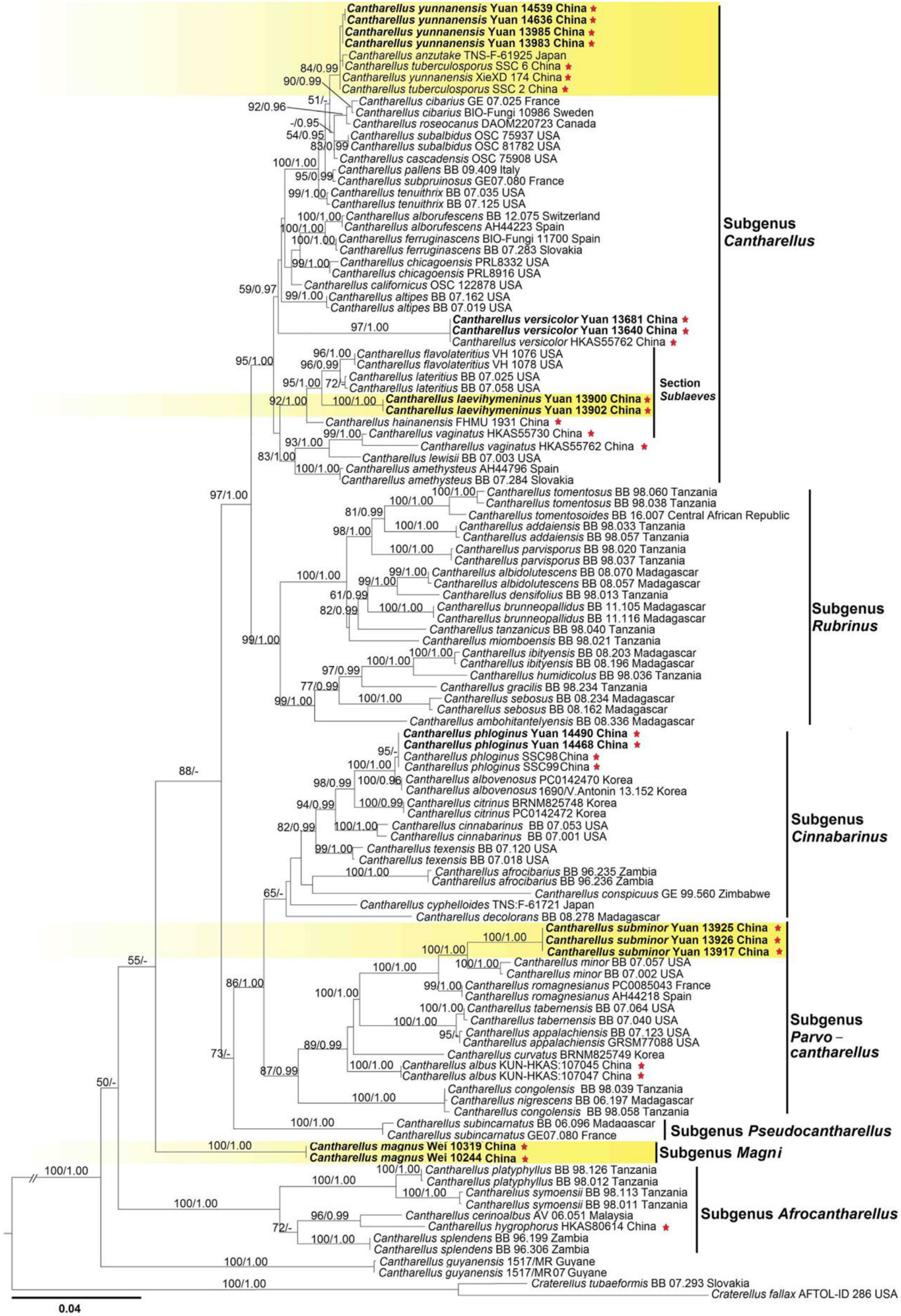

Fig. 2. Maximum Likelihood tree based on the combined 5.8S + nLSU + mtSSU + *RPB2* + *TEF1* sequence dataset illustrating the phylogeny of the genus *Cantharellus*. The new taxa have a yellow background; newly acquired samples in this study are in bold; samples from China are marked with red stars. Branches are labelled with Maximum Likelihood bootstrap higher than 50 % and Bayesian Posterior Probabilities > 0.95.

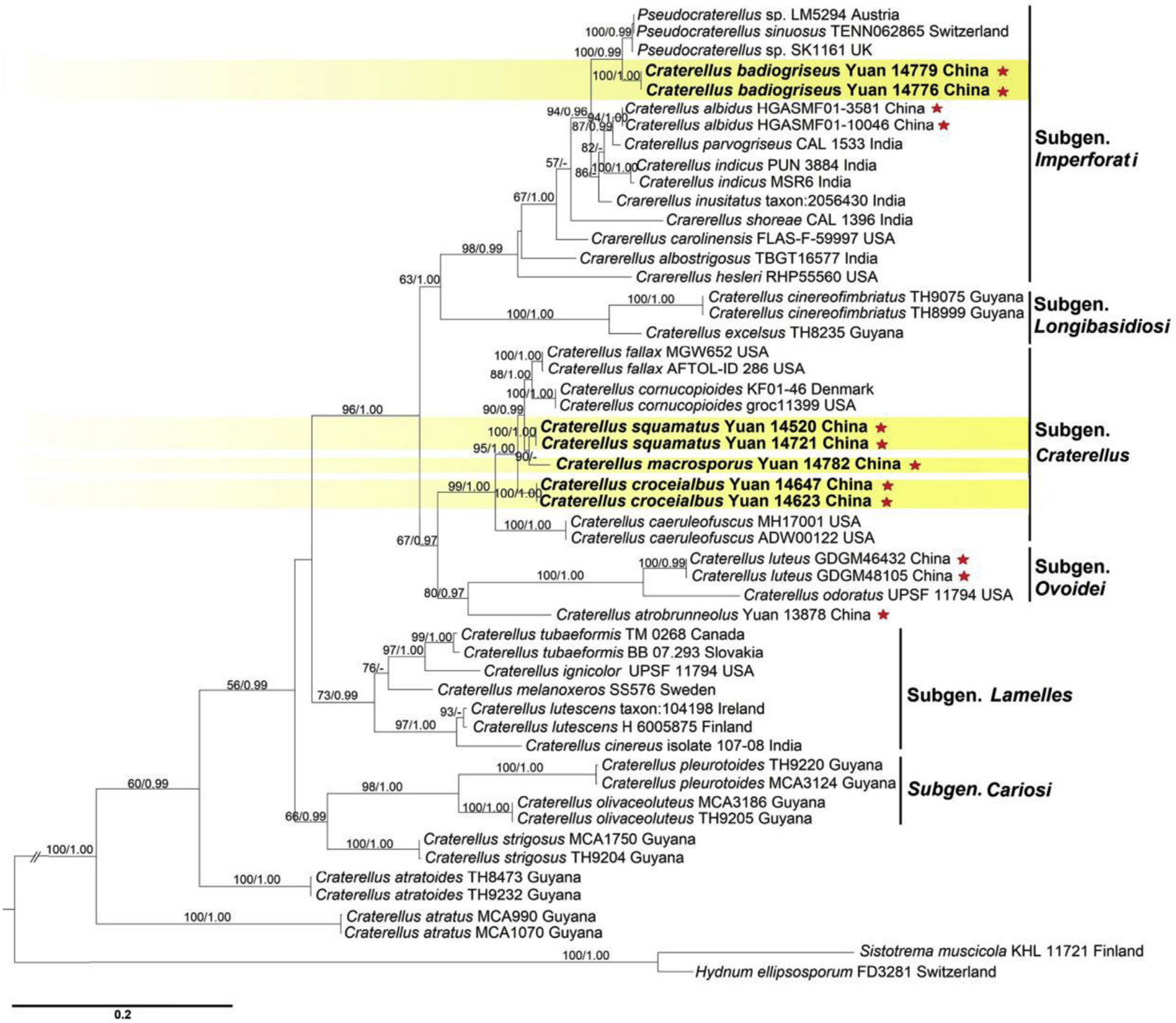

Fig. 3. Maximum Likelihood tree based on the combined nLSU + ITS sequence dataset illustrating the phylogeny of the genus *Craterellus*. The new taxa have a yellow background; newly acquired samples in this study are in bold; samples from China are marked with red stars. Branches are labelled with Maximum Likelihood bootstrap higher than 50 % and Bayesian Posterior Probabilities > 0.95.

electrophoresis gel stained with ethidium bromide (Stöger *et al.* 2006) and sequenced at the Beijing Genomics Institute (BGI) with the same primers as used in PCR. The newly generated DNA sequences were assembled and manually modified with the software DNAMAN8 (Lynnon Biosoft, Quebec, Canada). The sequence quality control followed the guidelines by Nilsson *et al.* (2012). All sequences newly obtained were submitted to GenBank (Sayers *et al.* 2020).

Phylogenetic analyses

Sequences for phylogenetic analysis were found in GenBank (http://www.ncbi.nlm.gov) using the BLAST option and downloaded (Table 1). DNA alignments were performed using the MAFFT v. 7.471 online service (https://mafft.cbrc.jp/alignment/server/index.html; Katoh *et al.* 2019). Intron regions of *RPB2* and *TEF1* as well as low-homology regions of ITS1 and ITS2 were removed before phylogenetic analyses, and the two sequence datasets were combined using BioEdit v. 7.2.6 (Hall 2005).

We assembled four datasets for phylogenetic analyses: the *Cantharellales* dataset based on a five-locus concatenated alignment which included nLSU, ITS, mtSSU, *RPB2* and *TEF1*; the *Cantharellus* dataset based on a five-locus concatenated alignment which included 5.8S, nLSU, mtSSU, *RPB2* and *TEF1*; the *Craterellus* and *Hydnum* datasets both based on a two-locus (nLSU and ITS) concatenated alignment. The four datasets were all partitioned by gene and codon position and the best-fit models were determined by jModelTest v. 2.1.10 (Darriba *et al.* 2012) based on the Corrected Akaike Information Criterion (AICc). The first dataset (*Cantharellales*) was divided into nine data partitions and the best-fit models were: GTR + I + G for nLSU, GTR + G for ITS, TrN + G for mtSSU, GTR + I + G for *RPB2* 1st, 2nd, 3rd and *TEF1* 1st, K80 + G for *TEF1* 2nd and 3rd; the second (*Cantharellus*) was divided into nine: TPM1 + G for 5.8S, TIM1 + I + G for nLSU, F81 + I for mtSSU, TrNef + I + G for *PRB2* 1st, TrN + G for *PRB2* 2nd and *PRB2* 3rd, TIM1ef + I + G for *TEF1* 1st, JC for *TEF1* 2nd and TPM2 + I + G for *TEF1* 3rd; the third (*Craterellus*) was divided into four: ITM1 + I + G for nLSU, TrN + I for ITS1, JC

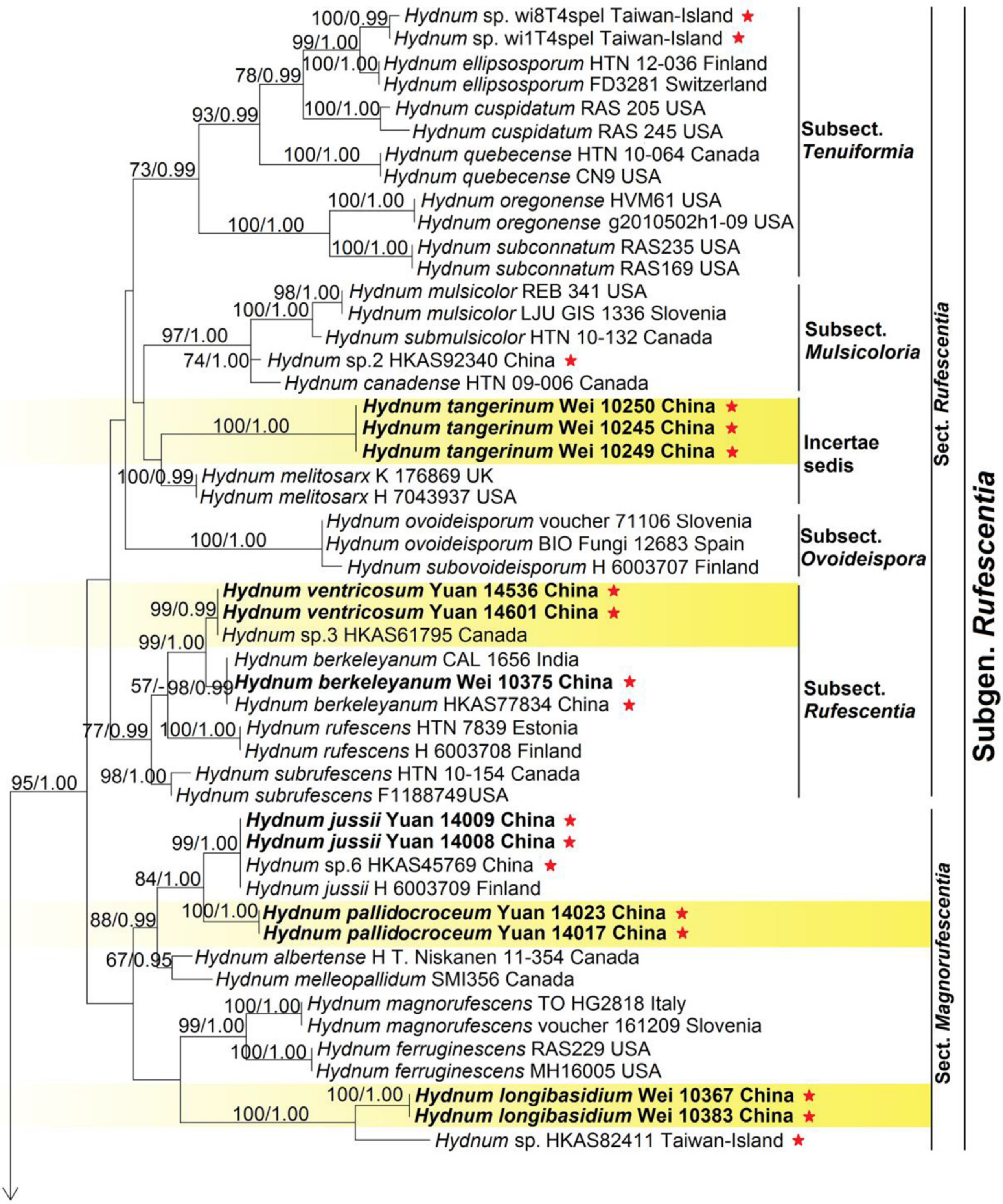

Fig. 4. Maximum Likelihood tree based on the combined nLSU + ITS sequence dataset illustrating the phylogeny of the genus *Hydnum*. The new taxa have a yellow background; newly acquired samples in this study are in bold; samples from China are marked with red stars. Branches are labelled with Maximum Likelihood bootstrap higher than 50 % and Bayesian Posterior Probabilities > 0.95.

for 5.8S and TrN + G for ITS2 and the fourth (*Hydnum*) was divided into four: GIR + I + G for nLSU, JC for ITS1, K80 for 5.8S and TrN + G for ITS2.

Phylogenetic analyses for each dataset were conducted using Bayesian Inference (BI) analysis and Maximum Likelihood (ML) methods. All characters were weighted, and gaps were treated as missing data. BI analysis with MrBayes v. 3.2.7 (Ronquist *et al.* 2012) implemented the Markov Chain Monte Carlo (MCMC) technique. Four simultaneous Markov chains were run with 15, 10, 5, 5 million generations for the four datasets respectively, starting from random trees and keeping one tree every 100th generation until the average standard deviation of split frequencies was below 0.01. The value of burn-in was set to discard 25 % of trees when calculating the posterior probabilities. Bayesian Posterior Probabilities (BPP) were obtained from the 50 % majority rule consensus of the trees kept. An ML analysis used the same datasets as the BI analysis and was performed in RAxML v. 8.2.4 (Stamatakis 2014). The best tree was obtained

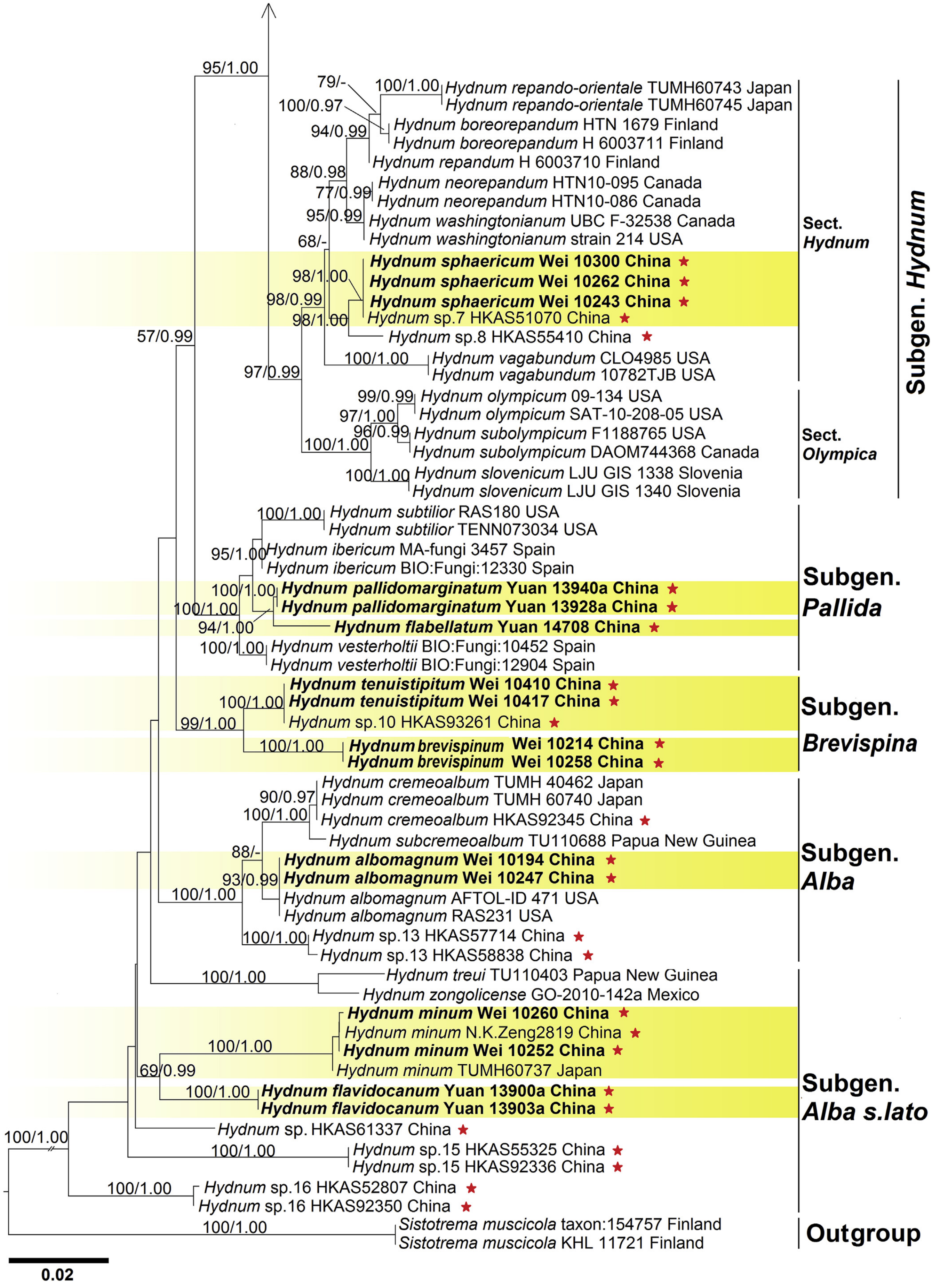

Fig. 4. (continued).

Table 2. Taxonomic information of the genera of *Hydnaceae*.

Genera	Morphology of basidiocarps	Nutritional modes	Distribution	Number of species[1]	References
Bergerella	Bulbil-forming	Lichenicolous	Austria	1	Lawrey *et al.* (2020)
Bryoclavula	Clavarioid	Lichenised	Japan	1	Masumoto & Degawa (2020a)
Bulbilla	Bulbil-forming	Lichenicolous	South America	1	Diederich *et al.* (2014)
Burgella	Bulbil-forming	Lichenicolous	North and South America	2	Diederich & Lawrey (2007), Diederich *et al.* (2014)
Burgellopsis	Bulbil-forming	Lichenicolous	Scotland	1	Diederich *et al.* (2014)
Burgoa	Bulbil-forming	Lichenicolous	Asia, Europe	10	Diederich & Lawrey (2007)
Cantharellus	Cantharelloid	Ectomycorrhizal	Worldwide	328	Buyck *et al.* (2014)
Clavulina	Clavarioid coralloid/ infundibuliform, resupinate, or effused	Ectomycorrhizal	Worldwide	88	Smith *et al.* (2011), Tibpromma *et al.* (2017)
Corallofungus	Clavarioid	-	Japan	2	He *et al.* (2019)
Craterellus	Cantharelloid, Tuberiform	Ectomycorrhizal	Worldwide	73	Henkel *et al.* (2014), Hembrom *et al.* (2017), Kirk & Larsson (2013), Das *et al.* (2017)
Gloeomucro	Geotropic, mucous to watery-gelatinous, lanceolate	Saprotrophic	North and South America, Asia	10	He *et al.* (2019)
Hydnum	Pileate-stipitate	Ectomycorrhizal	Worldwide	49	Feng *et al.* (2016)
Ingoldiella	-	Saprotrophic	Australia,Canada, Malaysia	3	He *et al.* (2019)
Membranomyces	Resupinate	Ectomycorrhizal	Asia, Middle East, Europe, Canada, USA	2	Argüelles-Moyao *et al.* (2017), Jülich (1975), Kotiranta & Saarenoksa (1993)
Minimedusa	Bulbil-forming	Lichenicolous, Saprophytic	North America, Europe, Asia	3	Lawrey *et al.* (2007)
Multiclavula	Clavarioid	Saprotrophic, Lichenised	Worldwide	16	Masumoto & Degawa (2020b)
Neoburgoa	Bulbil-forming	Lichenicolous	Alps, Russia	1	Lawrey *et al.* (2016), Zhurbenko Pino-Bodas (2017)
Parastereopsis	Tuberiform	-	Malaysia	1	He *et al.* (2019)
Osteomorpha	-	Saprotrophic	France, Russia	1	He *et al.* (2019)
Repetobasidiellum	Resupinate	Saprotrophic	Northern Europe	1	He *et al.* (2019)
Rogersiomyces	Hypochnoid	Saprotrophic	USA, Asia	2	Mel'nik *et al.* (2015), Psurtseva *et al.* (2016)
Sistotrema	Resupinate, stipitate	Saprotrophic, Ectomycorrhizal, Endophyte	Worldwide	55	Kirk & Larsson (2013), Hibbett *et al.* (2014)
Sistotremella	Resupinate	Saprotrophic	Europe	3	Eriksson *et al.* (1984), Boidin & Gilles (1994)

[1]The number of the species based on the http://www.indexfungorum.org/, and He *et al.* 2019 (Note and outline of *Basidiomycota*).

by performing 1 000 rapid bootstrap inferences followed by a thorough search for the most likely tree (Stamatakis *et al.* 2008). Phylogenetic trees were checked and modified in FigTree v. 1.4 (Rambaut 2012). The alignments and trees were deposited in TreeBASE (No. S28157).

RESULTS

Sequences and alignments produced in this study

We generated a total of 169 sequences from 20 species of three genera in *Hydnaceae* which included 50 of nLSU, 17 of mtSSU, 42 of ITS, 24 of *RPB2* and 36 of *TEF1* sequences.

Phylogenetic analyses

The ML and BI analyses for the four datasets produced similar topologies and therefore, only the ML tree for each dataset is shown (Figs 1–4).

The *Cantharellales* dataset included 110 samples *i.e.*, 109 of 77 species of 28 genera in six families, and one as the outgroup (*Dacrymyces australis*). The data matrix comprised 347 sequences and had an aligned length of 3 410 bases. The BI analysis resulted in an average standard deviation of split frequencies = 0.004722. The *Cantharellales* clade had high support (86 % ML and 1.00 BPP) in the tree (Fig. 1). *Hydnaceae* together with *Tulasnellaceae*, *Botryobasidiaceae*, and *Ceratobasidiaceae* nested in *Cantharellales* and all with full support. *Hydnaceae* was placed as a sister clade to *Tulasnellaceae*. Seventeen genera were confirmed in *Hydnaceae*.

Fig. 5. Basidiocarps of new taxa in *Hydnaceae*. **A–B.** *Cantharellus laevihymeninus* (IFP 019441). **C–D.** *Cantharellus magnus* (IFP 019443). **E.** *Cantharellus subminor* (IFP 019445). **F.** *Craterellus badiogriseus* (IFP 019452). **G.** *Craterellus croceialbus* (IFP 019454). **H.** *Craterellus macrosporus* (IFP 019456). **I.** *Craterellus squamatus* (IFP 019457). **J.** *Hydnum brevispinum* (IFP 019464). **K–L.** *Hydnum flabellatum* (IFP 019459). **M–N.** *Hydnum flavidocanum* (IFP 019460). **O.** *Hydnum longibasidium* (IFP 019462). **P–Q.** *Hydnum pallidocroceum* (IFP 019466). **R–S.** *Hydnum pallidomarginatum* (IFP 019468). **T–U.** *Hydnum sphaericum* (IFP 019470). **V.** *Hydnum tangerinum* (IFP 019473). **W.** *Hydnum tenuistipitum* (IFP 019476). **X–Y.** *Hydnum ventricosum* (IFP 019478). Scale bars: A, B, E–Y = 1 cm; C, D = 2 cm.

The *Cantharellus* dataset comprises 113 samples *i.e.*, 111 from 61 *Cantharellus* species and 2 as outgroups (*Craterellus tubaeformis* and *C. cornucopioides*). The data matrix comprised 385 sequences and had an aligned length of 2 675 bases. The BI analysis resulted in an average standard deviation of split frequencies = 0.003862. A new subgenus *Magnus* and three new species *Cantharellus magnus*, *Ca. laevihymeninus* and *Ca. subminor* are revealed, and two synonyms, *Ca. anzutake* and *Ca. tuberculosporus* as *Ca. yunnanensis* are recognised according to the analysis. The phylogenetic tree was divided into eight clades which correspond to subgenus *Cantharellus*, subgen. *Rubrinus*, subgen. *Parvocantharellus*, subgen. *Cinnabarinus*, subgen. *Pseudocantharellus*, subgen. *Magni*, subgen. *Afrocantharellus* and *Ca. guyanensis*, respectively. Ten sections also had high support in the tree. The result of the present study is similar to Buyck *et al.* (2014). Besides, it is noted that *Cantharellus* species from China are distributed throughout the genus except for subgen. *Rubrinus* (Fig. 2).

The *Craterellus* dataset comprises 52 samples *i.e.*, 50 of 31 *Cantharellus* species and two as outgroups (*Hydnum ellipsosporum* and *Sistotrema muscicola*). The data matrix comprised 81 sequences and had an aligned length of 1 701 bases. The BI

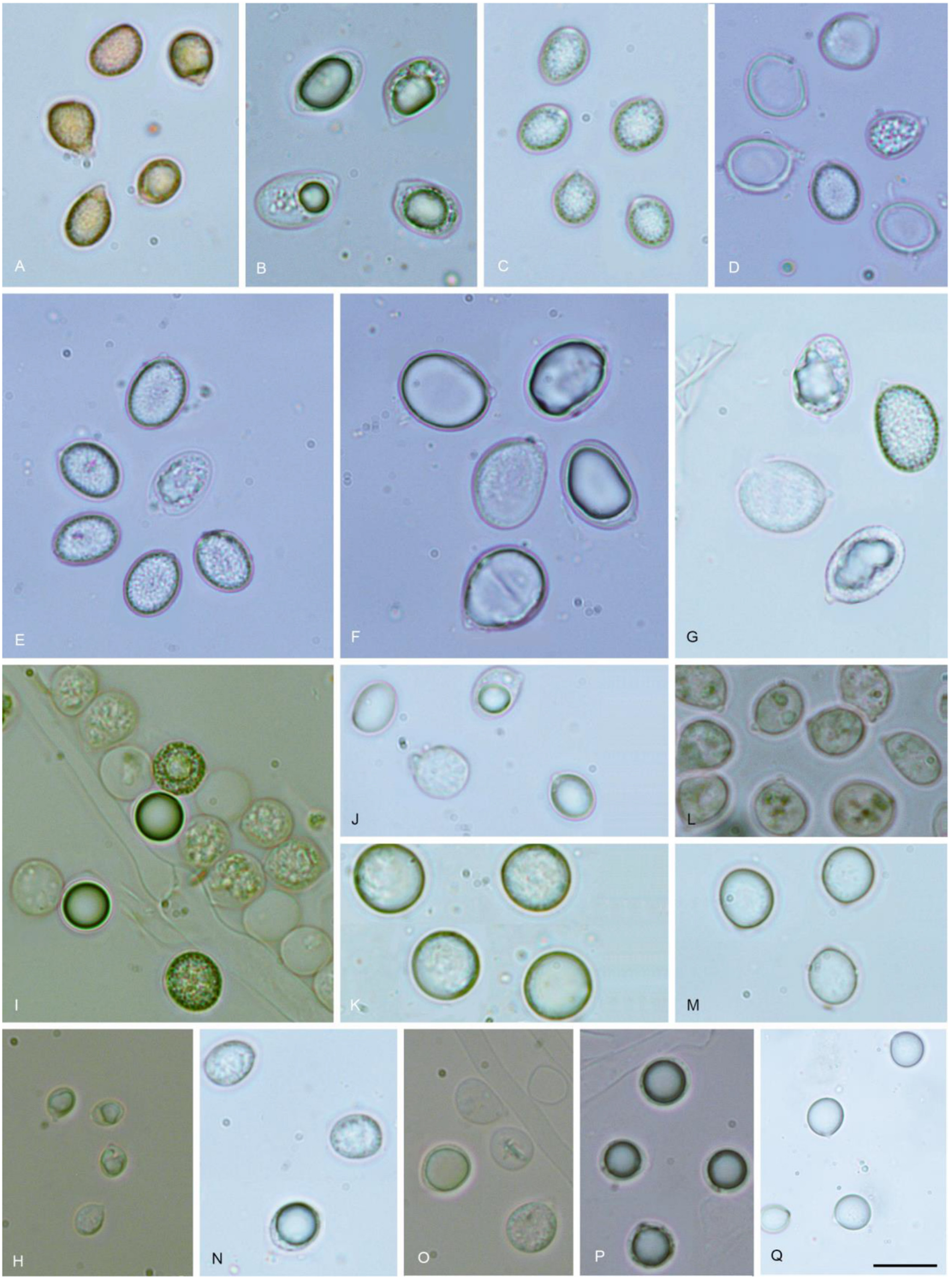

Fig. 6. Microscopic structures of basidiospores. **A.** *Cantharellus laevihymeninus* (IFP 019441). **B.** *Cantharellus magnus* (IFP 019443). **C.** *Cantharellus subminor* (IFP 019445). **D.** *Craterellus badiogriseus* (IFP 019452). **E.** *Craterellus croceialbus* (IFP 019454). **F.** *Craterellus macrosporus* (IFP 019456). **G.** *Craterellus squamatus* (IFP 019457). **H.** *Hydnum brevispinum* (IFP 019464). **I.** *Hydnum flabellatum* (IFP 019459). **J.** *Hydnum flavidocanum* (IFP 019460). **K.** *Hydnum longibasidium* (IFP 019462). **L.** *Hydnum pallidocroceum* (IFP 019466). **M.** *Hydnum pallidomarginatum* (IFP 019468). **N.** *Hydnum sphaericum* (IFP 019470). **O.** *Hydnum tangerinum* (IFP 019473). **P.** *Hydnum tenuistipitum* (IFP 019476). **Q.** *Hydnum ventricosum* (IFP 019478). Scale bar = 10 µm.

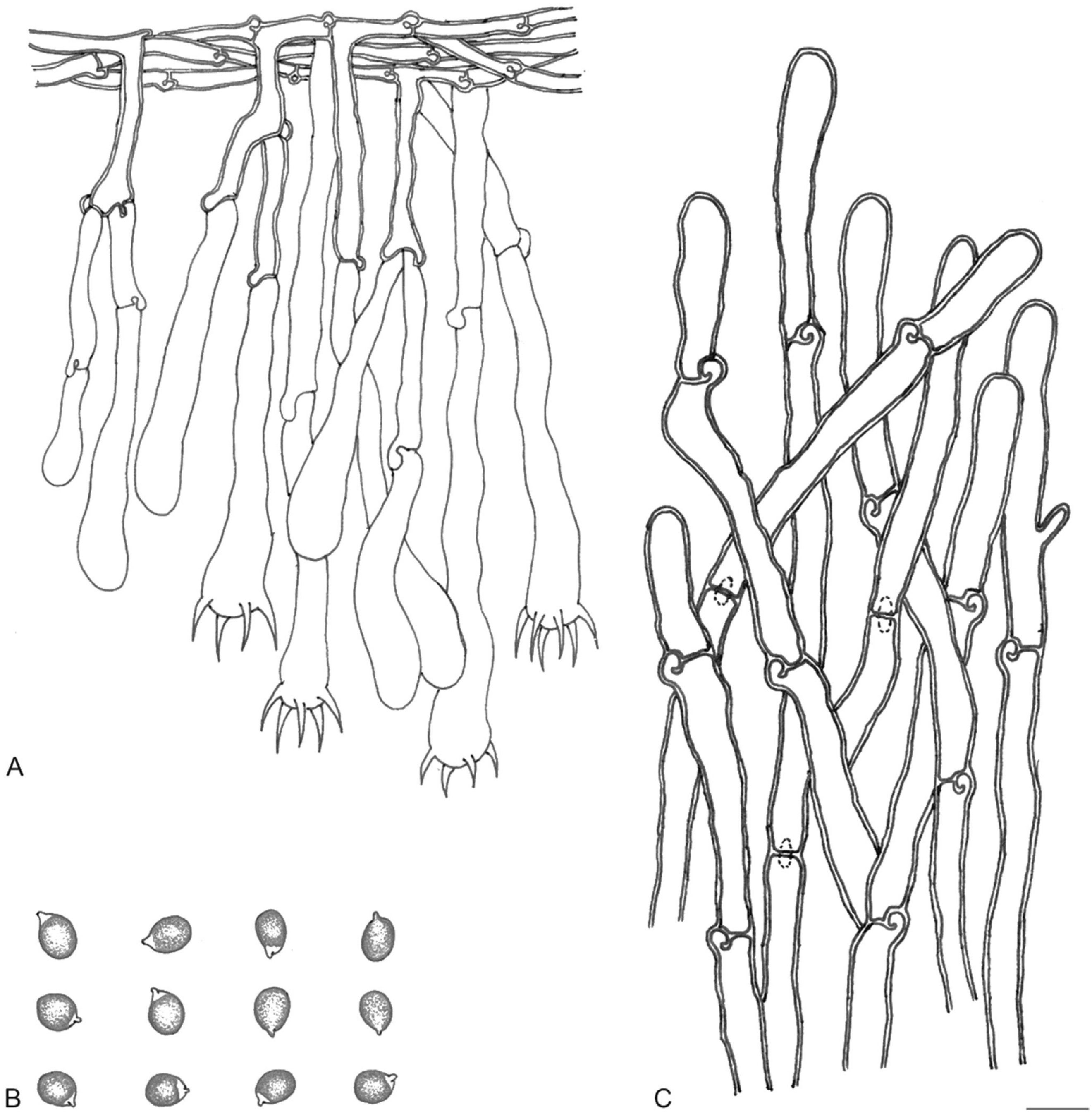

Fig. 7. Microscopic structures of *Cantharellus laevihymeninus* (IFP 019441). **A.** Hymenium and subhymenium. **B.** Basidiospores. **C.** Pileipellis. Scale bar = 10 µm.

analysis resulted in an average standard deviation of split frequencies = 0.002033. Six subgenera including subgen. *Cariosi,* subgen. *Craterellus*, subgen. *Imperforati*, subgen. *Lamelles*, subgen. *Longibasidiosi*, subgen. *Ovoidei*, in *Craterellus* are proposed and four new species (*Craterellus badiogriseus*, *Cr. croceialbus*, *Cr. macrosporus* and *Cr. squamatus*) are revealed in the genus according to the tree (Fig. 3).

The *Hydnum* dataset comprises 111 samples *i.e.*, 109 from 56 *Hydnum* species and two samples of *Sistotrema muscicola* as outgroups. The data matrix comprised 157 sequences and had an aligned length of 1 460 bases. The BI analysis resulted in an average standard deviation of split frequencies = 0.003647. The four subgenera *Alba*, *Hydnum*, *Pallida* and *Rufescentia*, two sections *Hydnum* and *Olympica* as well as the five subsections in section *Rufescentia* suggested by Niskanen *et al.* (2018), and a new subgenus *Brevispina* have been confirmed and suggested here with high support. However, the two sections *Rufescentia* and *Magnorufescentia* have weak support which is probably due to the addition of several samples from China. The taxa from China in the tree consist of ten new species (*Hydnum brevispinum*, *H. flabellatum*, *H. flavidocanum*, *H. longibasidium*, *H. pallidocroceum*, *H. pallidomarginatum*, *H. sphaericum*, *H. tangerinum*, *H. tenuistipitum* and *H. ventricosum*) as well as two newly recorded species (*H. albomagnum* and *H. minum*) from this study and ten undescribed samples by Feng *et al.* (2016) and these Chinese taxa have been found in every subgenus (Fig. 4).

Taxonomy

New taxa of Hydnaceae in this study

Cantharellus Adans. ex Fr., Syst. Mycol. (Lundae) 1: 316. 1821. MycoBank MB 17236.

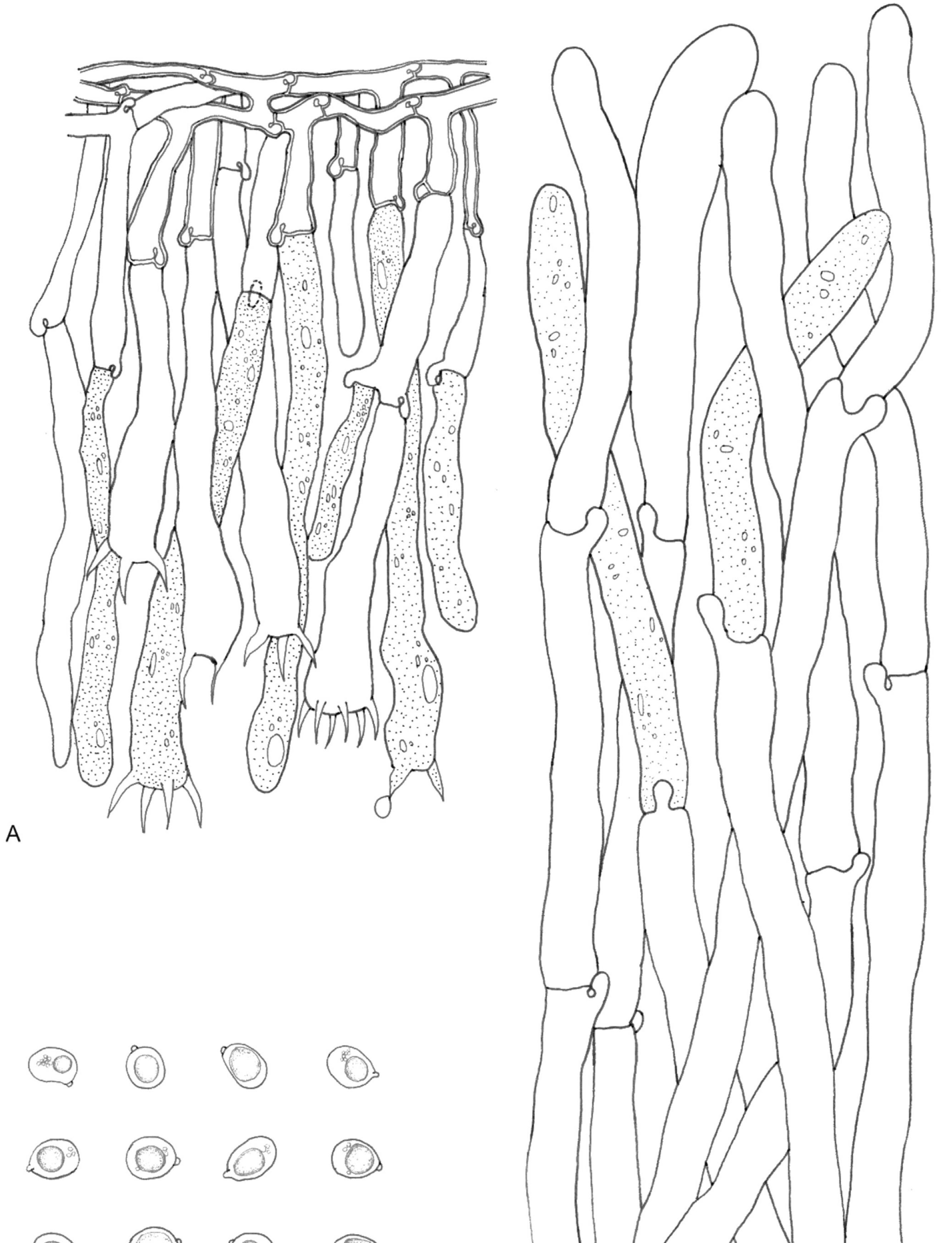

Fig. 8. Microscopic structures of *Cantharellus magnus* (IFP 019443). **A.** Hymenium and subhymenium. **B.** Basidiospores. **C.** Pileipellis. Scale bar = 10 μm.

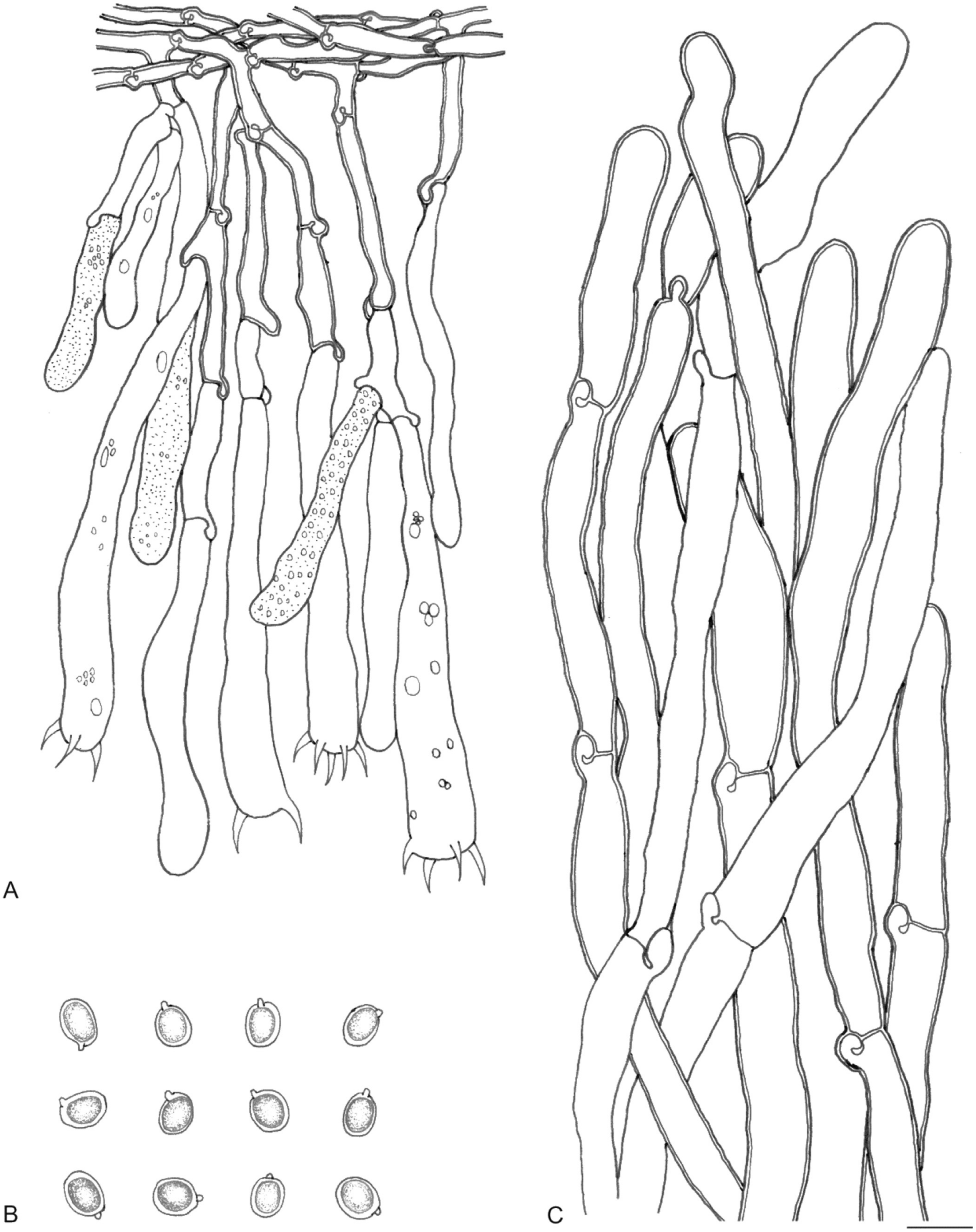

Fig. 9. Microscopic structures of *Cantharellus subminor* (IFP 019445). **A.** Hymenium and subhymenium. **B.** Basidiospores. **C.** Pileipellis. Scale bar = 10 µm.

Synonym: *Afrocantharellus* (Eyssart. & Buyck) Tibuhwa, IMA Fungus 3: 33. 2012. MycoBank MB 518687.
Goossensia Heinem., Bull. Jard. Bot. État Brux 28: 424. 1958. MycoBank MB 17690.

Type species: *Cantharellus cibarius* Fr., Syst. Mycol. (Lundae) 1: 318. 1821. MycoBank MB 200345.

Notes: *Cantharellus* was described by Fries (1821), with *Cantharellus cibarius* selected as the type species by Earle (1909). It is a large ectomycorrhizal genus of the *Hydnaceae*, comprising many edible species (Moncalvo *et al.* 2006, Hibbett *et al.* 2014), and belongs in the core lineage of the cantharelloid clade. Our study reproduced the infrageneric classification of the genus

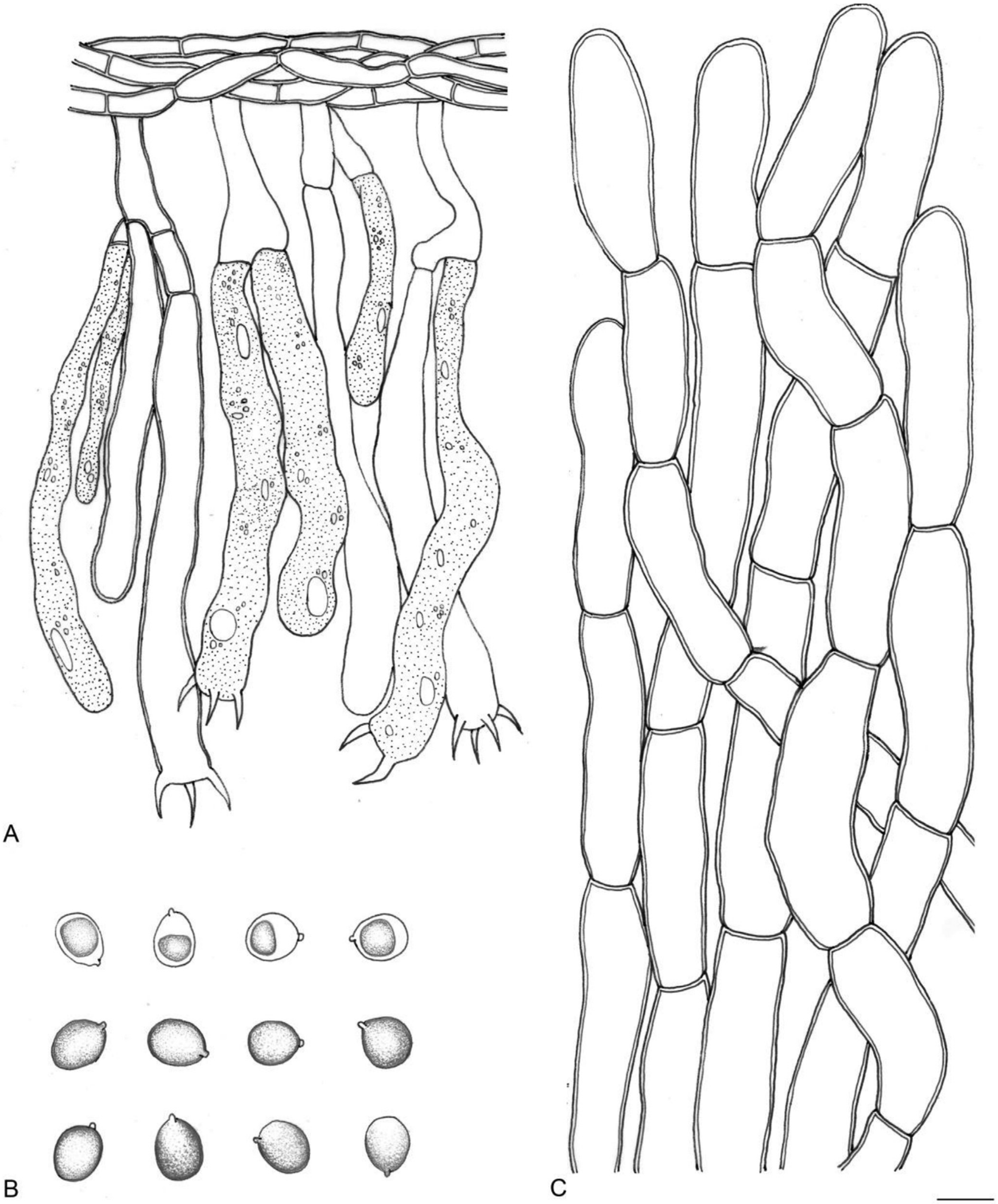

Fig. 10. Microscopic structures of *Craterellus badiogriseus* (IFP 019452). **A.** Hymenium and subhymenium. **B.** Basidiospores. **C.** Pileipellis. Scale bar = 10 µm.

based on a multiple-marker database (including 5.8S, nLSU, mtSSU and two protein coding genes *RPB2* and *TEF1*) (Fig. 2) and the result is similar to Buyck *et al.* (2014). The phylogenetic status of *Cantharellus* in the family proposed by Moncalvo *et al.* (2006) and Hibbett *et al.* (2014) is also confirmed by our tree (Fig. 1). *Cantharellus* groups with *Craterellus* and these two genera as well as *Hydnum* and several samples of *Sistotrema* form a strongly supported subclade in *Hydnaceae*.

Cantharellus is characterised by fleshy basidiocarps, a colourful pileus, nearly smooth to obvious veined hymenophore, long and stichic basidia, cylindrical hyphal endings in the pileipellis and a solid stipe (Cairney & Chambers 1999, Pine *et al.* 1999, Buyck 2014, Buyck *et al.* 2014). The boundary between *Cantharellus* and its sister group *Craterellus* had been resolved with molecular data by Dahlman *et al.* (2000) and Moncalvo *et al.* (2006). Furthermore, the basidiocarps mostly have a solid stipe

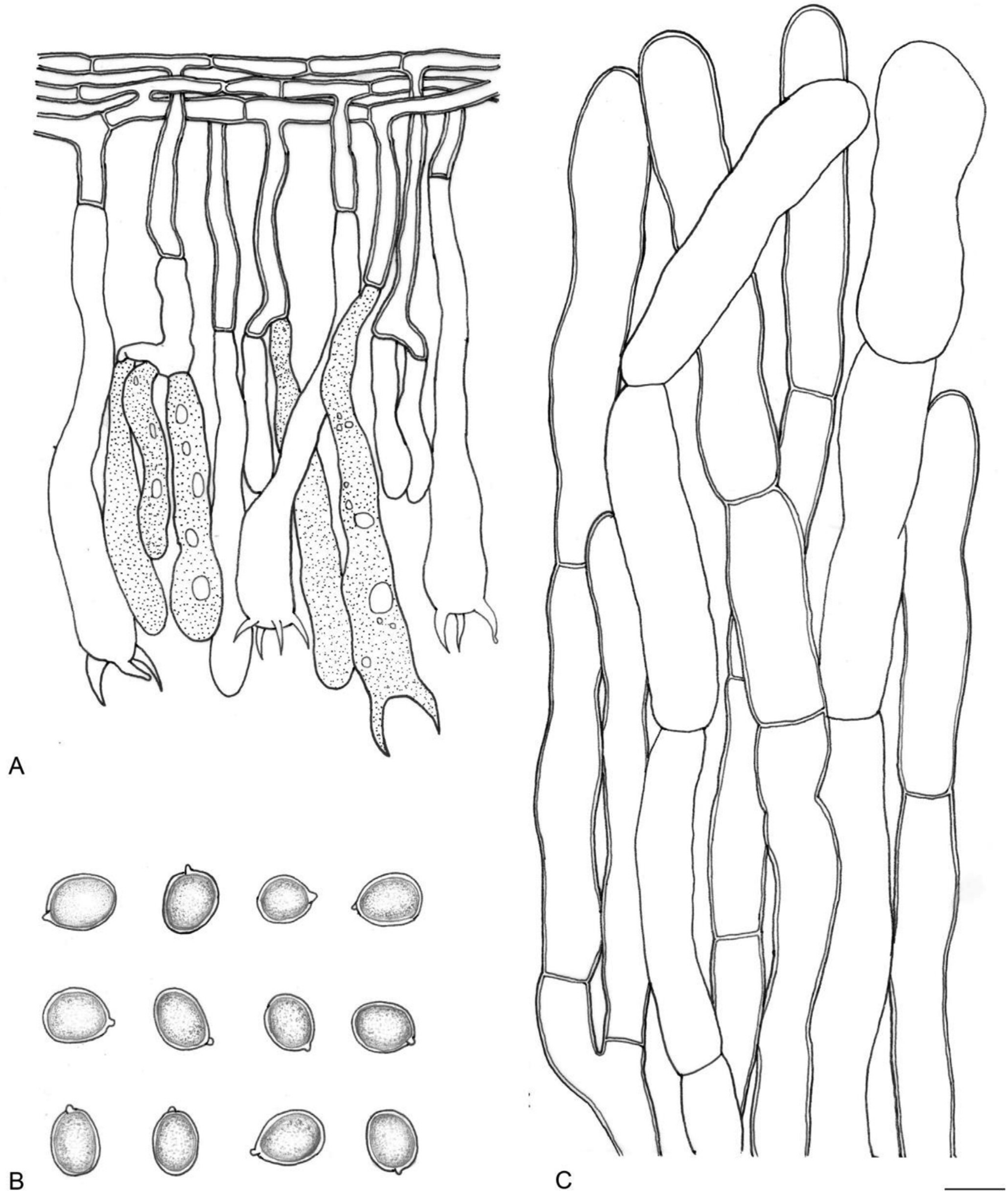

Fig. 11. Microscopic structures of *Craterellus croceialbus* (IFP 019454). **A.** Hymenium and subhymenium. **B.** Basidiospores. **C.** Pileipellis. Scale bar = 10 µm.

which also differentiates *Cantharellus* from *Craterellus* (Buyck *et al.* 2014). Many new taxa of *Cantharellus* have been published from around the world in the past two decades; for the overview of the detailed references see He *et al.* (2019). As of now, there are six subgenera, ca. ten sections (Buyck *et al.* 2014) and up to 300 species recognised in the genus (http://www.indexfungorum.org/). Species of *Cantharellus* are distributed worldwide but only nine species have been described from China (Chiu 1973, Zang 1980, Shao *et al.* 2011, 2014, 2016a, b, Tian *et al.* 2012, An *et al.* 2017, Jian *et al.* 2020) and a key to them was provided by Jian *et al.* (2020).

As significant ectomycorrhizal (ECM) fungi (Table 2), species of *Cantharellus* have many host species such as the trees of *Fagaceae*, *Pinaceae*, *Betulaceae*, *Salicaceae*, *Juglandaceae*, *Polygonaceae*, *Leguminosae*, *Phyllanthaceae*, *Fabaceae* etc. (De Kesel *et al.* 2011, Kumari *et al.* 2011, Bahram *et al.* 2012, Tian *et al.* 2012, Buyck *et al.* 2012, 2014, 2016a, b, Henkel *et al.* 2014, Shao *et al.* 2014, De Kesel *et al.* 2016, Leacock *et al.*

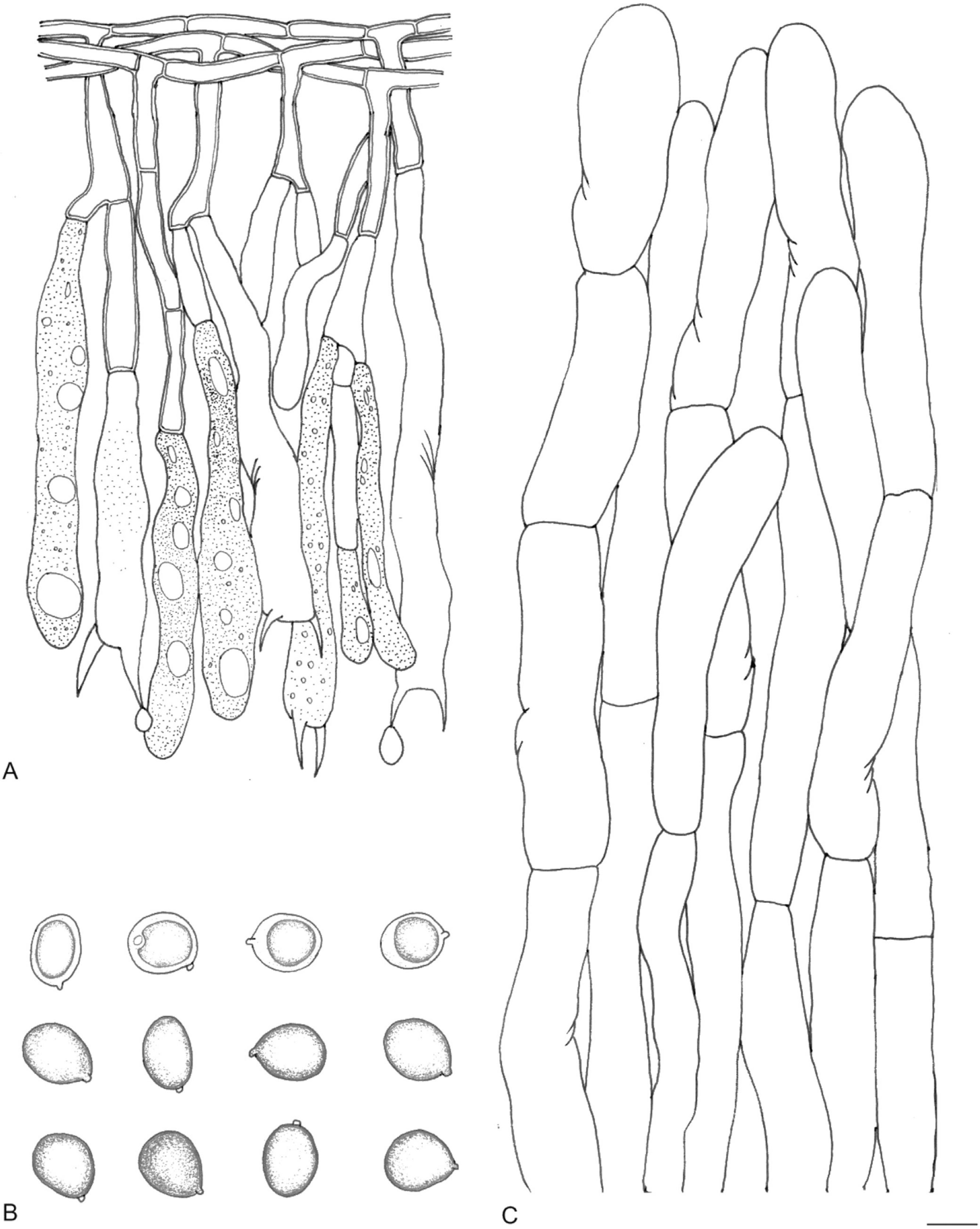

Fig. 12. Microscopic structures of *Craterellus macrosporus* (IFP 019456). **A.** Hymenium and subhymenium. **B.** Basidiospores. **C.** Pileipellis. Scale bar = 10 µm.

2016, Thorn *et al.* 2017, Das *et al.* 2018, Parad *et al.* 2018, Hyde *et al.* 2019, Buyck *et al.* 2020). In general, the candidate host of *Cantharellus* is related to species, regional disparities, and varies with altitude gradient.

Cantharellus* subg. *Magni T. Cao & H.S. Yuan, ***subg. nov.*** MycoBank MB 839393; Fig. 2

Etymology: *Magni* (Lat.), as the name of the type species.

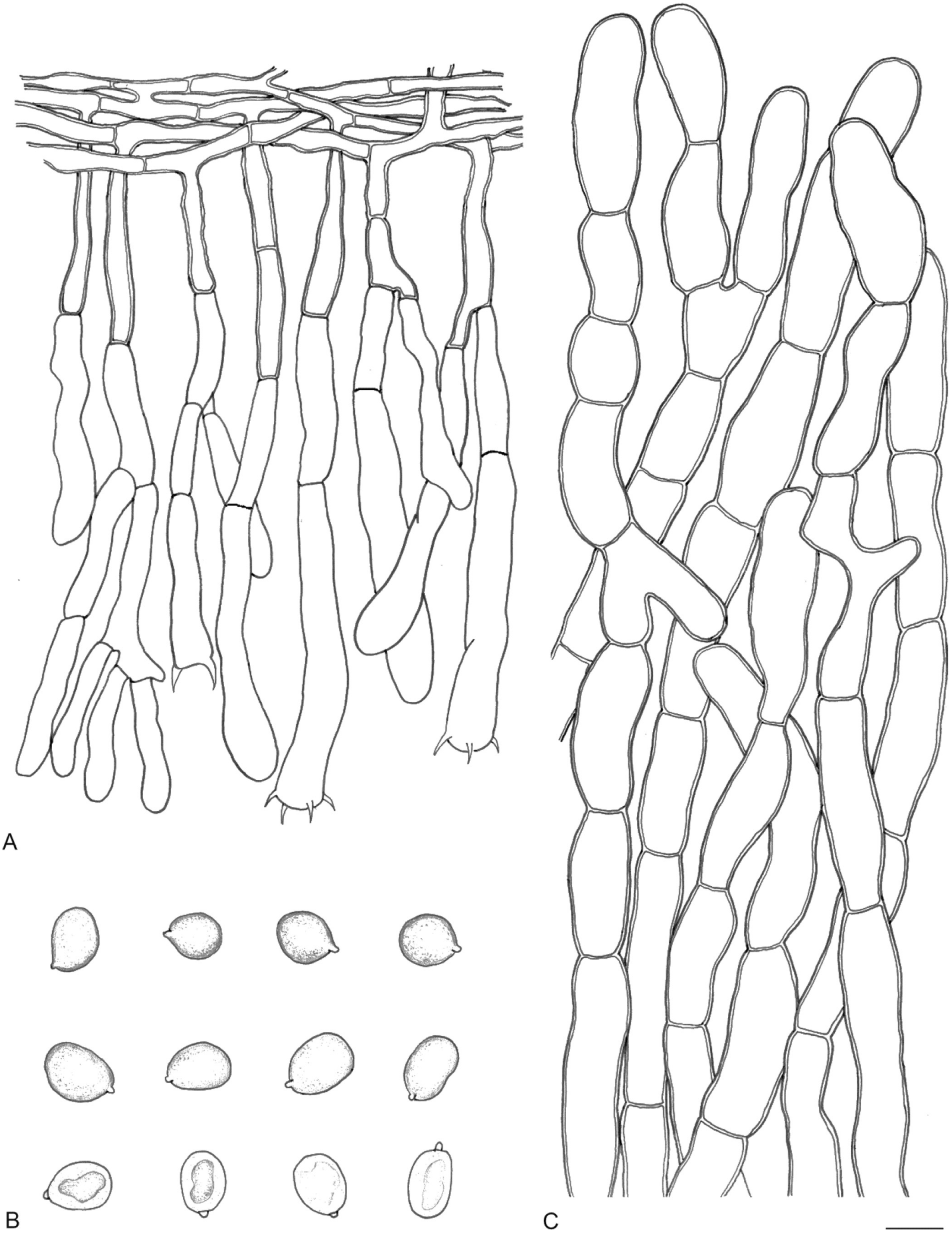

Fig. 13. Microscopic structures of *Craterellus squamatus* (IFP 019457). **A.** Hymenium and subhymenium. **B.** Basidiospores. **C.** Pileipellis. Scale bar = 10 µm.

Type species: *Cantharellus magnus* T. Cao & H. S. Yuan, MycoBank MB 839407.

Notes: *Cantharellus* subg. *Magni* is characterised by a large basidiocarp; smooth, azonate, deep yellow to deep orange pileal surface; always incised pileal margin; decurrent and almost perfectly smooth hymenophore; broadly ellipsoid basidiospores, absence of cystidia, thin- to slightly thick-walled terminal cells of pileipellis hyphae and presence of clamps. The type species,

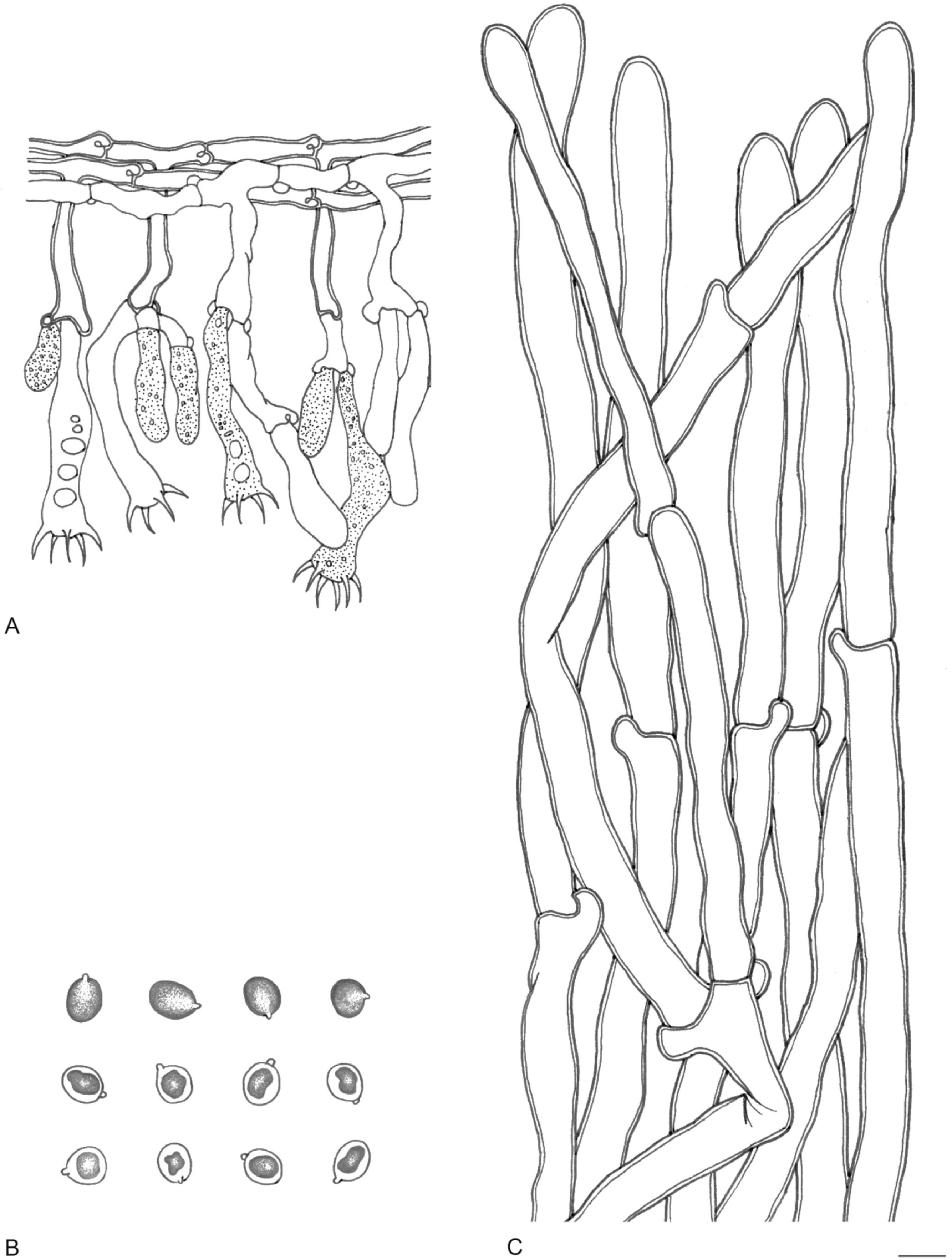

Fig. 14. Microscopic structures of *Hydnum brevispinum* (IFP 019464). **A.** Hymenium and subhymenium. **B.** Basidiospores. **C.** Pileipellis. Scale bars: A, C = 10 µm; B = 5 µm.

Cantharellus magnus, is distinctly different from the species of the other six subgenera based on morphological characteristics. The subgenus *Afrocantharellus* Buyck & V. Hofstetter includes small to large species (up to 180 mm wide and 100 mm high, like *Cantharellus splendens*), and they are differentiated from *C. magnus* by having four-spored basidia and absence of clamps. *C. magnus* resembles species of subgenus *Cantharellus* in having abundant clamps, smooth hymenophore (partly in some

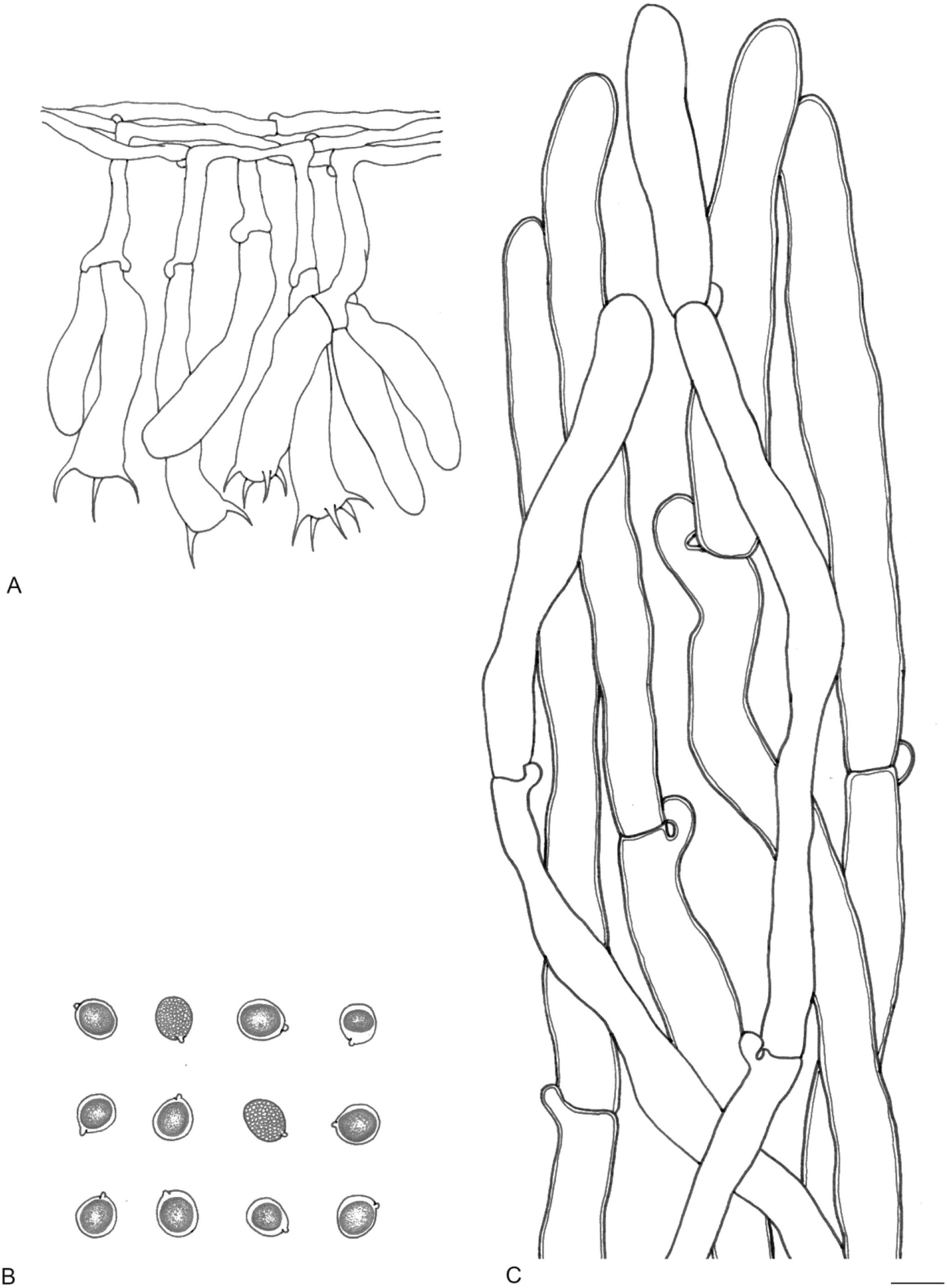

Fig. 15. Microscopic structures of *Hydnum flabellatum* (IFP 019459). **A.** Hymenium and subhymenium. **B.** Basidiospores. **C.** Pileipellis. Scale bar = 10 µm.

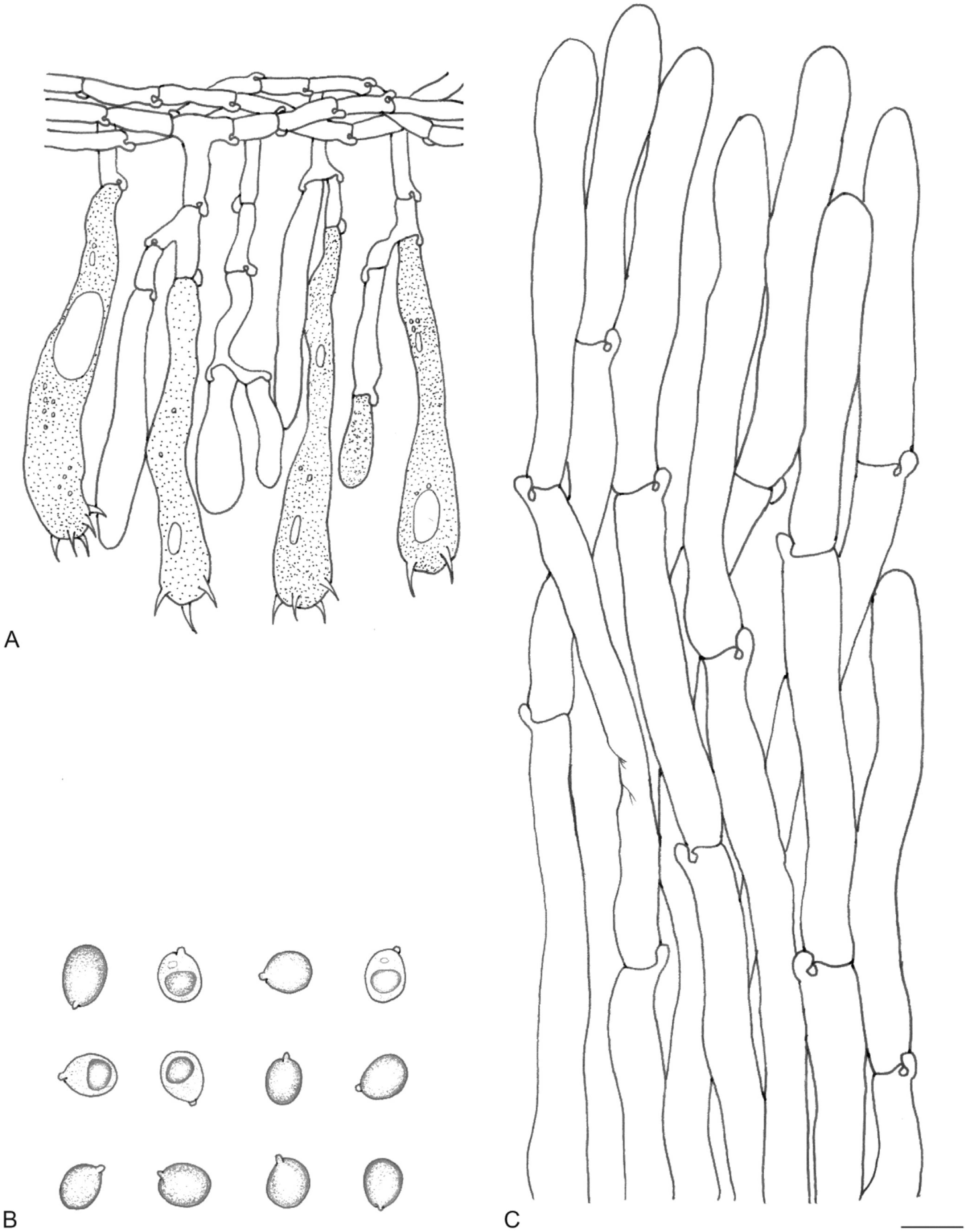

Fig. 16. Microscopic structures of *Hydnum flavidocanum* (IFP 019460). **A.** Hymenium and subhymenium. **B.** Basidiospores. **C.** Pileipellis. Scale bar = 10 µm.

species) and yellowish pileus but differs by the extremely large basidiocarps and thin- to slightly thick-walled pileipellis hyphae. The species of subgenus *Rubrinus* Buyck & V. Hofstetter can be obviously distinguished from *Cantharellus magnus* by small to medium-sized basidiocarps and absence of clamps. The species of subgenus *Cinnabarinus* Buyck & V. Hofstetter are similar to *C. magnus* in having abundant clamps but differ by the thin-walled terminal cells of the pileipellis hyphae and small to medium-sized basidiocarps (except *C. afrocibarius*). In addition, *Cantharellus magnus* differs from species of subgenus *Parvocantharellus* and subgenus *Pseudocantharellus* Buyck & V. Hofstetter by having large basidiocarps and nearly smooth hymenophore (Buyck 2014).

Cantharellus laevihymeninus T. Cao & H. S. Yuan, ***sp. nov.*** MycoBank MB 839405; Figs 1, 2, 5A–B, 6A, 7

Etymology: *Laevihymeninus* (Lat.), refers to the almost perfectly smooth hymenophore.

Typus: **China**, Yunnan Province, Shizong County, Junzishan Mt., on soil in angiosperm and *Pinus* sp. mixed forest, 8 Aug. 2019, H. S. Yuan & J. R. Yu, **holotype,** Yuan 13902 (IFP 019441).

Diagnosis: Differs from *Cantherallus hainanensis* in having larger pilei (30–65 mm *vs.* 25–55 mm wide in *C. hainanensis*), discoloured stipes when injured, broader spores (5–6.1 μm *vs.* 4.5–5 μm wide) and shorter terminal cells (15–38.5 μm *vs.* 23–82 μm long) of the pileipellis.

Description: *Basidiocarps* concrescent, medium, fleshy, leathery when fresh, becoming soft corky and light in weight upon drying. *Pilei* 30–65 mm wide, convex when young, with maturity becoming slightly plano-convex and slightly depressed in the center. *Pileal surface* dry, subglabrous, smooth to irregularly wrinkled, pale orange to orange (5A3–5A6) when moist, drying light brown (6D6/7D5/7D6). *Pileal margin* slightly decurved when young, undulate with maturity, involute or irregularly folded, sometimes incised. *Pileal context* 0.5–3 mm thick, thin towards the pileus margin, light yellow (4A4). *Hymenophore* decurrent, almost perfectly smooth to a few faint ridges or folds, pale orange to light orange (5A3/5A4). *Stipes* central, often concrescent, confluent with pilei, 25–45 mm long, 10–18 mm wide, subcylindrical, sometimes hollow; surface glabrous to finely rugulose, orange-white (5A2/6A2) when moist, bruising darker when injured, drying brown to dark brown (6E7–6F8); stipe base slightly enlarged and with a small amount of white basal mycelium. *Odour* typically of apricots. *Taste* mild.

Basidiospores ellipsoid, (6.8–)7.0–8.8(–9.0) × (4.8–)5.0–6.1(–6.2) μm, L_m = 7.87 μm, W_m = 5.52 μm, Q = 1.35–1.42 (n = 60/2), smooth, thin-walled, IKI–, hyaline, some with granular contents; hilar appendix 0.5–1.0 μm long. *Basidia* subcylindric, subclavate to clavate, 22.5–75 × 6.5–10 μm, sometimes with large guttules or finely granulose contents; sterigmata 4–6, up to 10 μm long, 1–2.5 μm wide at base, slightly curving. *Basidioles* cylindrical to subclavate, smaller than basidia. *Subhymenium trama* filamentous, hyphae 2–7 μm wide, thin- to slightly thick-walled, olive yellow in KOH. *Cystidia* absent. *Pileipellis* composed of cylindrical hyphae, 3–9 μm wide, thick-walled, interwoven, rarely branched; terminal elements rounded at apex, cells 15–38.5 × 3–10 μm. *Stipitipellis* composed of cylindrical hyphae, thick-walled, densely interwoven to subparallel, 4.9–7.4 μm wide, terminal elements rounded at apex. *Clamp connections* present.

Material examined: China. Yunnan Province, Shizong County, Junzishan Mt., on soil in angiosperm and Pinus sp. mixed forest, 8 Aug. 2019, H. S. Yuan & J. R. Yu, paratype, Yuan 13902 (IFP 019442).

Notes: The new species, *Cantharellus laevihymeninus*, fell in subgenus *Cantharellus* and together with three other smooth chanterelles *viz.*, *C. hainanensis*, *C. flavolateritius* and *C. lateritius* made up section *Sublaeves* with a strong support (100 % ML, 1.00 BPP) based on our phylogenetic tree. Members of section *Sublaeves* usually share the almost smooth hymenophore (apart from *C. lateritius* which is only partly smooth) (Buyck 2014).

Cantharellus hainanensis is another Chinese species in section *Sublaeves* and was described from Hainan Province. Morphologically, *Cantharellus hainanensis* is like *C. laevihymeninus* in having a decurrent and almost smooth hymenophore, sometimes hollow stipes, clavate to subcylindrical basidia and 4–6 sterigmata. But *Cantharellus laevihymeninus* is quite distinct due to its larger pilei (30–65 mm *vs.* 25–55 mm wide in *C. hainanensis*), discoloured stipes when injured, broader spores (5–6.1 μm *vs.* 4.5–5 μm wide) and shorter terminal cells (15–38.5 μm *vs.* 23–82 μm long) of the pileipellis (An *et al.* 2017).

Cantharellus flavolateritius was described from North Carolina in the USA and resembles *C. laevihymeninus* in having a decurrent and almost smooth hymenophore, stipes bruising darker when injured, absence of cystidia and presence of clamps. However, *Cantharellus flavolateritius* differs from the new species by having slenderer basidiospores (4.2–5.2 μm), longer basidia (up to 85 μm), 5 sterigmata and longer terminal cells (up to 70 μm long) of the pileipellis (Buyck *et al.* 2016b). *Cantharellus lateritius* is similar to *C. laevihymeninus* in having yellow to orange fruit bodies, sometimes concrescent stipes, ellipsoid spores and absence of cystidia, but differs by larger basidiocarps (up to 9 cm wide and 12 cm high), partly smooth hymenophore, thin-walled hyphae in pileipellis and (3–)4–5 sterigmata (Petersen 1979a, Buyck 2014).

Cantharellus magnus T. Cao & H. S. Yuan, ***sp. nov.*** MycoBank MB 839407; Figs 1, 2, 5C–D, 6B, 8

Etymology: *Magnus* (Lat.), refers to the large basidiocarps.

Typus: **China**, Hunan Province, Sangzhi County, Badagong Nature Reserve, on soil in angiosperm forest, 23 Sep. 2020, T. Cao & Y. L. Wei, **holotype**, Wei 10225 (IFP 019443).

Diagnosis: Differs from *Cantherallus miomboensis* in having a larger pileus (200 mm *vs.* 150 mm wide) and smooth hymenophore.

Description: *Basidiocarps* solitary, fleshy and fragile when fresh, becoming soft corky and light in weight upon drying. *Pilei* up to 200 mm wide, convex when young, becoming plano-convex and depressed in the center, infundibuliform when mature. *Pileal surface* dry, subglabrous to velutinate, smooth, azonate, deep yellow to deep orange (4A8–5A8) when moist, drying become light yellow to greyish orange (4A5–5B4). *Pileal margin* always incised, decurved when young, becoming strongly and irregularly folded and undulate with age. *Pileal context* 5–15 mm thick, yellowish white (3A2). *Hymenophore* decurrent, almost perfectly smooth to a few faint ridges or folds, pale yellow to greyish yellow (4A3–4B4) when fresh, pale orange to brownish orange (5A4–5C8) upon drying. *Stipes* central, confluent with pilei, 30–100 mm long, 6–25 mm wide, subcylindrical, somewhat curved, solid; surface subglabrous to finely rugulose, orange to yellowish white to white (3A1–3A2) when moist, drying pale yellow (4A3); stipe base equal and covered with a small amount of white basal mycelium. *Odour* typically of apricots. *Taste* mild.

Basidiospores broadly ellipsoid, (8.5–)9.0–11.0(–11.5) × (6.5–)6.8–7.5(–8.0) μm, L_m = 9.73 μm, W_m = 7.26 μm, Q = 1.34–1.37 (n = 60/2), smooth, thin-walled, IKI–, hyaline, some with granular contents; hilar appendix 0.5 μm long. *Basidia* subcylindric, subclavate to clavate, 85–120 × 10–18 μm,

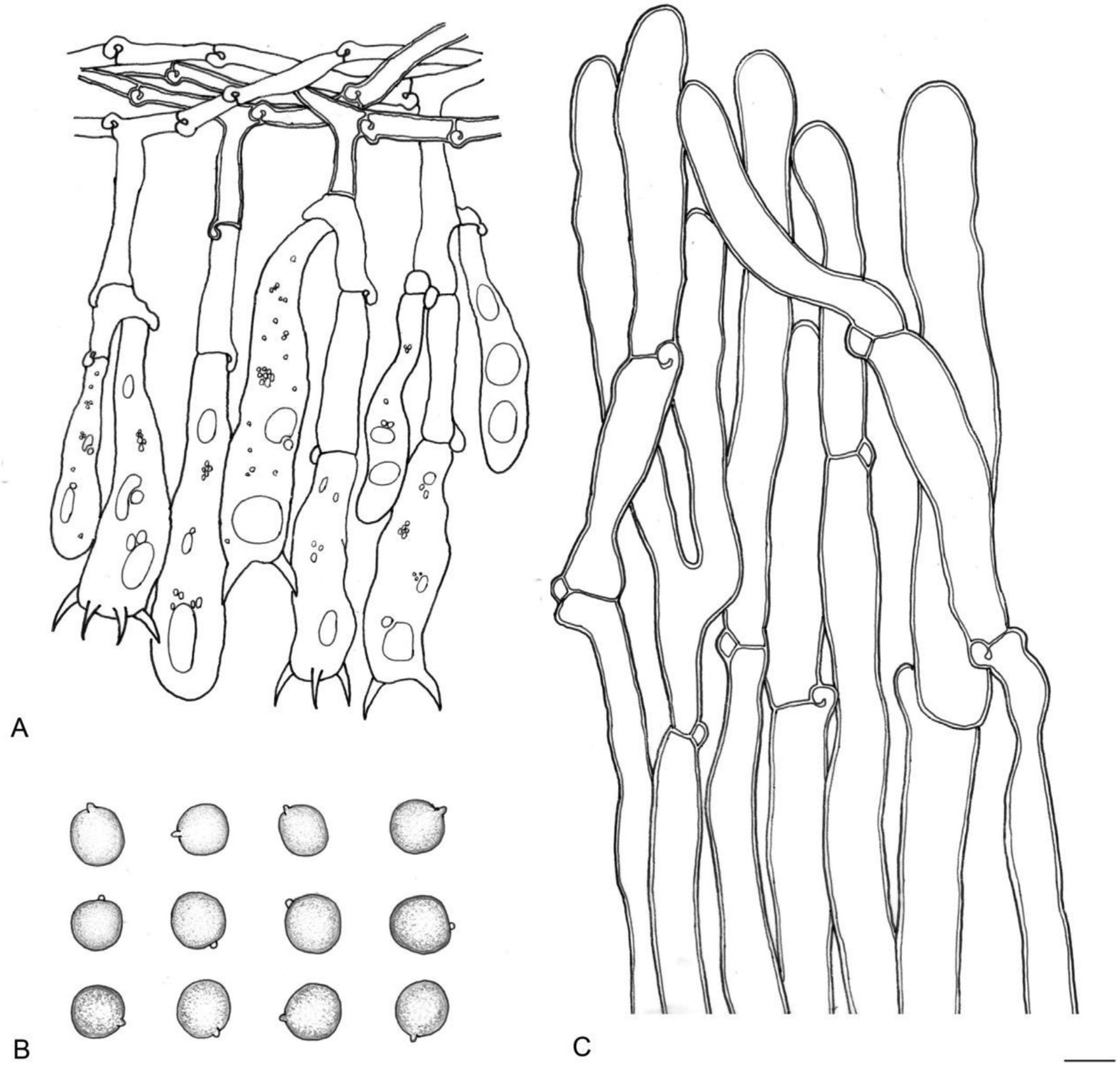

Fig. 17. Microscopic structures of *Hydnum longibasidium* (IFP 019462). **A.** Hymenium and subhymenium. **B.** Basidiospores. **C.** Pileipellis. Scale bar = 10 µm.

sometimes with large guttules or finely granulose contents; sterigmata 2–6, up to 10 µm long, 1.5–5 µm wide at base, somewhat curving. *Basidioles* numerous, subcylindrical to subclavate, smaller than basidia, 30–98 × 3–11 µm. *Subhymenium trama* filamentous, hyphae 3.5–6 µm wide, thin- to slightly thick-walled, olive yellow in KOH. *Cystidia* absent. *Pileipellis* composed of cylindrical hyphae, 6–13 µm wide, thin- to slightly thick-walled, interwoven, rarely branched; terminal elements rounded at apex, cells 92–160 × 7–15 µm. *Stipitipellis* composed of cylindrical hyphae, thick-walled, densely interwoven to subparallel, 7.5–11 µm wide, terminal elements rounded at apex. *Clamp connections* present.

Material examined: **China**, Hunan Province, Sangzhi County, Badagong Nature Reserve, on soil in angiosperm forest, 23 Sep. 2020, T. Cao & Y. L. Wei, paratype, Wei 10244 (IFP 019444).

Notes: *Cantharellus magnus* was collected from a subtropical forest in central China. The phylogenetic analysis shows that it nests in the genus *Cantharellus* but does not belong to any recognised subgenus. *Cantharellus magnus* has large basidiocarps, with a deep yellow to deep orange pileal surface, decurrent and smooth hymenophore, broadly ellipsoid spores and large, thin- to slightly thick-walled terminal cells of the pileipellis. *Cantharellus magnus* resembles *C. afrocibarius* (up to 180 mm wide) and *C. miomboensis* (up to 150 mm wide) in having large basidiocarps, but the new species can be differentiated from these two species by having an almost smooth hymenophore (Buyck *et al.* 2012).

Cantharellus subminor T. Cao & H. S. Yuan, ***sp. nov.*** MycoBank MB 839409; Figs 1, 2, 5E, 6C, 9

Etymology: Subminor (Lat.), refers to the affinity with *C. minor*.

Typus: **China**, Yunnan Province, Luoping County, Huangnigou Village, on soil in angiosperm and *Pinus* sp. mixed forest, 9 Aug. 2019, H. S. Yuan, **holotype**, Yuan 13917 (IFP 019445).

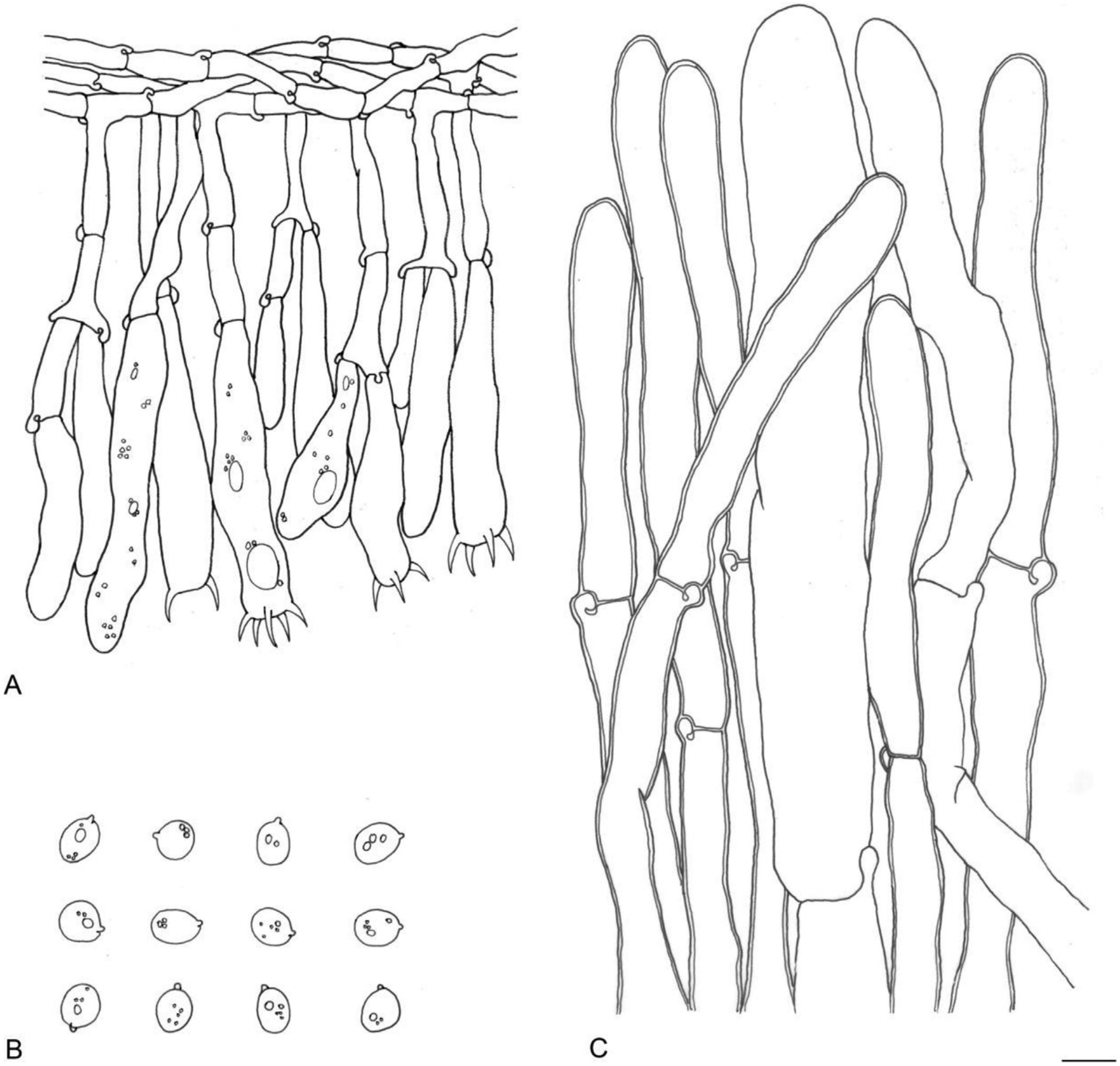

Fig. 18. Microscopic structures of *Hydnum pallidocroceum* (IFP 019466). **A.** Hymenium and subhymenium. **B.** Basidiospores. **C.** Pileipellis. Scale bar = 10 µm.

Diagnosis: Differs from *Cantharellus minor* in the intervenose hymenophore, shorter and broader stipes (15–30 × 2–5 *vs.* 20–50 × 1–2 mm) and smaller basidiospores (7.8–8.8 × 5.2–5.8 *vs.* 6–11.5 × 4–6.5 µm).

Description: *Basidiocarps* solitary, soft and leathery when fresh, becoming brittle upon drying. *Pilei* thin, 5–15 mm wide, convex to plano-convex and slightly depressed in the center when young, becoming broadly uplifted and infundibuliform with age. *Pileal surface* dry, subglabrous, smooth to irregularly wrinkled, vivid yellow to light yellow (3A8/3A5) when moist, drying become brownish orange to light brown (6C6–6D7). *Pileal margin* entire and decurved when young, becoming plane, uplifted, sometimes incised with age. *Pileal context* thin, ca. 0.2 mm thick. *Hymenophore* decurrent, composed of low forking veins, sometimes intervenose at margin, concolorous with pileal surface. *Stipes* central, confluent with pilei, 15–30 mm long, 2–5 mm wide, subcylindrical, solid; surface glabrous to finely rugulose, orange to golden yellow (5B7–5B8) when moist, drying brownish orange to light brown (6C5–7D7), deeper than the pileal surface; leathery or fleshy when fresh, become hard upon drying; stipe base slightly enlarged and covered with a small amount of white basal mycelium. *Odour* faintly fruity. *Taste* mild.

Basidiospores ellipsoid, (7.5–)7.8–8.8(–9.0) × (4.8–) 5.2–5.8 (–6.0) µm, L_m = 8.38 µm, W_m = 5.57 µm, Q = 1.47–1.50 (n = 60/2), smooth and thin-walled, IKI–, hyaline, some with granular contents; hilar appendix 0.3–0.8 µm long. *Basidia* subcylindric, subclavate to clavate, 43–96.5 × 6.5–10 µm, sometimes with large guttules or finely granulose contents; sterigmata 4–5, up to 10 µm long, 1–3 µm wide at base, somewhat curving. *Basidioles* numerous, cylindrical to subclavate, smaller than basidia, 10–62.5 × 2–10 µm. *Subhymenium trama* filamentous, hyphae 3–5.5 µm wide, thin- to slightly thick-walled, olive yellow in KOH. *Cystidia* absent. *Pileipellis* composed of cylindrical hyphae, 8.5–12 µm wide, thin- to slightly thick-walled, interwoven, rarely branched; terminal elements rounded at apex, cells 22–96 × 8.5–15 µm. *Stipitipellis*

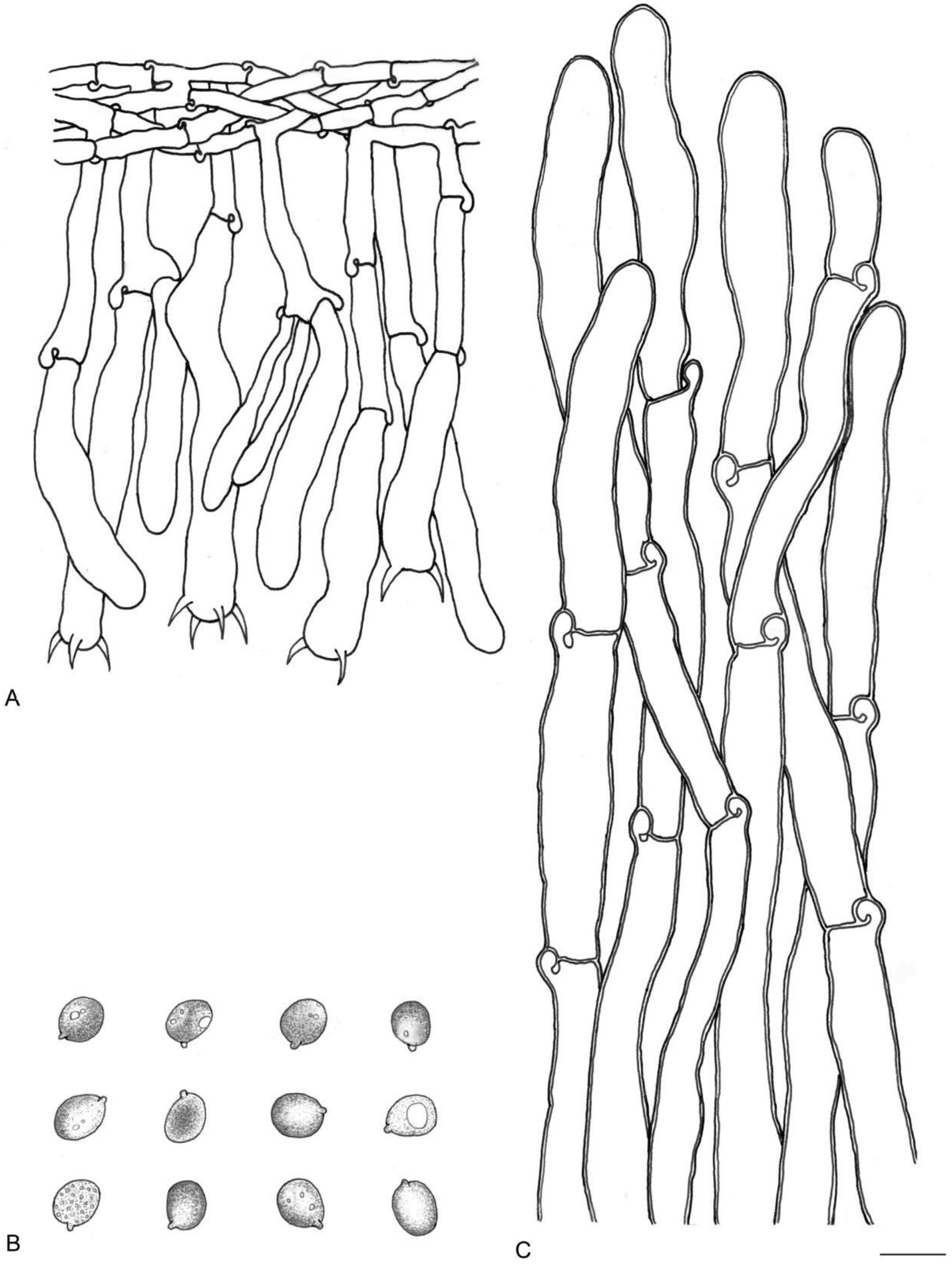

Fig. 19. Microscopic structures of *Hydnum pallidomarginatum* (IFP 019468). **A.** Hymenium and subhymenium. **B.** Basidiospores. **C.** Pileipellis. Scale bar = 10 µm.

composed of cylindrical hyphae, thick-walled, densely interwoven to subparallel, 5–13.5 µm wide, terminal elements rounded at apex. *Clamp connections* present.

Material examined: **China**, Yunnan Province, Qujing City, Luoping County, Huangnigou Village, on soil in angiosperm and *Pinus* sp. mixed forest, 9 Aug. 2019, H. S. Yuan, paratype, Yuan 13925 (IFP 019446); Yuan 13926 (IFP 019447).

Notes: *Cantharellus subminor* is the smallest species of *Cantharellus* described from China. In the phylogenetic tree, *C. subminor* is embedded in subg. *Parvocantharellus* and forms a clade with two other small chanterelles, *C. minor* and *C. romagnesianus*.

Morphologically, *Cantharellus subminor* is closely related to *C. minor* by having a smooth and yellowish pileal surface, small pileus (less than 15 mm wide) and 4–5 sterigmata, ellipsoid basidiospores and presence of clamps, but *C. minor* differs by the non-intervenose hymenophore, longer and slenderer stipes (20–50 × 1–2 mm) and larger basidiospores (6–11.5 × 4–6.5 µm) (Peck 1873, Lao *et al.* 2019). *Cantharellus romagnesianus* is like *C. subminor* in having subcylindrical stipes, subcylindric basidia, absence of cystidia and presence of clamps, however, it is differentiated by having a larger pileus (up to 25 mm wide), discoloured context when injured, slenderer basidiospores (4.5–5 µm wide) and 5–6 sterigmata (Eyssartier & Buyck 1999). *Cantharellus albus* is another Chinese species embeded in subg. *Parvocantharellus*, but it can be distinctly differentiated from *C. subminor* in having a larger pileus (up to 50 mm wide and 70 mm high) and snow white basidiocarps (Jian *et al.* 2020). The Mexican *Cantharellus parvoflavus* M. Herrera, Bandala & Montoya is also a member of subg. *Parvocantharellus* and has small size basidiocarps as *C. subminor*, however, it differs from *C. subminor* by having orangish pilei, slenderer basidiospores (Q = 1.52–1.57 *vs.* 1.47–1.50), shorter basidia (50–89 *vs.* 43–96.5 µm long) and smaller terminal elements (23–80 × 3.5–8 *vs.* 22–96 × 8.5–15 µm) of pileipellis. Besides, the similarity of *TEF1* sequences between *C. parvoflavus* and *C. subminor* is 94.69 %.

Cantharellus yunnanensis W.F. Chiu, Acta Microbiol. Sin. 13(2): 129. 1973. MycoBank MB 310378.

Synonym: *Cantharellus tuberculosporus* M. Zang, Acta Microbiol. Sin. 20(1): 31. 1980. MycoBank MB 118474.
Cantharellus anzutake W. Ogawa, N. Endo, M. Fukuda and A. Yamada, Mycoscience 59: 158. 2017. MycoBank MB 813057.

Typus: **China**, Yunnan Province, Kunming City, Xishan Forest Park, on soil in angiosperm and *Pinus* sp. mixed forest, 11 Aug. 1942, S. J. Shen, **holotype**, Tsinghua 8090 (HMAS 4090).

Materials examined: **China**, Yunnan Province, Kunming City, Xishan Forest Park, on soil in angiosperm and *Pinus* sp. mixed forest, 15 Aug. 2019, T. Cao, Yuan 13983 (IFP 019448), 13985 (IFP 019449); Liaoning Province, Fushun City, Xinbin County, Gangshan Mt., on soil in angiosperm and *Pinus* sp. mixed forest, 12 Aug. 2020, H. S. Yuan, Yuan 14539 (IFP 019450); 14636 (IFP 019451).

Notes: *Cantharellus yunnanensis* is the first species of the genus to be described from China (Chiu 1973). Shao *et al.* (2021) have selected the epitype (Herrera 263C) and redescribed the species. In this study, we collected several samples (Yuan 13983 and Yuan 13985) from Xishan Forest Park of Kunming, where the type material of *C. yunnanensis* (HMAS 4090, Tsinghua 8090) and epitype (Herrera 263C) were collected and we recognised them as the same taxa as *C. yunnanensis* based on phylogenetical and morphological evidences. Phylogenetic analyses shows that four samples (Yuan 13983, 13985, 14539, 14363) which were collected from Liaoning Province, group with *C. yunnanensis* (XieXD 174), *C. tuberculosporus* (HKAS58195 and HKAS58196) and *C. anzutake* (TNS-F-61925). The eight samples form a strongly supported (84 % in ML, 0.99 BPP) isolated lineage (Fig. 2). Furthermore, Yuan 13983 showed a high similarity of *TEF1* sequences to KU720337 (XieXD 174), KM893834 (HKAS58195), KM893835 (HKAS58196) and LC179800 (TNS-F-61925) with 99.01 %, 99.12 %, 99.01 % and 98.76 % respectively.

According to the original description, *Cantharellus yunnanensis* possesses small basidiocarps with a white to pale salmon hymenophore and small basidiospores (4–5 × 2–3.5 µm) (Chiu 1973). The verification of the epitype specimen (Herrera 263C) shows that the basidiospore size, 6.5–8.5 × 5–6.5 µm overlaps the spore size of the newly collected specimens Additionally, according to the observations of the specimens (epitype, Yuan 13983 and Yuan 13985), the size of the basidiocarps of *C. yunnanensis* is also larger than the original description, and the hymenophore can be white, pale salmon or even yellow in some individuals.

Cantharellus anzutake, described from Japan, was collected from a forest of Japanese red pine and is characterised by a pale yellow to orange-yellow pileal surface, white to pale yellow hymenophore, 4–6 spored basidia and ellipsoid basidiospores. The spore size of the *C. yunnanensis* epitype (Herrera 263C, 6.5–8.5 × 5–6.5 µm), Yuan 13983 and Yuan 13985 (7.5–9 × 5–6.5 µm) overlaps with those of *C. anzutake* (5.8–9.2 × 4–6.3 µm), and the pileal and hymenophore colour of *C. anzutake* often change with weather conditions; having a pale-yellow pileus and white hymenophore in drier conditions or yellow in wet is very similar to *C. yunnanensis* (Ogawa *et al.* 2018). Phylogenetic analyses (Fig. 2) suggest the type *Cantharellus anzutake* (TNS-F-61925) and several samples of *C. yunnanensis* belong to a separate lineage which confirms *C. anzutake* is the later synonym of *C. yunnanensis*.

Cantharellus tuberculosporus was described from Xizang, China. According to the original description, the species is characterised by a bright yellow pileal surface and hymenophore as well as tuberculate basidiospores (Zang 1980). Shao (2011) corrected the type specimen number (HKAS5412) to HKAS 28930 and redescribed the species as the spores of HKAS 28930 are smooth, 7–8 × 5–6 µm, and obviously different from the tuberculate spores in the original description. The tuberculate spores may be due to the shrinkage caused by dehydration (Shao 2011). The anatomical features of *C. tuberculosporus* are closely related to *C. anzutake* and *C. yunnanensis*. In addition, the macroscopic morphology of the fruitbody and molecular evidence in our study both strongly support that *C. tuberculosporus* is the same species as *C. anzutake* and *C. yunnanensis*. *Cantharellus yunnanensis* has priority, therefore, *C. tuberculosporus* and *C. anzutake* are later synonyms of *C. yunnanensis*.

Craterellus Pers., Mycol. Eur. (Erlanga) 2: 4. 1825. MycoBank MB 17398.

Synonym: *Pseudocraterellus* Corner, Beih. Sydowia 1: 268. 1958. MycoBank MB 18388.

Pterygellus Corner, Monogr. Cantharelloid Fungi: 166. 1966. MycoBank MB 18424.

Type species: *Craterellus cornucopioides* (L.) Pers., Mycol. Eur. (Erlanga) 2: 5. 1825. MycoBank MB 153130.

Notes: *Craterellus* was described in 1825, with *C. cornucopioides* as the type species (Persoon 1825). The genus is traditionally characterised by funnel-shaped basidiocarps with a hollow stipe that may also be much reduced (Petersen 1979a). The genus belongs to *Hydnaceae* according to Hibbett *et al.* (2014) which is also supported by our analysis based on dataset 4 (this study provides four markers for genus *Craterellus*: nLSU, ITS, *RPB2* and *TEF1*) (Fig. 1). *Craterellus* with the sister genus *Cantharellus* form a fully supported lineage which is closely related to the genera *Hydnum* and *Sistotrema*. *Pseudocraterellus* and *Pterygellus* Corner, two other genera in *Hydnaceae*, have been recognised as synonyms of *Craterellus.* Although in the tree (Fig. 3) three samples of *Pseudocraterellus* have been appropriately embeded in *Craterellus*, the validity of the recombined species and research on typification in the two genera are needed to confirm their status (Feibelman *et al.* 1997, Yomyart *et al.* 2012, Henkel *et al.* 2014, Hembrom *et al.* 2017). Approximately 140 taxa names are recorded for *Craterellus*, and up to 70 species are currently accepted (http://www.indexfungorum.org). The species in the genus often possess an ectomycorrhizal nutritional mode and are distributed worldwide. Most of the known species are edible and show diversity in colour (Dahlman *et al.* 2000, Dunham *et al.* 2003, Porter *et al.* 2008, Wright *et al.* 2009, Matheny *et al.* 2010, Wilson *et al.* 2012, Osmundson *et al.* 2013, Henkel *et al.* 2014, Raja *et al.* 2017, Bijeesh *et al.* 2018, Zhong *et al.* 2018). Up to now, there are only four species described from China (Berkeley & Curtis 1860, Zhong *et al.* 2018, Zhang *et al.* 2020, Cao *et al.* 2021).

Although the molecular evidence has been widely used in taxonomy of *Craterellus* since Dahlman *et al.* (2000), most studies do a phylogenetic analysis using only nLSU or ITS sequences but our study is based on the combined nLSU and ITS dataset (dataset 2). There are six distinct clades with high support have been recognised in the phylogenetic tree (Fig. 3). The species in the same clade often share several similar morphological characteristics, thus we propose them as six subgenera in the genus *Craterellus*.

Craterellus **subg.** ***Cariosi*** T. Cao & H. S. Yuan, ***subgen. nov.*** MycoBank MB 839396; Fig. 3

Etymology: Cariosi (Lat.), refers to the habit of fruiting on decayed wood.

Type species: *Craterellus pleurotoides* (T.W. Henkel, Aime & S.L. Mill.) A.W. Wilson, Mycologia 104: 1475. 2012. MycoBank MB 510239.

Notes: The subgenus consists of two South American species, *Craterellus pleurotoides* and *C. olivaceoluteus.* Although *Craterellus* is an ECM genus, the two species in subgen. *Cariosi*, *C. pleurotoides* and *C. olivaceoluteus* both fruit on very decayed wood and they also share the characteristics of small-sized basidiocarps, smooth hymenophore and presence of clamps (Henkel *et al.* 2006, 2014).

Craterellus **subg.** ***Craterellus*** MycoBank MB 839401; Fig. 3

Etymology: Craterellus (lat.), refers to the subgenus in which the type species of the genus is located.

Type species: *Craterellus cornucopioides* (L.) Pers., Mycol. Eur. (Erlanga) 2: 5. 1825. MycoBank MB 153130.

Notes: This subgenus includes the genus type *Craterellus cornucopioides* as well as five other ‘black trumpet’ species *viz*., *C. badiogriseus*, *C. caeruleofuscus*, *C. croceialbus*, *C. macrosporus* and *C. squamatus*, and they all have tuberiform to infundibuliform blackish brown basidiocarps. However, the yellow individuals (*e.g.*, *C. konradii* Bourdot & Maire) rule out blackish brown basidiocarps as an iconic feature of this group. The species in clade *Craterellus* often have a fully perforated pileus with smooth or wrinked hymenophore and lack distinct stipes. Although lacking molecular evidence, we suspect other species in the *C. cornucopioides* complex (*e.g., C. cornucopioides* var. *cornucopioides* (L.) Pers., *C. cornucopioides* var. *crispus* Sacc., *C. cornucopioides* var. *flavicans* Sacc., *C. cornucopioides* var. *mediosporus* Corner, *C. cornucopioides* var. *parvisporus* Heinem., *C. cornucopioides* var. *roseus* R. Heim, *C. philippinensis* Bres. and *C. verrucosus* Massee) also belong to subgenus *Craterellus*. *Craterellus cornucopioides*, *C. fallax*, *C. macrosporus* and *C. squamatus* form a well-supported subclade in Clade III and they share the large basidiospore size (up to 14 µm long) (Smith 1968, Gulden & Høiland 1989, Matheny *et al.* 2010).

Craterellus **subg.** ***Imperforati*** T. Cao & H. S. Yuan, ***subgen. nov.*** MycoBank MB 839397; Fig. 3

Etymology: *Imperforati* (Lat.), refers to the non-perforated pileus.

Type species: *Craterellus carolinensis* R.H. Petersen, Persoonia 5(2): 217. 1968. MycoBank MB 329222.

Notes: This subgenus is comprised of our new species *Craterellus badiogriseus* and eight other species *viz*., *C. albidus*, *C. albostrigosus*, *C. carolinensis*, *C. hesleri*, *C. indicus*, *C. inusitatus*, *C. parvogriseus*, *C. shoreae* and *Pseudocraterellus sinuosus* (Fig. 3). They often have variably coloured pilei but share the small basidiocarps (less than 40 mm wide and high), non-perforated pilei, smooth or slightly wrinked hymenophore, broadly ellipsoid basidiospores and absence of clamps (Reid 1962, Petersen 1969, Petersen 1975, Deepika *et al.* 2012, Henkel *et al.* 2014, Das *et al.* 2017, Hembrom *et al.* 2017, Bijeesh *et al.* 2018, Zhang *et al.* 2020).

Craterellus **subg.** ***Lamelles*** T. Cao & H. S. Yuan, ***subgen. nov.*** MycoBank MB 839398; Fig. 3

Etymology: *Lamelles* (Lat.), refers to the hymenophore with folds or well-developed false gills.

Type species: *Craterellus cinereus* R.H. Petersen, Mycol. Eur. (Erlanga) 2: 6. 1825. MycoBank MB 357303.

Notes: There are five species in subgenus *Lamelles viz*., *Craterellus cinereus*, *C. ignicolor*, *C. lutescens*, *C. melanoxeros* and *C. tubaeformis*. They often have medium to large basidiocarps, perforated or occasionally perforated pilei and presence of clamps. Most species in this clade have a hymenophore with

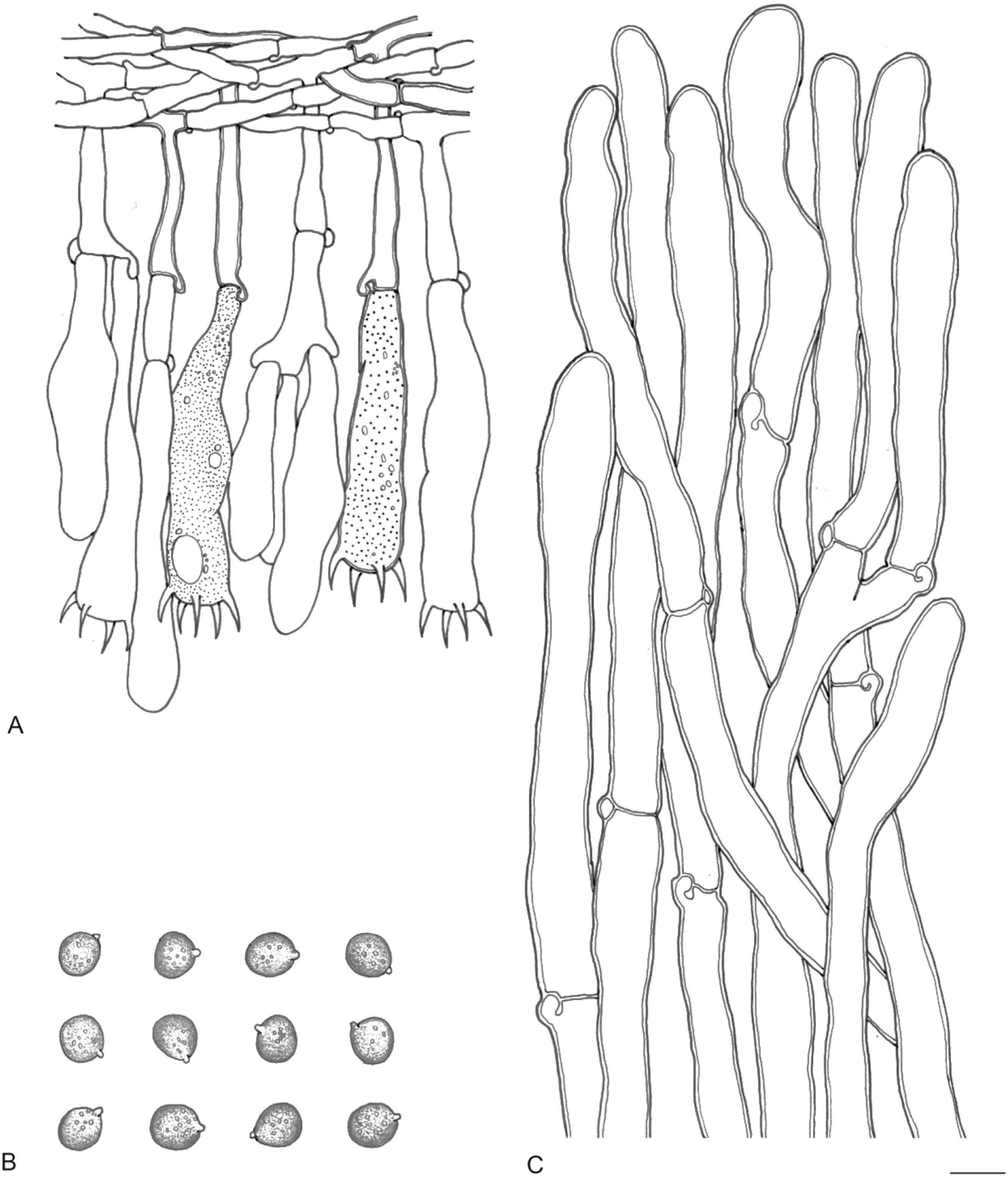

Fig. 20. Microscopic structures of *Hydnum sphaericum* (IFP 019470). **A.** Hymenium and subhymenium. **B.** Basidiospores. **C.** Pileipellis. Scale bar = 10 µm.

folds or well-developed false gills, but *C. lutescens* has a smooth hymenophore (Dahlman *et al.* 2000, Redhead *et al.* 2002, Contu *et al.* 2009).

Craterellus* subg. *Longibasidiosi T. Cao & H. S. Yuan, ***subgen. nov.*** MycoBank MB 839399; Fig. 3

Etymology: Longibasidiosi (Lat.), refers to the long basidia.

Type species: *Craterellus excelsus* T.W. Henkel & Aime, Mycotaxon 107: 202. 2009. MycoBank MB 510899.

Notes: There are two species in this subgenus characterised by medium to large basidiocarps (up to 65 mm wide in *Craterellus cinereofimbriatus* and 150 mm in *C. excelsus*), greyish brown and often perforated pilei, smooth hymenophore, long basidia (up to 100 µm long), broadly ellipsoid basidiospores and absence of clamps. Besides, both species grow on soil under *Dicymbe corymbosa* (Henkel *et al.* 2009, 2014).

Craterellus* subg. *Ovoidei T. Cao & H. S. Yuan, ***subgen. nov.*** MycoBank MB 839400; Fig. 3

Etymology: Ovoidei (Lat.), refers to the narrowly ellipsoid to ovoid basidiospores.

Type species: *Craterellus odoratus* (Schwein.) Fr., Epicr. Syst. Mycol. (Upsaliae): 532. 1838. MycoBank MB 190345.

Notes: *Craterellus luteus* and *C. odoratus* constitute sugenus *Ovoidei* and the perforated pilei, smooth hymenophore, narrowly ellipsoid to ovoid basidiospores (8.5–12.5 × 5.7–7.8 μm in *C. luteus* and 8.9–11.8 × 4.4–6.3 μm in *C. odoratus*) and absence of clamps are the common features. In addition, the two species both have brightly coloured basidiocarps (light yellow and bright orange) (Petersen 1979b, Zhong *et al.* 2018).

Craterellus badiogriseus T. Cao & H. S. Yuan, ***sp. nov.*** MycoBank MB 839410; Figs 1, 3, 5f, 6d, 10

Etymology: *Badiogriseus* (Lat.), refers to the brownish grey pileal surface.

Typus: **China**, Liaoning Province, Qingyuan County, on soil in angiosperm and *Pinus* sp. mixed forest, 7 Sep. 2019, H. S. Yuan, **holotype**, Yuan 14776 (IFP 019452).

Diagnosis: Differs from *Craterellus indicus* in having a brownish grey to black pileal surface, longer basidia (55–106 *vs.* 48–85 μm long) and broader terminal cells of pileipellis hyphae (5–10 *vs.* 2.5–8 μm long).

Description: *Basidiocarps* concrescent, infundibuliform, leathery when fresh, becoming brittle and light in weight upon drying. *Pilei* 10–15 mm wide, convex-expanded towards the margin, slightly or deeply depressed in the center but not perforated. *Pileal surface* dry, velutinate, brownish grey (8F2) to black when moist, drying greyish brown (7D3–7F3). *Pileal margin* thin, slightly involute or irregularly involute, orange-grey (5B2), lighter than pileal surface. *Pileal context* 0.3–0.5 mm thick, orange-grey to brownish orange (5B2–5C3). *Hymenophore* decurrent, smooth, brownish grey to grey (4C1–4C2) when moist drying yellowish grey to orange-grey (4B2–5B2). *Stipes* 10–15 mm long, 3–5 mm wide, subcylindrical, hollow; surface glabrous, concolorous with hymenophore; stipe base equal or slightly enlarged and rarely covered with basal mycelium. *Odour* fruity.

Basidiospores broadly ellipsoid, (7.5–)8.0–10.5(–11.0) × (6.5–)6.8–7.5(–8.0) μm, L_m = 9.35 μm, W_m = 7.33 μm, Q = 1.25–1.28 (n = 60/2), smooth, thin-walled, IKI–, hyaline, some with granular contents, inamyloid; hilar appendix 0.3–0.8 μm long. *Basidia* subcylindric, subclavate to clavate, 55–106 × 8–12 μm, sometimes with large guttules or finely granulose contents; sterigmata 2–4, up to 10 μm long, 2–5 μm wide at base, slightly curving. *Basidioles* numerous, subcylindrical to subclavate, smaller than basidia, 15–95 × 5–10 μm. *Subhymenium trama* filamentous, hyphae 3–5 μm wide, thick-walled, olive yellow in KOH; *pileal trama* hyphae 3–6 μm wide, thick-walled, secondary septation absent. *Cystidia* absent. *Pileipellis* composed of cylindrical hyphae, 5–15 μm wide, thick-walled, interwoven to subparallel, rarely branched; terminal elements rounded at apex, cells 20–65 × 6–15 μm. *Clamp connections* absent.

Material examined: **China**, Liaoning Province, Qingyuan County, on soil in angiosperm and *Pinus* sp. mixed forest, H. S. Yuan, 7 Sep. 2019, paratype, Yuan 14779 (IFP 019453).

Notes: The new species, *Craterellus badiogriseu*s, was discovered from a temperate forest in northeast China. In the phylogenetic tree, *Craterellus badiogriseus* and three samples of *Pseudocraterellus* Corner form a lineage with strong support (100 % ML and 0.99 BPP). Although *Pseudocraterellus* was regarded as a later synonym of *Craterellus* by Feibelman *et al.* (1997), the molecular and morphological evidence of the type material in the genus are unconvincing. *P. sinuosus* is similar to *C. badiogriseus* in having dark greyish brown and non-perforated pileus, a smooth hymenophore and absence of clamps. However, it can be distinctly differentiated from the new species in having a larger pileus (12–25 mm wide), longer stipes (up to 37 mm long) and presence of secondary hyphal septation (Henkel *et al.* 2014).

Craterellus badiogriseus and *Pseudocraterellus* group with two other Asiatic species *C. indicus* and *C. parvogriseus* and form a large clade with support, 87 % in ML and 0.95 BPP. *Craterellus badiogriseus* resembles *C. indicus* in having a non-perforated pileus, smooth hymenophore, broadly ellipsoid basidiospores, 2–4 sterigmata and absence of clamps, but the latter differs from the new species by the light brownish pileal surface, shorter basidia (48–85 μm long) and slenderer terminal cells (2.5–8 μm wide) of the pileipellis hyphae. *Craterellus parvogriseus* is related to *C. badiogriseus* in having a brownish grey pileal sueface, broadly ellipsoid basidiospores and absence of clamps, however, the former can be distinguished from *C. badiogriseus* by the irregularly folded hymenophore, longer stipes (up to 27 mm long), 2–6 sterigmata and smaller basidia (47–78 × 8–9 μm) (Das *et al.* 2017).

Craterellus croceialbus T. Cao & H. S. Yuan, ***sp. nov.*** MycoBank MB 839411; Figs 1, 3, 5G, 6E, 11

Etymology: *Croceialbus* (Lat.), refers to the orange-white pileal margin.

Typus: **China**, Liaoning Province, Xinbin County, Gangshan Mt., on soil in angiosperm and *Pinus* sp. mixed forest, 26 Aug. 2020, H. S. Yuan, Yuan 14623 (**holotype** IFP 019454).

Diagnosis: Differs from *Craterellus cornucopioides* in having smaller basidiocarps (up to 2 cm *vs.* 15 cm wide), 2–4 sterigmata and smaller basidiospores (up to 12.5 μm *vs.* 14 μm long).

Description: *Basidiocarps* solitary to concrescent, infundibuliform, leathery when fresh, becoming brittle upon drying. *Pilei* 10–20 mm wide, convex-expanded towards the margin, broadly and deeply depressed in the center and perforation continuous with hollow stipe. *Pileal surface* dry, glabrous to velutinate, smooth, brownish grey to greyish brown (6D2–6D3) when moist, drying greyish brown (6F3–7E3). *Pileal margin* thin, slightly revolute and undulate, orange-white (5A2), distinctly lighter than pileal surface. *Pileal context* 0.3–1 mm thick, orange-white (5A2). *Hymenophore* decurrent, almost perfectly smooth to having a few faint ridges or folds, moist pale grey to grey (1B1–3B1), drying yellowish grey to orange-grey (4B2–5B2). *Stipes* indistinct, confluent with pileus, 20–35 mm long and 3–8 mm wide, subconic, hollow; surface glabrous, concolorous with the hymenophore; stipe base equal or slightly enlarged and rarely covered with basal mycelium. *Odour* fruity.

Basidiospores ellipsoid, (9.0–)10.0–12.0(–12.5) × (6.5–)6.8–8.0(–8.2) μm, L_m = 10.31 μm, W_m = 7.33 μm,

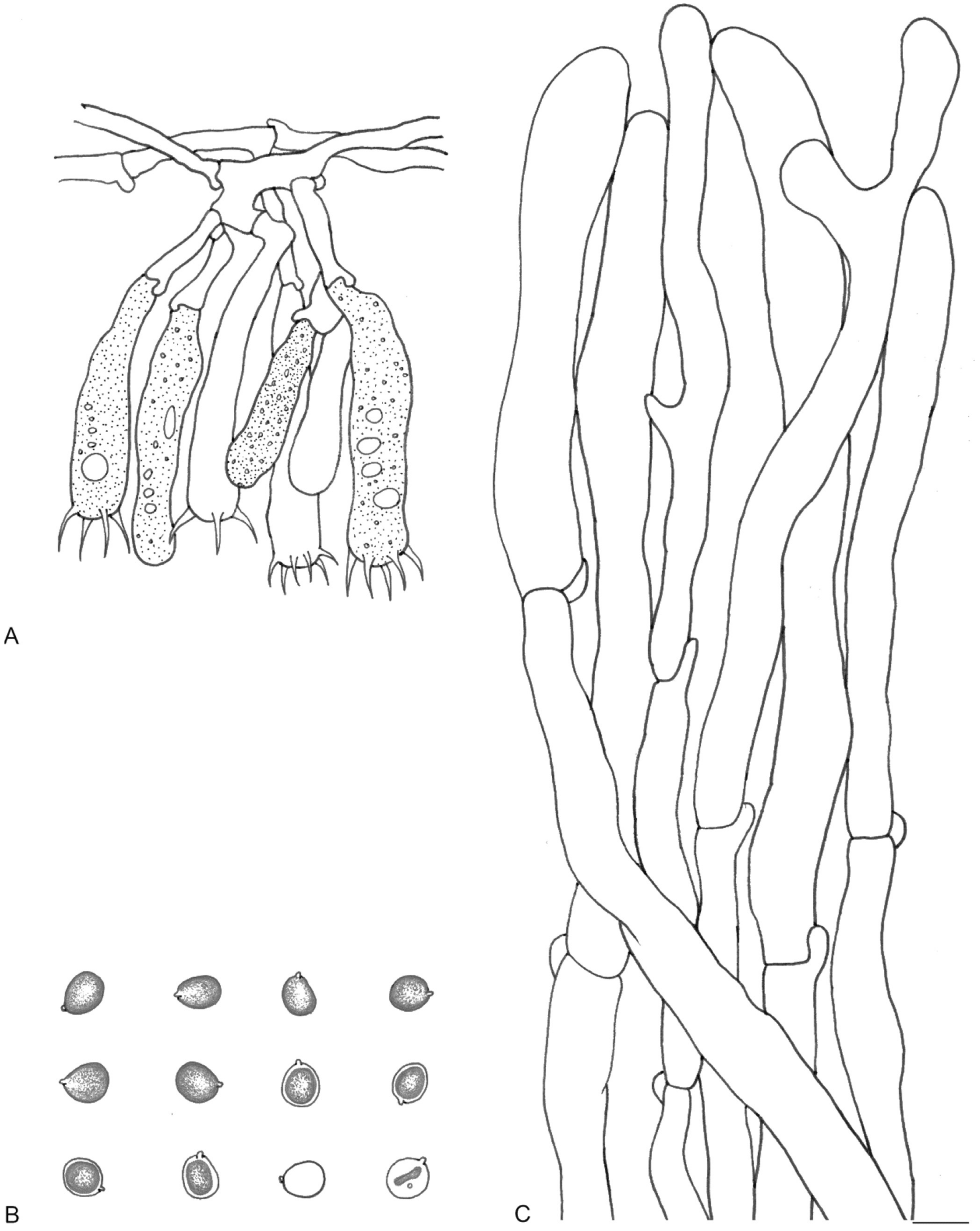

Fig. 21. Microscopic structures of *Hydnum tangerinum* (IFP 019473). **A.** Hymenium and subhymenium. **B.** Basidiospores. **C.** Pileipellis. Scale bar = 10 µm.

Q = 1.41–1.44 (n = 60/2), smooth, thin-walled, IKI–, hyaline, some with granular contents, inamyloid; hilar appendix 0.5 µm long. *Basidia* subcylindric, subclavate to clavate, 60–85 × 10–12 µm, sometimes with large guttules or finely granulose contents; sterigmata 2–4, up to 10 µm long, 1–4 µm wide at base, somewhat curving. *Basidioles* numerous, subcylindrical to subclavate, smaller than basidia, 16–75 × 5–10 µm. *Subhymenium trama* filamentous, hyphae 3–5 µm wide, thick-walled, brownish yellow in KOH; *pileal trama* hyphae 3–5.5 µm wide, thick-walled, secondary septation absent. *Cystidia* absent. *Pileipellis* composed of cylindrical hyphae, 9–20 µm wide, thin- to slightly thick-walled, subparallel, rarely

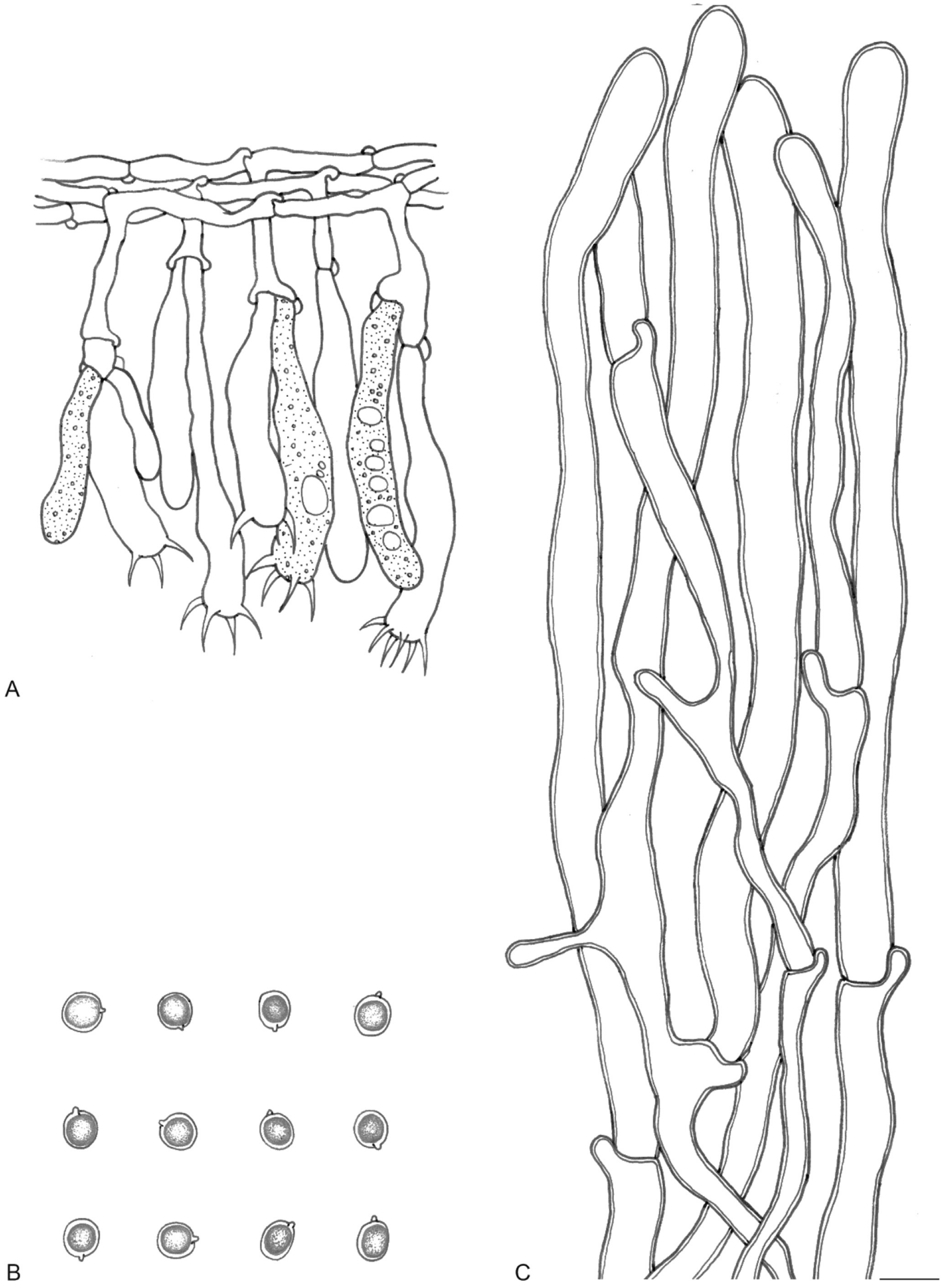

Fig. 22. Microscopic structures of *Hydnum tenuistipitum* (IFP 019476). **A.** Hymenium and subhymenium. **B.** Basidiospores. **C.** Pileipellis. Scale bar = 10 µm.

branched; terminal elements rounded at apex, cells 35–75 × 10–23 µm. *Clamp connections* absent.

Material examined: **China**, Liaoning Province, Fushun City, Xinbin County, Gangshan Mt., on soil in angiosperm and *Pinus* sp. mixed forest, 26 Aug. 2020, H. S. Yuan, paratype, Yuan 14647 (IFP 019455).

Notes: *Craterellus croceialbus* resembles *C. cornucopioides* in the brownish grey pileus, hollow stipes, ellipsoid basidiospores and absence of clamps, but the latter species differs from *C. croceialbus* in having larger basidiocarps (pileus up to 15 cm wide), basidia with 2 sterigmata and larger basidiospores (up to 14 µm long) (Smith 1968, Smith *et al.* 1979, Gulden & Høiland 1989, Hansen & Knudsen 1997, Matheny *et al.* 2010, Kumari *et al.* 2011, Tibuhwa 2018).

Craterellus macrosporus T. Cao & H. S. Yuan, ***sp. nov.*** MycoBank MB 839412; Figs 3, 5H, 6F, 12

Etymology: *Macrosporus* (Lat.), refers to the large basidiospores.

Typus: **China**, Liaoning Province, Qingyuan County, on soil in angiosperm and *Pinus* sp. mixed forest, 7 Sep. 2019, T. Cao, **holotype**, Yuan 14782 (IFP 019456).

Diagnosis: Differs from *Craterellus cornucopioides* in having smaller basidiocarps (less than 35 mm wide and 60 mm high), velutinate and smooth pileal surface and broader basidiospores (up to 11.5 µm wide).

Description: *Basidiocarps* solitary, infundibuliform, leathery when fresh, becoming brittle and light in weight upon drying. *Pilei* 30–35 mm wide, convex-expanded towards the margin, broadly and deeply depressed in the center and perforation continuous with hollow stipe. *Pileal surface* dry, glabrous to velutinate, smooth, brownish grey to greyish brown (5C2–5D3) when moist, drying brown (6E4–6E5). *Pileal margin* thin, slightly revolute and undulate, brownish grey (7F2–8F2), deeper than pileal surface. *Pileal context* 1–2 mm thick, brownish grey to greyish brown (8E2–8E3). *Hymenophore* decurrent, almost perfectly smooth or forming a few faint ridges or folds, grey (3B1) when moist, drying greyish brown to brownish grey (6D3–7C2). *Stipes* indistinct, confluent with pilei, 55–60 mm long and 8–15 mm wide, subconic, slightly curved, hollow; surface glabrous, concolorous with the hymenophore; stipe base equal or slightly enlarged and rarely with basal mycelium. *Odour* fruity.

Basidiospores broadly ellipsoid, (12.5–)12.8–14.5(–15.0) × (8.8–)9.0–11.0(–11.5) µm, L_m = 13.46 µm, W_m = 10.27 µm, Q = 1.31–1.37 (n = 30/1), smooth, thin-walled, IKI–, hyaline, some with granular contents, inamyloid; hilar appendix 0.5 µm long. *Basidia* subcylindric, subclavate to clavate, 80–105 × 9–13.5 µm, sometimes with large guttules or finely granulose contents; sterigmata 2, up to 10 µm long, 3–5 µm wide at base, slightly curving. *Basidioles* numerous, subcylindrical to subclavate, smaller than basidia, 13–85 × 5–10 µm. *Subhymenium trama* filamentous, hyphae 3–5 µm wide, thick-walled, pale yellow in KOH; *pileal trama* hyphae 4–5 µm wide, thick-walled, secondary septation absent. *Cystidia* absent. *Pileipellis* composed of cylindrical hyphae, 10–23 µm wide, thin-walled, subparallel, rarely branched; terminal elements rounded at apex, cells 35–98 × 10–25 µm. *Clamp connections* absent.

Notes: *Craterellus macrosporus* resembles *C. cornucopioides* in the infundibuliform basidiocarps, dark brownish pileus with almost smooth hymenophore, hollow stipes, absence of clamps, and basidia with 2 sterigmata, but *C. cornucopioides* differs in having scaly pileal surfaces, larger basidiocarps (up to 15 cm wide), shorter basidia (less than 96 µm long) and narrower basidiospores (less than 9 µm wide) (Smith 1968, Smith *et al.* 1979, Gulden & Høiland 1989, Hansen & Knudsen 1997, Matheny *et al.* 2010, Kumari *et al.* 2011, Tibuhwa 2018). The large (up to 15 µm long) spores of *Craterellus macrosporus* are like those of *C. konradii*. The European *Craterellus konradii* has the habit of *C. cornucopioides* and may be a member of the *C. cornucopioides* complex. However, *Craterellus konradii* has yellowish basidiocarps (Gulden & Høiland 1989). *Craterellus cornucopioides* var. *parvisporus* Heinem. is similar to *C. macrosporus* in the blackish brown pileal surface but differs by the smaller basidiospores (6.8–8.5 × 4.3–6 µm) (Heinemann 1958). Another new species from a temperate forest in northeast China, *Craterellus croceialbus*, is similar to *C. macrosporus* in having greyish brown basidiocarps, smooth pileal surface, grey hymenophore and absence of clamps, but *C. macrosporus* differs from *C. croceialbus* in having a larger pileus (30–35 mm wide), longer and wider stipes (55–60 mm long and 8–15 mm wide), larger basidiospores (12.8–14.5 × 9–11 µm), and longer basidia (80–105 × 9–13.5 µm) with 2 sterigmata.

Craterellus squamatus T. Cao & H. S. Yuan, ***sp. nov.*** MycoBank MB 839413; Fig. 1, 3, 5I, 6G, 13

Etymology: *Squamatus* (Lat.), refers to the scaly pileus.

Typus: **China**, Liaoning Province, Kuandian County, Baishilazi Nature Reserve, ground in angiosperm forest, 8 Aug. 2020, H.S. Yuan, **holotype**, Yuan 14520 (IFP 019457).

Diagnosis: Differs from *Craterellus cornucopioides* in having smaller basidiocarps (pileus less than 13 mm wide and stipes less than 35 mm long), broader basidiospores (up to 10 µm long) and basidia with 2–4 sterigmata.

Description: *Basidiocarps* solitary to concrescent, tuberiform to infundibuliform, leathery when fresh, becoming brittle and light in weight upon drying. *Pilei* 5–15 mm wide, broadly and deeply depressed in the center and perforation continuous with hollow stipe. *Pileal surface* dry, glabrous, grey, light brown to dark brown (6B1/7D4/7F2) when moist, drying become dark brown (7F3–7F4); scabrous, often with darker brown raised scales. *Pileal margin* thin, slightly undulate, decurved or involute. *Pileal context* 1–3 mm thick, orange-white to orange-grey (5A2–5B2). *Hymenophore* decurrent, almost perfectly smooth or forming a few faint ridges or folds, orange-grey (5B1–6B2). *Stipes* indistinct, confluent with pilei, 15–35 mm long, 2–5 mm wide, subcylindrical, somewhat curved and irregular, hollow; surface glabrous, concolorous with the hymenophore; stipe base enlarged and covered with white basal mycelium. *Odour* fruity.

Basidiospores ellipsoid, (11.5–)12.0–13.8(–14.0) × (8.2–)8.5–9.5(–10.0) µm, L_m = 13.03 µm, W_m = 8.89 µm, Q = 1.46–1.51 (n = 60/2), smooth, thin-walled, IKI–, hyaline, some with granular contents, inamyloid; hilar appendix 0.5–0.8 µm long. *Basidia* subcylindric, subclavate to clavate, 35–62 × 5–7.5 µm, sometimes with large guttules or finely granulose contents; sterigmata 2–4, up to 5 µm long, 1.5–3 µm wide at base, slightly curving. *Basidioles* numerous, subcylindrical to subclavate, smaller than basidia, 13.5–45 × 3–6.2 µm. *Subhymenium trama* filamentous, hyphae 3–8 µm wide, thick-walled, olive yellow in KOH; *pileal trama* hyphae 4–8 µm wide, thick-walled, secondary septation absent. *Cystidia* absent. *Pileipellis* composed of cylindrical hyphae,

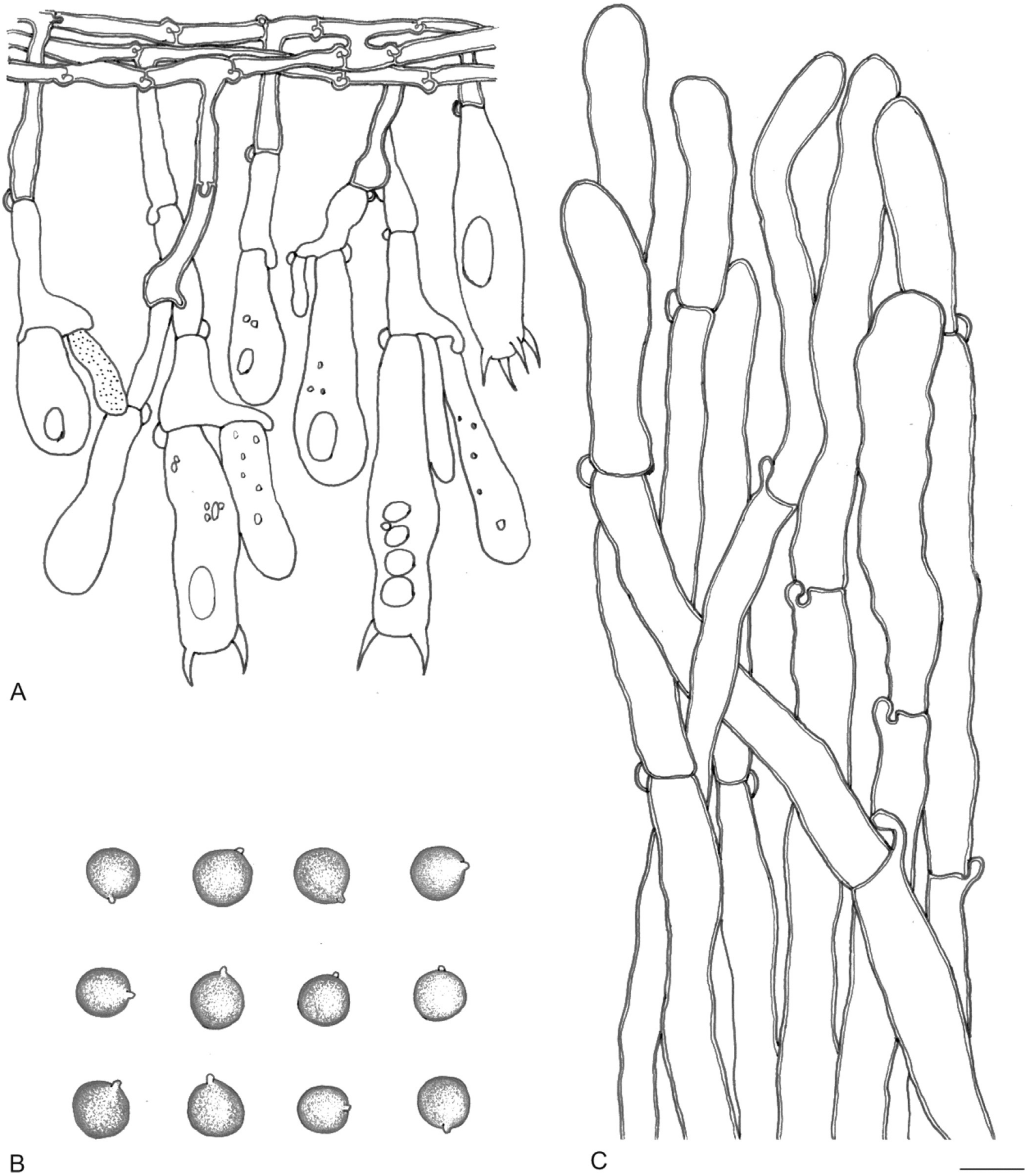

Fig. 23. Microscopic structures of *Hydnum ventricosum* (IFP 019478). **A.** Hymenium and subhymenium. **B.** Basidiospores. **C.** Pileipellis. Scale bar = 10 µm.

6–15 µm wide, thick-walled, interwoven to subparallel, frequently branched; terminal elements rounded at apex, cells 15–53.5 × 9–20 µm. *Clamp connections* absent.

Material examined: **China**, Liaoning Province, Kuandian County, Baishilazi Nature Reserve, on soil in angiosperm forest, 3 Sep. 2020, H. S. Yuan, paratype, Yuan 14721 (IFP 019458).

Notes: Morphologically, *Craterellus squamatus* is reminiscent of the *C. cornucopioides* complex clade (including *C. cornucopioides* and *C. fallax* A.H. Sm.) (Dahlman *et al.* 2000, Moncalvo *et al.* 2006) which is also confirmed by the molecular evidence. In the phylogenetic tree (Fig. 3), *C. squamatus* and *C. macrosporus* clustered together with the *C. cornucopioides* complex and formed a group with moderate support (77 % ML and 0.96 BPP). *Craterellus squamatus* is similar to the genus type species, *C. cornucopioides*, in having a dark-coloured pileus (except for the yellow individuals from Europe) (Dahlman *et al.* 2000), scaly pileal surface, almost perfectly smooth hymenophore, hollow stipes and absence of clamp connections. However, the latter species differs from *C. squamatus* by the larger basidiocarps (up to 15 cm wide), longer basidia (up to 96 μm long) and basidia with 2 sterigmata (Smith 1968, Smith *et al.* 1979, Gulden & Høiland 1989, Hansen & Knudsen 1997, Matheny *et al.* 2010, Kumari *et al.* 2011, Tibuhwa 2018). Additionally, there is the molecular similarity of ITS sequences between *C. squamatus* (Yuan 14520, holotype) and the two sequences of *C. cornucopioides* (KT693262 and UDB000053) with 95.43 % and 94.95 %, respectively. *Craterellus fallax* is regarded as a more recent synonym of *C. cornucopioides*. The morphological features of *C. fallax* are very similar to the latter, expect for the yellowish to orangy spore print of *C. fallax* (which in *C. cornucopioides* is white) and the presence of secondary septation (which in *C. cornucopioides* is absent) (Smith 1968, Petersen 1975, Bigelow 1978). However, phylogenetic analysis supports it as a species distinct from *C. cornucopioides* (Matheny *et al.* 2010). The presence of the secondary septation in *C. fallax* distinctly distinguishes it from *C. squamatus* and three new species of *Craterellus* in this study. Among the described varieties of *Craterellus cornucopioides*, several species also have black pilei, but the European *C. cornucopioides* var. *cornucopioides* (L.) Pers. can be distinguished by its regularly bi-sterigmate and long basidia (up to 100 μm long) (Corner 1966), the Malaysian *C. cornucopioides* var. *mediosporus* Corner differs by the 6-sterigmate basidia and blackish brown hymenophore (Corner 1966) and the Congolese *C. cornucopioides* var. *parvisporus* has smaller basidiospores (6.8–8.5 × 4.3–6 μm) than *C. squamatus* (Heinemann 1958).

Craterellus croceialbus, *C. squamatus*, *C. macrosporus*, and the *C. cornucopioides* complex clustered together and formed a large subclade with strong support (96 % ML and 0.95 BPP). *Craterellus croceialbus* is closely related to *C. squamatus* in having an almost perfectly smooth hymenophore, hollow stipes, basidia with 2–4 sterigmata, and absence of cystidia. However, *Craterellus croceialbus* can be distinctly differentiated from *C. squamatus* by the larger pilei (10–20 mm), velutinate and smooth pileal surface, smaller spores (10–12 × 6.8–8 μm), larger basidia (60–85 × 10–12 μm) and larger terminal cells (35–75 × 10–23 μm) of the pileipellis hyphae. *Craterellus macrosporus* and *C. squamatus* form a well-supported lineage (Fig. 3). The similarity of the ITS sequences between *C. squamatus* and *C. macrosporus* is 97.70 % and they share several morphological characteristics including the infundibuliform basidiocarps, almost perfectly smooth hymenophore, absence of cystidia and clamp connections. But *C. macrosporus* differs *C. squamatus* by having a larger plieus (30–35 mm wide), longer and wider stipes (55–60 mm long and 8–15 mm wide), smooth pileal surface, larger basidia (80–105 × 9–13.5 μm) with 2 sterigmata, broader basidiospores (Q = 1.31–1.37) and larger terminal cells (35–98 × 10–25 μm) of pileipellis hyphae. *Craterellus macrosporus* is a separate species distinctly different from *C. squamatus* based on the phylogenetic and morphological analyses.

Hydnum L., Sp. pl. 2: 1178. 1753. MycoBank MB 17797.

Synonym: Malacodon Bataille, Bull. Soc. Mycol. Fr. 39: 203. 1923. MycoBank MB 22227.

Type species: *Hydnum repandum* L., Sp. Pl. 2: 1178. 1753. MycoBank MB 225014.

Notes: *Hydnum* typified by *H. repandum* and traditionally characterised by stipitate and pileate basidiocarps with aculeate hymenophore, stichic basidia, fleshy and azoned monomitic context, smooth and subglobose to obovoid-elliptic basidiospores and usually the absence of cystidia (Vizzini *et al.* 2013, Niskanen *et al.* 2018, Swenie *et al.* 2018). *Hydnum* form ECM associations with a variety of host species including members of *Betulaceae*, *Dipterocarpaceae*, *Fagales*, *Magnoliaceae*, *Malvaceae*, *Myrtaceae*, *Pinaceae*, *Salicaceae* and *Ulmaceae* (McNabb 1971, Agerer *et al.* 1996, Lee *et al.* 2002, Feng *et al.* 2016, Niskanen *et al.* 2018, Swenie *et al.* 2018).

The genus was placed in *Cantharellales* by Kreisel (1969) based on its stichic basidia and this was confirmed by several subsequent molecular analyses (Pine *et al.* 1999, Moncalvo *et al.* 2006, Matheny *et al.* 2007, Hibbett *et al.* 2014). As the type genus of *Hydnaceae*, *Hydnum* is the sister clade of *Sistotrema confluens-subconfluens* lingeage and closely related to *Cantharellus* as well as *Craterellus* in the tree (Fig. 1) which is similar to a previous study (Hibbett *et al.* 2014). Four subgenera, four sections and several subsections have been recognised within the genus (Niskanen *et al.* 2018), the four subgenera, section *Hydnum,* section *Olympica*, and five subsections get strong support in the tree (Fig. 4) which is similar to Niskanen *et al.* (2018).

There are up to 900 taxa bearing the name *Hydnum* (http://www.indexfungorum.org), however, only ca. 40 species from Europe, North America and Asia have been described using modern molecular phylogenetic analyses and morphological features (Grebenc *et al.* 2009, Olariaga *et al.* 2012, Vizzini *et al.* 2013, Yanaga *et al.* 2015, Buyck *et al.* 2017, Niskanen *et al.* 2018, Swenie *et al.* 2018, Wang *et al.* 2018). Feng *et al.* (2016) estimated the global survey of diversity in *Hydnum* and recognised at least 31 phylogenetic species from Asia, Central America (Honduras), Europe, North America, Oceania, and South America (Venezuela) according to molecular evidence, but the samples in Africa are poorly investigated. Around less than half of the global diversity of *Hydnum* has been discovered and the diversity and distribution of *Hydnum* should be further explored (Niskanen *et al.* 2018).

Until 2016, the few species of *Hydnum* in China that been recorded were *H. repandum, H. repandum* var. *album* and *H. rufescens* (Le *et al.* 1993, Bi *et al.* 1994, Zang *et al.* 1996). Feng *et al.* (2016) recognised at least 19 taxa from China based on molecular phylogeny evidence, among which around 6 taxa fell in the named-clade and 13 lineages/taxa are non-named and seem to be new taxa. Several samples were described as *H. berkeleyanum*, *H. jussii* and *H. cremeoalbum* (Niskanen *et al.* 2018, Wang *et al.* 2018). We added 16 samples from Feng *et al.* (2016) in our study and the phylogenetic tree of the genus *Hydnum* shows the current status of *Hydnum* species in China.

Hydnum* subg. *Brevispina T. Cao & H. S. Yuan, ***subgen. nov.*** MycoBank MB 839402; Fig. 4

Etymology: *Brevispina* (Lat.), following the name of the type species.

Type species: *Hydnum brevispinum* T. Cao & H. S. Yuan. MycoBank MB 839417.

Notes: Two species, *Hydnum brevispinum* and *H. tenuistipitum*, comprise the subgenus and they share the following features: basidiocarps small to medium, solitary or concrescent, fleshy when fresh; pilei rounded, pileal surface velutinate, smooth, azonate to subzonate, pure whitish to yellowish white or orange-white, pileal margin often entire and slightly decurved; spines non-decurrent to subdecurrent; basidia with 2–6 sterigmata; basidiospores often subglobose to broadly ellipsoid, cystidia absent, terminal cells of pileipellis hyphae thick-walled, stipitipellis hyphae slightly thick-walled and clamps present. *Hydnum* subgenus *Alba* resembles subg. *Brevispinum* in having whitish basidiocarps, non-decurrent to subdecurrent spines but differs by having broader basidiospores (Q avg. = 1.00–1.10). Besides, subg. *Alba* contains some species with large basidiocarps (*e.g., H. albomagnum*) while subg. *Brevispinum* only has (very) small to medium ones. Three other subgenera, subg. *Hydnum*, subg. *Pallida* and subg. *Rufescentia* can be differentiated from subg. *Brevispinum* by the mostly yellow or orange-coloured pileus (except for a few whitish ones).

Hydnum brevispinum T. Cao & H. S. Yuan, ***sp. nov.*** MycoBank MB 839417; Figs 4, 5J, 6H, 14

Etymology: *Brevispinum* (Lat.), refers to the short spines.

Typus: **China**, Hunan Province, Sangzhi County, Badagong Nature Reserve, on soil in angiosperm forest, 23 Sep. 2020, T. Cao, **holotype**, Wei 10214 (IFP 019464).

Diagnosis: Differs from *Hydnum minum* in having shorter spines (0.2–0.8 mm 0.2–0.8 mm *vs.* up to 1.7 mm long), longer stipes (25 *vs.* 15 mm long), broader pileipellis hyphae (5–12 *vs.* 4–6 µm), larger basidia (20–40 × 3–10 µm 20–30 × 4–7 µm) with 4–6 sterigmata.

Description: *Basidiocarps* solitary or concrescent, fleshy when fresh, becoming brittle and light in weight upon drying. *Pilei* 10–15 mm wide, round, convex to plano-convex, shallowly depressed in the center. *Pileal surface* dry, velutinate, smooth, azonate to subzonate, pure white to yellowish white (4A2), drying yellowish white to greyish orange (4A2/5B4). *Pileal margin* thin, entire and slightly decurved, concolorous with the pileal surface. *Pileal context* 1–3 mm thick, pure white. *Hymenophore* hydnoid, spines non-decurrent to subdecurrent, crowded, evenly distributed; surface pure white when fresh, yellowish white (4A2) when dry; fibrous, subulate, acute, straight to somewhat flexuous, solitary, 0.2–0.8 mm long, shortest near the pileus margin, 5–9 per mm, brittle when dry. *Stipe* central or eccentric, up to 25 mm long, 2–4 mm wide, subcylindrical, solid; surface glabrous, white; stipe base enlarged and covered with a small amount of white basal mycelium. *Odour* mild.

Basidiospores broadly ellipsoid, (4.5–)5–5.8(–6) × (3.5–)3.8–4.8(–5) µm, L_m = 5.28 µm, W_m = 4.16 µm, Q = 1.27–1.31 (n = 60/2), smooth, thin-walled, IKI–, hyaline, some with granular contents; hilar appendix 1 µm long. *Basidia* fusiform to subcylindric, ventricose, 20–40 × 3–10 µm, sometimes with large guttules or finely granulose contents; sterigmata 4–6, up to 7 µm long, 1.5 µm wide at base, somewhat curving. *Basidioles* numerous, ventricose, subcylindrical or subclavate, smaller than basidia, 10–35 × 3–7.5 µm. *Cystidia* absent. *Subhymenium trama* filamentous, hyphae 2–4 µm wide, thin- to slightly thick-walled, olive in KOH. *Hyphae of spines* 2–3 µm, thin-walled, apex cylindrical. *Pileipellis* composed of cylindrical hyphae, thick-walled, subparallel, occasionally branched; terminal elements rounded at apex, cells 80–145 × 5–12 µm. *Stipitipellis* composed of subcylindrical hyphae, slightly thick-walled, interwoven, 5–16.5 µm wide, terminal elements rounded at apex. *Clamp connections* present.

Material examined: **China**, Hunan Province, Sangzhi County, Badagong Nature Reserve, on soil in angiosperm forest, 23 Sep. 2020, T. Cao, paratype, Wei 10258 (IFP 019465).

Notes: There are several almost pure white species in genus *Hydnum* such as *H. minum*, *H. treui*, *H. zongolicense* and the species in subgenus *Alba* (*e.g., H. cremeoalbum*, *H. subcremeoalbum* and *H. albomagnum*). *Hydnum brevispinum* is also a white species with small basidiocarps which are reminiscent of *H. minum*, however, *H. minum* differs from *H. brevispinum* in having longer spines (up to 1.7 mm long), shorter stipes (less than 1.5 cm long), slenderer pileipellis hyphae (4–6 µm wide), and smaller basidia (20–30 × 4–7 µm) with 5–8 sterigmata (Yanaga *et al.* 2015); *Hydnum albomagnum* can be differentiated from *H. brevispinum* by larger basidiocarps (pilei 60–110 mm wide), longer spines (1–6 mm long), ellipsoid basidiospores (Q up to 2.17) and slenderer pileipellis hyphae (2.5–5 µm wide) (Swenie *et al.* 2018); *Hydnum brevispinum* differs from *H. zongolicense* by a smaller pileus (10–15 *vs.* 17–35 mm wide), shorter spines (0.2–0.8 *vs.* 0.5–2 mm long), broadly ellipsoid and smaller basidiospores (subglobose and 5–5.8 × 3.8–4.8 µm in *H. zongolicense*) and basidia with 4–6 sterigmata (2–5 in *H. zongolicense*) (Niskanen *et al.* 2018). The small whitish basidiocarps and small basidiospores of *H. albidum* are similar to *H. brevispinum*, but the former species differs from the latter by having the bumpy or mottled pileal surface, longer spines (1–6 mm long) and presence of 7-spored basidia (Niskanen *et al.* 2018), besides, the similarity of the ITS sequences between the type materials (NR_164025 of *H. albidum* and MW980578 of *H. brevispinum*) of two species is only 92.79 %.

Hydnum flabellatum T. Cao & H. S. Yuan, ***sp. nov.*** MycoBank MB 839414; Figs 4, 5K–L, 6I, 15

Etymology: *Flabellatum* (Lat.), refers to the flabelliform to semicircular pileus.

Typus: **China**, Liaoning Province, Xinbin County, Qingsongling Mt., on soil in angiosperm and *Pinus* sp. mixed forest, 5 Sep. 2020, H. S. Yuan, **holotype**, Yuan 14708 (IFP 019459).

Diagnosis: Differs from *Hydnum subtilior* in the smaller pilei (30–45 mm *vs.* up to 90 mm wide), shorter spines (0.6–2 mm *vs.* up to 8 mm long), longer basidia (35–60 µm *vs.* less than 44 µm) and broader pileipellis hyphae (5–16 *vs.* 3–7 µm).

Description: *Basidiocarps* solitary, fleshy and leathery when fresh, becoming soft corky and light in weight upon drying. *Pilei* 30–45 mm wide, flabelliform to semicircular, convex. *Pileal surface* dry, glabrous, irregularly bumpy or mottled, subzonate towards margin, yellowish white, pale yellow to greyish yellow (4A2/4A3/4B3), drying pale orange (5A3); scabrous, often with some brownish orange (6C7/6C8) scales. *Pileal margin* thin, entire and straight, concolorous with the pileal surface. *Pileal context* 1–5 mm thick, yellowish white (4A2). *Hymenophore* hydnoid, spines non-decurrent or subdecurrent, crowded, evenly distributed; surface orange-white (5A2) when fresh, greyish orange (5B5) when dry; subulate, acute, straight to somewhat flexuous, solitary, 0.6–2 mm long, shortest near the pileus margin, 3–5 per mm, brittle when dry. *Stipes* eccentric, up to 50 mm long, 8–13 mm wide, subcylindrical, hollow; surface glabrous, white, staining orange-white (5A2) when handled; stipe base enlarged and covered with a small amount of white basal mycelium. *Odour* mild.

Basidiospores broadly ellipsoid, (7.8–)8.5–9.5(–10) × (6–)6.5–7.8(–8) µm, L_m = 9.07 µm, W_m = 7.04 µm, Q = 1.26–1.29 (n = 30/1), smooth, thin-walled, IKI–, hyaline, some with granular contents; hilar appendix 1 µm long. *Basidia* subcylindric, subclavate to clavate, 35–60 × 6–11 µm, sterigmata 2–5, up to 10 µm long, 1–1.5 µm wide at base, slightly curving. *Basidioles* numerous, subcylindrical or subclavate, smaller than basidia, 12–45 × 3.5–9 µm. *Cystidia* absent. *Subhymenium trama* filamentous, hyphae 2–5 µm wide, thin-walled, greenish yellow in KOH. *Hyphae of spines* 1.5–3 µm, thin-walled, apex cylindrical. *Pileipellis* composed of cylindrical hyphae, thin- to slightly thick-walled, subparallel, rarely branched; terminal elements rounded at apex, cells 50–185 × 5–16 µm. *Stipitipellis* composed of subcylindrical hyphae, thick-walled, interwoven, 5–12 µm wide, terminal elements rounded at apex. *Clamp connections* present.

Notes: *Hydnum flabellatum* was collected from a temperate forest in northeast China. It is embedded in the subgenus *Pallida* and shares the small to medium basidiocarps, cream-coloured to ochraceous with very pale orange pileus, stipes bruising brownish when handled, non-decurrent or subdecurrent spines and broadly ellipsoid basidiospores with other species of this subgenus (Niskanen *et al.* 2018). However, *Hydnum flabellatum* can be differentiated from *H. iberidum* in having larger basidiospores (avg. = 9.07 × 7.04 *vs.* 8.2 × 6.4 µm) and basidia with 2–5 sterigmata (Niskanen *et al.* 2018). *Hydnum subtilior* differs from *H. flabellatum* by having a larger pileus (up to 90 mm wide), longer spines (up to 8 mm long), shorter basidia (less than 44 µm) and slenderer pileipellis hyphae (3–7 µm wide) (Swenie *et al.* 2018). The subgenus type species, Europe *Hydnum vesterholtii* differs from *H. flabellatum* in having one-spored basidia (sometimes), thin-walled pileipellis hyphae with yellowish content and thin-walled and slenderer stipitipellis hyphae (4–8 µm wide) (Olariaga *et al.* 2012).

Hydnum flavidocanum T. Cao & H. S. Yuan, ***sp. nov.*** MycoBank MB 839415; Figs 1, 4, 5M–N, 6J, 16

Etymology: *Flavidocanum* (Lat.), refers to the yellowish grey tint at the centre of the pileal surface.

Typus: **China**, Yunnan Province, Shizong County, Junzishan Mt., on soil in angiosperm and *Pinus* sp. mixed forest, 8 Aug. 2019, J. R. Yu & T. Cao, **holotype**, Yuan 13903a (IFP 019460).

Diagnosis: Differs from *Hydnum minum* in having a subzonate pileal surface, larger basidia (33.5–55 × 5–10 *vs.* 20–30 × 4–7 µm) with 2–5 sterigmata, larger basidiospores (7.2–8.8 × 5.5–6.5 *vs.* 4.5–5.5 × 3–4.5 µm) and broader pileipellis cells (5–10 *vs.* 4–6 µm).

Description: *Basidiocarps* solitary to concrescent, fleshy and leathery when fresh, becoming soft corky and light in weight upon drying. *Pilei* 20–30 mm wide, round, convex to plano-convex, shallowly depressed in the center. *Pileal surface* dry, glabrous, smooth, subzonate, yellowish white or yellowish grey (4A2–4B2) at center and whitish towards margin when moist, azonate upon drying. *Pileal margin* thin, entire and slightly incurved, concolorous with the pileal surface. *Pileal context* 1–3 mm thick, yellowish white to pale yellow (4A2–4A3). *Hymenophore* hydnoid, spines non-decurrent or subdecurrent, crowded, evenly distributed; surface orange-white (5A2) when fresh, greyish orange (5B4–5B6) when dry; fibrous, subulate, acute, straight to somewhat flexuous, solitary, 0.5–2 mm long, shortest near the pileus margin, 3–5 per mm, brittle when dry. *Stipes* central, confluent with pilei, 25–40 mm long, 8–10 mm wide, subcylindrical, solid; surface glabrous, concolorous with the spine surface; stipe base enlarged and covered with a small amount of white basal mycelium. *Odour* mild and fruity.

Basidiospores broadly ellipsoid, (7.0–)7.2–8.8(–8.9) × (5.2–)5.5–6.5(–6.8) µm, L_m = 7.75 µm, W_m = 6.01 µm, Q = 1.29–1.31 (n = 60/2), smooth, thin-walled, IKI–, hyaline, some with granular contents; hilar appendix 0.3–1 µm long. *Basidia* subcylindric, subclavate to clavate, 33.5–55 × 5–10 µm, sometimes with large guttules or finely granulose contents; sterigmata 2–5, up to 5 µm long, 1–3 µm wide at base, somewhat curving. *Basidioles* numerous, subcylindrical or subclavate, smaller than basidia, 12.5–48 × 3–10 µm. *Cystidia* absent. *Subhymenium trama* filamentous, hyphae 3–5 µm wide, thin-walled, olive yellow in KOH. *Hyphae of spines* 1.5–4 µm, thin-walled, apex cylindrical. *Pileipellis* composed of cylindrical hyphae, 5–10 µm wide, thin-walled, densely interwoven to subparallel, rarely branched; terminal elements rounded at apex, cells 20–73 × 5–10 µm. *Stipitipellis* composed of subcylindrical hyphae, thin- to slightly thick-walled, interwoven, 7–13.5 µm wide, terminal elements rounded at apex. *Clamp connections* present.

Material examined: **China**, Yunnan Province, Shizong County, Junzishan Mt., on soil in angiosperm and *Pinus* sp. mixed forest, 8 Aug. 2019, J. R. Yu & T. Cao, paratype, Yuan 13900a (IFP 019461).

Notes: *Hydnum flavidocanum* forms a group with *H. minum*. Morphologically, *Hydnum minum* resembles *H. flavidocanum* by a non-decurrent hymenophore, absence of cystidia and presence of clamps, but differs from it by the azonate pileal surface, smaller basidia (20–30 × 4–7 µm) with 5–8 sterigmata, smaller basidiospores (4.5–5.5 × 3–4.5 µm) and slenderer pileipellis cells (4–6 µm wide) (Yanaga *et al.* 2015).

Hydnum longibasidium T. Cao & H. S. Yuan, ***sp. nov.*** MycoBank MB 839416; Figs 1, 4, 5O, 6K, 17

Etymology: *Longibasidium* (Lat.), refers to the long basidia.

Typus: **China**, Hunan Province, Sangzhi County, Badagong Mt. Nature Reserve, on soil in angiosperm forest, 24 Sep. 2020, T. Cao, Wei10383 (**holotype** IFP 019462).

Diagnosis: Differs from *Hydnum ferruginescens* in having a subzonate to zonate pileal surface, smaller basidiocarps, larger basidiospores (8.5–11 × 7.8–9.8 *vs.* 6–8 × 5–7.5 µm), larger basidia (45–82 × 10–14 *vs.* 39–56 × 7.5–9 µm) as well as thick-walled and broader (8–18 *vs.* 5–7 µm) pileipellis hyphae.

Description: *Basidiocarps* solitary to concrescent, leathery when fresh, becoming brittle and light in weight upon drying. *Pilei* 10–15 mm wide, irregularly round, plano-convex, shallowly depressed in the center. *Pileal surface* dry, subglabrous to velutinate, subzonate or zonate towards margin, orange-white to greyish orange (5A2–5B5) when fresh, greyish orange to brownish yellow (5C7–5C8) upon drying. *Pileal margin* entire and incurved when young, slightly decurved, straight and somewhat lobed in age, orange-white to orange-grey (6A2–6B2). *Pileal context* 0.5–1 mm thick, white to yellowish white (4A1–4A2). *Hymenophore* hydnoid, spines non-decurrent or subdecurrent, crowded, evenly distributed; surface orange-white to pale orange (5A2/5A3) when fresh, concolorous with the pileal surface when dry; fibrous, subulate, acute, straight to somewhat flexuous, solitary, 1–4 mm long, shortest near the pileus margin, 2–3 per mm, brittle when dry. *Stipes* central, 15–25 mm long and 3–8 mm wide, subcylindrical, solid; surface glabrous, white, staining pale yellow when handled; stipe base enlarged and white basal mycelium absent. *Odour* mild and fruity.

Basidiospores broadly ellipsoid to subglobose, (8.0–) 8.5–11.0(–11.5) × (7.5–)7.8–9.8(–10.0) µm, L_m = 9.81 µm, W_m = 9.03 µm, Q = 1.09–1.13 (n = 60/2), smooth, thin-walled, IKI–, hyaline, some with granular contents; hilar appendix 0.5–1 µm long. *Basidia* subcylindric or subclavate, 45–82 × 10–14 µm, sometimes with large guttules or finely granulose contents; sterigmata 2–4, up to 8 µm long, 1.5–3.5 µm wide at base, slightly curving. *Basidioles* numerous, subclavate to clavate, smaller than basidia, 15–56 × 5–14 µm. *Cystidia* absent. *Subhymenium trama* filamentous, hyphae 2–5.5 µm wide, thin- to slightly thick-walled, olive yellow in KOH. *Hyphae of spines* 4.5–6 µm, thin-walled, apex cylindrical. *Pileipellis* composed of cylindrical hyphae, 8–18 µm wide, thick-walled, interwoven to subparallel, occasionally branched; terminal elements rounded at apex, cells 40–138 × 8–18 µm. *Stipitipellis* composed of subcylindrical hyphae, thick-walled, subparallel, 7–25 µm wide, terminal elements rounded at apex. *Clamp connections* present.

Material examined: **China**, Hunan Province, Sangzhi County, Badagong Mt. Nature Reserve, on soil in angiosperm forest, 24 Sep. 2020, T. Cao, paratype, Wei 10367 (IFP 019463).

Notes: *Hydnum longibasidium* falls in subg. *Rufescentia* and is closely related to *Hydnum* sp. (HKAS82411) (Taiwan Island), *H. ferruginescens* (southeastern US) and *H. magnorufescens* (Italian) (Feng *et al.* 2016, Niskanen *et al.* 2018). In terms of molecular and morphology characteristics, *Hydnum ferruginescens* and *H. magnorufescens* are very similar and they both resemble *H. longibasidium* in having an entire and incurved pileal margin when young, non-decurrent or subdecurrent spines, white basal mycelium covering stipe base, absence of cystidia and presence of clamps. However, *Hydnum ferruginescens* and *H. magnorufescens* can both be differentiated from *H. longibasidium* by the azonate pileal surface, larger basidiocarps (pileus up to 60 mm wide and stipes up to 40 mm long in *H. ferruginescens*, up to 55 mm wide and 50 mm long in *H. magnorufescens*), smaller spores (6–8 × 5–7.5 µm in former and 7–8.5 × 6.8–8 µm in latter), smaller basidia (39–56 × 7.5–9 µm and 38–46 × 7.5–9.5 µm respectively) as well as thin-walled and slenderer pileipellis hyphae (mostly 5–7 µm and 5–7 µm wide respectively) (Swenie *et al.* 2018, Niskanen *et al.* 2018).

Hydnum pallidocroceum T. Cao & H. S. Yuan, ***sp. nov.*** MycoBank MB 839418; Figs 1, 4, 5P–Q, 6L, 18

Etymology: *Pallidocroceum* (Lat.), refers to the pale orange pileal surface.

Typus: **China**, Xinjiang Auto. R, Kanasi National Geopark, on soil in *Pinus* sp. and *Picea* sp. forest, 6 Aug. 2019, Xu Lu & Y. H. Mu, **holotype**, Yuan 14023 (IFP 019466).

Diagnosis: Differs from *Hydnum jussii* in having a smaller pileus (25–40 *vs.* up to 60 mm wide), non-decurrent spines, slenderer spores (Q= 1.32–1.35 *vs.* 1.03–1.18) and larger basidia (42–55 × 8–11 *vs.* 43–48 × 7–9 µm).

Description: *Basidiocarps* solitary, fleshy and leathery when fresh, becoming brittle and light in weight upon drying. *Pilei* 25–40 mm wide, irregularly round, plano-convex, shallowly depressed in the center. *Pileal surface* dry, subglabrous, azonate, orange-white to pale orange (5A2–5A3). *Pileal margin* entire and slightly incurved or straight, concolorous with pileal surface. *Pileal context* 1–3 mm thick, yellowish white to yellowish grey (4A2–4B2). *Hymenophore* hydnoid, spines non-decurrent, crowded, evenly distributed; surface light yellow (4A4) when fresh, concolorous with pileal surface when dry, fibrous, subulate, acute, straight to somewhat flexuous, solitary, 1–5 mm long, shortest near the pileus margin, 2–6 per mm, brittle when dry. *Stipes* central or eccentric, 30–55 mm long, 5–10 mm wide, subcylindrical, solid; surface glabrous, concolorous with spine surface, staining brownish when handled; stipe base somewhat narrower than the apex. *Odour* mild and fruity.

Basidiospores broadly ellipsoid, (7.5–) 7.8–9.5(–10.0) × (5.5–)6.0–7.5(–8.0) µm, L_m = 9.09 µm, W_m = 6.72 µm, Q = 1.32–1.35 (n = 60/2), smooth, thin-walled, IKI–, hyaline, some with granular contents; hilar appendix 0.5–1 µm long. *Basidia* subcylindric or subclavate, 42–55 × 8–11 µm, sometimes with large guttules or finely granulose contents; sterigmata 2–5, up to 5 µm long, 1–3 µm wide at base, slightly curving. *Basidioles* numerous, subclavate to clavate, smaller than basidia, 15–48 × 3–10 µm. *Cystidia* absent. *Subhymenium trama* filamentous, hyphae 3–5 µm wide, thin-walled, pale yellow in KOH. *Hyphae of spines* 3–6 µm, thin-walled, apex cylindrical. *Pileipellis* composed of cylindrical hyphae, 8–23 µm wide, thin- to slightly thick-walled, interwoven to subparallel, rarely branched; terminal elements rounded at apex, cells 73–100 × 8.5–25 µm. *Stipitipellis* composed of subcylindrical hyphae, thick-walled, subparallel, 7–18 µm wide, terminal elements rounded at apex. *Clamp connections* present.

Material examined: **China**, Xinjiang Auto. Reg., Kanasi National Geopark, on soil in *Pinus* sp. and *Picea* sp. forest, 6 Aug. 2019, Xu Lu & Y. H. Mu, paratype, Yuan 14017 (IFP 019467).

Notes: *Hydnum pallidocroceum* was discovered from the Xinjiang Autonomous Region and the two samples form a strongly supported (93 % in ML and 1.00 BPP) group with the *H. jussii* lineage which includes two other samples from Xinjiang (Yuan 14008 and Yuan 14009). *Hydnum jussii* is widely distributed, being known from Finland, as well as from Xizang and Xinjiang in China. Morphologically, *Hydnum jussii* is closely related to the new species in having a pale orange pileal surface, thin-walled hyphae at the spine apex and stipes bruising brownish when handled but differs by the larger pileus (up to 60 mm wide), somewhat decurrent spines, broader spores (Q = 1.03–1.18) and smaller basidia (43–48 × 7–9 µm) (Niskanen *et al.* 2018).

In the phylogenetic tree, *Hydnum pallidocroceum*, and *H. jussii* clustered together with *H. melleopallidum* as well as *H. albertense*. *Hydnum melleopallidum* is similar to *H. pallidocroceum* in having a convex pileus, pale orange pileal surface and thin-walled hyphae at the spine apex but can be differentiated from it by smaller basidiocarps (less than 35 mm wide and long), decurrent spines, broader spores (Q = 1.04–1.18) and smaller basidia (42–48 × 7.5–8.5 µm) (Niskanen *et al.* 2018). *Hydnum albertense* resembles *H. pallidocroceum* in having a convex pileus, incurved pileal margin and non-decurrent spines, however, it differs from the new species in having larger basidiocarps (pileus up to 100 mm wide and stipes up to 65 mm long), broader spores (Q = 1.06–1.22) and smaller basidia (40–47 × 6.5–8 µm) (Niskanen *et al.* 2018).

Hydnum pallidomarginatum T. Cao & H. S. Yuan, ***sp. nov.*** MycoBank MB 839419; Figs 1, 4, 5R–S, 6M, 19

Etymology: *Pallidomarginatum* (Lat.), refers to the light-coloured pileal margin.

Typus: **China**, Yunnan Province, Yimen County, on soil in angiosperm forest, 10 Aug. 2019, H. S. Yuan, **holotype**, Yuan 13928a (IFP 019468).

Diagnosis: Differs from *Hydnum ibericum* in having broader stipes (10–15 *vs.* 5–8 mm wide), basidia with 2–4 sterigmata and larger basidiospores (8.2–9.8 × 6.5–7.8 *vs.* 7.5–8.5 × 6–7 µm).

Description: *Basidiocarps* solitary to concrescent, sometimes multipileate, fleshy and leathery when fresh, becoming hard and light in weight upon drying. *Pilei* 20–35 mm wide, irregularly round or semicircular, infundibuliform, depressed in the center. *Pileal surface* dry, glabrous, smooth, orange-white to pale orange (6A2/6A3), with a light colour zone towards center, drying azonate. *Pileal margin* entire to incised, straight or slightly decurved, whitish, obviously lighter than the pileal surface. *Pileal context* 3–5 mm thick, yellowish white to pale yellow (4A2–4A3). *Hymenophore* hydnoid, spines decurrent, crowded, evenly distributed, surface orange-white to pale orange (5A2–5A3) when fresh, brownish orange (5C6) when dry; subulate, terete or flattened, straight to somewhat flexuous, solitary, 0.5–2 mm long, shortest near the pileus margin, 2–3 per mm, brittle when dry. *Stipes* central or eccentric, confluent with pilei, 25–30 mm long, 10–15 mm wide, subcylindrical, solid; surface glabrous, concolorous with the spine surface, bruising brownish when handled; stipe base slightly enlarged and covered with white basal mycelium. *Odour* mild and fruity.

Basidiospores broadly ellipsoid, (8.0–)8.2–9.8(–10.0) × (6.0–)6.5–7.8(–8.2) µm, L_m = 8.75 µm, W_m = 6.99 µm, Q = 1.25–1.28 (n = 60/2), smooth, thin-walled, IKI–, hyaline, some with granular contents; hilar appendix 0.3–0.5 µm long. *Basidia* subcylindric, subclavate to clavate, 32–65 × 6.5–11 µm, sometimes with large guttules or finely granulose contents; sterigmata 2–4, up to 10 µm long, 2–5 µm wide at base, slightly curving. *Basidioles* numerous, subcylindrical or subclavate, smaller than basidia, 23–60 × 3–10 µm. *Cystidia* absent. *Subhymenium trama* filamentous, hyphae 2.5–6 µm wide, thin-walled, pale yellow in KOH. *Hyphae of spines* 2–4 µm, thin-walled, apex cylindrical. *Pileipellis* composed of cylindrical hyphae, 6–10 µm wide, slightly thick-walled, interwoven, rarely branched; terminal elements rounded at apex, cells 35–110 × 6–11.5 µm. *Stipitipellis* composed of subcylindrical hyphae, thick-walled, densely interwoven to subparallel, 4.5–18 µm wide, terminal elements rounded at apex. *Clamp connections* present.

Material examined: **China**, Yunnan Province, Yimen County, on soil in angiosperm forest, 10 Aug. 2019, T. Cao, paratype, Yuan 13940a (IFP 019469).

Notes: The two samples of *Hydnum pallidomarginatum* form a fully supported lineage in the phylogenetic tree. They are embeded in subgenus *Pallida* and grouped with *H. ibericum*, *H. vesterholtii*, *H. subtilior* as well as another new Chinese species, *H. flabellatum*. Morphologically, the Spanish species. *Hydnum ibericum*, is closely related to *H. pallidomarginatum* in having a pileal surface with pale orange tints, decurrent spines, stipes bruising brownish and presence of clamps. However, it can be differentiated from the new species by the slenderer stipes (5–8 mm wide), basidia with 3–5 sterigmata and smaller basidiospores (7.5–8.5 × 6–7 µm). Additionally, *H. ibericum* grows on the soil of an angiosperm forest whereas *H. pallidomarginatum* grows in coniferous mixed forests (Niskanen *et al.* 2018). *Hydnum vesterholtii* is described from France and resembles *H. pallidomarginatum* in having zonate pileus with whitish margin, broadly ellipsoid basidiospores and absence of cystidia, but differs from it by the non-decurrent to slightly decurrent spines, basidia with 3–5 sterigmata, thin-walled and broader (up to 14 µm wide) terminal cells of pileipellis and slenderer stipitipellis hyphae (4–8 µm wide) (Olariaga *et al.* 2012). *Hydnum subtilior* is similar to *H. pallidomarginatum* in having a zonate pileal surface, broadly ellipsoid basidiospores, absence of cystidia and presence of clamps, but differs from it by a larger pileus (up to 90 mm wide), longer spines (up to 8 mm long), larger stipes (up to 60 mm long and 21 mm wide), smaller basidia (less than 44 µm long and 9 µm wide) and thin-walled terminal cells of pileipellis (Swenie *et al.* 2018).

Hydnum flabellatum and *H. pallidomarginatum* are found in the temperate and subtropical forests of China, respectively, and they share the pale orange-tinted pileal surface. However, the former species differs from *H. pallidomarginatum* in having a scabrous pileal surface, longer stipes (up to 50 mm long), basidia with 2–5 sterigmata, broader pileipellis hyphae (up to 16 µm wide) and slenderer stipitipellis hyphae (less than 12 µm wide). The two species from subtropical China, *H. pallidomarginatum* and *H. flavidocanum*, share the zonate pileal surface, enlarged stipe base, absence of cystidia and presence of clamps. However, *H. pallidomarginatum* can be differentiated from *H. flavidocanum* by the shorter but wider stipes (25–30 × 10–15 mm), longer basidia (up to 65 µm long) with 2–4 sterigmata, larger basidiospores (8.2–9.8 × 6.5–7.8 µm) and slightly thick-walled and larger terminal cells (35–110 × 6–11.5 µm) of pileipellis.

Hydnum sphaericum T. Cao & H. S. Yuan, ***sp. nov.*** MycoBank MB 839420; Figs 1, 4, 5T–U, 6N, 20

Etymology: *Sphaericum* (Lat.), refers to the subglobose pileus.

Typus: **China**, Hunan Province, Sangzhi County, Badagong Mt. Nature Reserve, on soil in angiosperm forest, 23 Sep. 2020, T. Cao, **holotype**, Wei10243 (IFP 019470).

Diagnosis: Differs from *Hydnum repandum* in the smaller pileus (20–35 *vs.* 110 mm wide), non-decurrent to subdecurrent spines and larger basidia (37–65 × 8–13.5 *vs.* 35–45 × 6–8 µm).

Description: *Basidiocarps* solitary to concrescent, fleshy and leathery when fresh, becoming brittle and light in weight upon drying. *Pilei* 20–35 mm wide, subglobose when young, becoming irregularly round with age. *Pileal surface* dry, subglabrous, azonate, orange-white (6A2) when moist, greyish orange to brownish orange (5B5–6C7) upon drying. *Pileal margin* entire and strongly incurved when young, slightly decurved and undulate in age, concolorous with the pileal surface. *Pileal context* 1–3 mm thick, white to yellowish white (4A1–4A2). *Hymenophore* hydnoid, spines non-decurrent to subdecurrent, crowded, evenly distributed; surface white (3A1–4A1) when fresh, brownish orange (6C4–6C6) when dry; fibrous, subulate, acute, straight to somewhat flexuous, solitary, 0.5–3 mm long, shortest near the pileus margin, 3–6 per mm, brittle when dry. *Stipe* central or eccentric, 18–25 mm long, 5–8 mm wide, subcylindrical, solid; surface glabrous, concolorous with the spine surface; stipe base enlarged and covered with a small amount of white basal mycelium. *Odour* mild and fruity.

Basidiospores broadly ellipsoid, (7.5–)8.0–8.8(–9.0) × (6.0–) 6.5–7.5(–8.0) µm, L_m = 8.36 µm, W_m = 6.94 µm, Q = 1.20–1.23 (n = 60/2), smooth, thin-walled, IKI–, hyaline, some with granular contents; hilar appendix 0.5 µm long. *Basidia* subcylindric or subclavate, 37–65 × 8–13.5 µm, sometimes with large guttules or finely granulose contents; sterigmata 4–5, up to 8 µm long, 2–2.5 µm wide at base, slightly curving. *Basidioles* numerous, subclavate, smaller than basidia, 15–53 × 4–11 µm. *Cystidia* absent. *Subhymenium trama* filamentous, hyphae 3–5 µm wide, thin- to slightly thick-walled, pale yellow in KOH. *Hyphae of spines* 3–5 µm, thin-walled, apex cylindrical. *Pileipellis* composed of cylindrical hyphae, 5–13 µm wide, thick-walled, interwoven to subparallel, occasionally branched; terminal elements rounded at apex, cells 70–105 × 5–14.5 µm. *Stipitipellis* composed of subcylindrical hyphae, thick-walled, subparallel, 8.5–20 µm wide, terminal elements rounded at apex. *Clamp connections* present.

Materials examined: **China,** Hunan Province, Sangzhi County, Badagong Mt. Nature Reserve, on soil in angiosperm forest, 23 Sep. 2020, T. Cao , paratype, Wei 10262 (IFP 019471); Wei 10300 (IFP 019472).

Notes: The three samples of *Hydnum sphaericum* cluster with HKAS51070 and all were collected from subtropical China. Although the coverage between the ITS sequences of Wei 10243 (holotype of *H. sphaericum*, 647 bp) and HKAS51070 (556 bp) is 85 %, they got 98.74 % similarity. The four samples form a separate lineage with strong support (97 % ML, 1.00 BPP) and we describe them as a new taxon.

In the phylogenetic tree, *Hydnum sphaericum* fell in subg. *Hydnum*. The genus type species *H. repandum* is also nested in this subgenus and it is closely related to *H. sphaericum* in having a cream colour to orange pileal surface, crowded spines, thin-walled hyphae in the spines, and presence of clamps. However, it differs from *H. sphaericum* in having a larger pileus (up to 110 mm wide), larger stipes (35–60 × 7–14 mm), mostly decurrent spines and smaller basidia (35–45 × 6–8 µm) (Niskanen *et al.* 2018).

Species of *Hydnum* subg. *Hydnum* usually have medium to large (pilei 40–110 mm wide) basidiomata (Niskanen *et al.* 2018), however, *H. sphaericum* has small ones (pilei 20–35 mm wide). Another relatively small species is *H. olympicum* (pilei 30–65 mm wide) and it resembles the new species in having whitish pileal surface, crowded spines, broadly ellipsoid basidiospores and presence of clamps, but *H. olympicum* differs from *H. sphaericum* in having larger basidiocarps (pileus up to 65 mm wide and stipes up to 60 mm long), smaller basidia (37–43 × 6.6–8.6 µm) with 4 sterigmata, and presence of pleurocystidia (Niskanen *et al.* 2018).

Hydnum tangerinum T. Cao & H. S. Yuan, ***sp. nov.*** MycoBank MB 839421; Figs 4, 5V, 6O, 21

Etymology: *Tangerinum* (Lat.), refers to the orange tint of pileal surface.

Typus: **China**, Hunan Province, Sangzhi County, Badagong Nature Reserve, on soil in angiosperm forest, 23 Sep. 2020, T. Cao, **holotype**, Wei 10245 (IFP 019473).

Diagnosis: Differs from *Hydnum melitosarx* in having shorter stipes (60 *vs.* 70 mm long), broadly ellipsoid basidiospores and basidia with 3–6 sterigmata.

Description: *Basidiocarps* solitary or concrescent, fleshy and leathery when fresh, becoming soft corky and light in weight upon drying. *Pilei* 10–50 mm wide, flabelliform, or irregularly round, convex to plano-convex, shallowly depressed in the center. *Pileal surface* dry, velutinate, smooth, azonate, pale orange, light orange, orange to brownish orange (5A3/5A4/6B8/6C8), drying greyish orange (5B5/5B6/6B5); scabrous, often with some scales towards center. *Pileal margin* thin, entire and undulate, concolorous with the pileal surface. *Pileal context* 1–5 mm thick, yellowish white (4A2). *Hymenophore* hydnoid, spines non-decurrent, crowded, evenly distributed; surface orange-white (6A2) when fresh, greyish orange (5B5/5B6) when dry; subulate, acute, straight to somewhat flexuous, solitary, 2–6 mm long, shortest near the pileus margin, 2–3 per mm, brittle when dry. *Stipes* central, up to 60 mm long, 3–7 mm wide, subcylindrical, solid; surface glabrous, white, staining pale orange (5A3) when handled; stipe base enlarged and covered with a small amount of white basal mycelium. *Odour* mild and fruity.

Basidiospores broadly ellipsoid, (7–)7.2–8.8(–9) × (5.5–) 5.8–7(–7.5) µm, L_m = 8.11 µm, W_m = 6.19 µm, Q = 1.23–1.31 (n = 60/2), smooth, thin-walled, IKI–, hyaline, some with granular contents; hilar appendix 1 µm long. *Basidia* subcylindric, subclavate to clavate, 29–45 × 5.5–10 µm, sometimes with large guttules or finely granulose contents; sterigmata 3–6, up to 6 µm long, 1.5 µm wide at base, somewhat curving. *Basidioles* numerous, subcylindrical or subclavate, smaller than basidia, 12.5–43.5 × 3–10 µm. *Cystidia* absent. *Subhymenium trama* filamentous, hyphae 3–5 µm wide, thin-walled, greenish yellow in KOH. *Hyphae of spines* 2–3.5 µm, thin-walled, apex cylindrical. *Pileipellis* composed of cylindrical hyphae, thin-walled, subparallel, occasionally branched; terminal elements rounded at apex, cells 75–210 × 4–18 µm. *Stipitipellis* composed of subcylindrical hyphae, slightly thick-walled, interwoven, 3.5–13 µm wide, terminal elements rounded at apex. *Clamp connections* present.

Material examined: **China**, Hunan Province, Sangzhi County, Badagong Nature Reserve, on soil in angiosperm forest, 23 Sep. 2020, T. Cao, paratype, Wei 10249 (IFP 019474); Wei 10250 (IFP 019475).

Notes: *Hydnum tangerinum* is nested in the subgenus *Rufescentia* and shares the small to medium basidiocarps, orange-tinted pileal surface, bruising stipes when handled, non-decurrent spines and broadly ellipsoid basidiospores, with most of the species in the subgenus. *Hydnum melitosarx* and *H. tangerinum* form a weakly supported lineage in the tree (Fig. 4), the former species is similar to *H. tangerinum* in the medium basidiocarps, orange-tinted pileal surface and non-decurrent spines but differs by having longer stipes (up to 70 mm long), subglobose basidiospores (Q avg. = 1.11) and basidia with 3 sterigmata (Niskanen *et al.* 2018). *Hydnum mulsicolor* and *H. submulsicolor* both share medium basidiocarps, orange-tinted pileal surface and non-decurrent spines with *H. tangerinum*, however, *H. mulsicolor* can be differentiated from *H. tangerinum* by having shorter basidiospores (L_m = 7.5); *H. submulsicolor* differs from *H. tangerinum* in having subglobose basidiospores (Q avg. = 1.13) and basidia with 3–4 sterigmata (Niskanen *et al.* 2018).

Hydnum tenuistipitum T. Cao & H. S. Yuan, ***sp. nov.*** MycoBank MB 839422; Figs 4, 5W, 6P, 22

Etymology: *Tenuistipitum* (Lat.), refers to the slender stipes.

Typus: **China**, Hunan Province, Sangzhi County, Badagong Nature Reserve, on soil in angiosperm forest, 23 Sep. 2020, T. Cao, **holotype**, Wei 10410 (IFP 019476).

Diagnosis: Differs from *Hydnum treui* in having longer stipes (uo to 60 mm *vs.* 15–20 mm long), and larger basidia (45–63 × 3–12 µm 35–42 × 6–7 µm) with 2–6 sterigmata

Description: *Basidiocarps* solitary or concrescent, fleshy when fresh, becoming brittle and light in weight upon drying. *Pilei* 10–30 mm wide, round, convex to plano-convex, shallowly depressed in the center. *Pileal surface* dry, glabrous, smooth, azonate, yellow-white to orange-white (4A2/5A2), drying pale orange to greyish orange (5A3/5B4). *Pileal margin* thin, entire and slightly decurved, concolorous with pileal surface. *Pileal context* 1–5 mm thick, white to yellowish white (4A2). *Hymenophore* hydnoid, spines non-decurrent to subdecurrent, crowded, evenly distributed; surface orange-white (5A2) when fresh, light brown (6D7/6D8) when dry; subulate, acute, straight to somewhat flexuous, solitary, 1–3 mm long, shortest near the pileus margin, 3–4 per mm, brittle when dry. *Stipes* central, up to 60 mm long, 2–6 mm wide, subcylindrical, solid; surface glabrous, white, staining pale orange (5A3) when handled; stipe base enlarged and covered with a small amount of white basal mycelium. *Odour* mild and fruity.

Basidiospores subglobose, (6.5–)6.8–7.2(–7.5) × (5.2–)5.5–6.5(–6.8) µm, L_m = 7.08 µm, W_m = 6.09 µm, Q = 1.07–1.16 (n = 60/2), smooth, thin-walled, IKI–, hyaline, some with granular contents; hilar appendix 1 µm long. *Basidia* subcylindric, subclavate to clavate, 45–63 × 3–12 µm, sometimes with large guttules or finely granulose contents; sterigmata 2–6, up to 10 µm long, 1.5 µm wide at base, slightly curving. *Basidioles* numerous, subcylindrical or subclavate, smaller than basidia, 12–50 × 3–10 µm. *Cystidia* absent. *Subhymenium trama* filamentous, hyphae 3–5 µm wide, thin-walled, greenish yellow in KOH. *Hyphae of spines* 2–4 µm, thin-walled, apex cylindrical. *Pileipellis* composed of cylindrical hyphae, thick-walled, subparallel, frequently branched; terminal elements rounded at apex, cells 98–260 × 4–15 µm. *Stipitipellis* composed of subcylindrical hyphae, slightly thick-walled, interwoven, 3.5–13 µm wide, terminal elements rounded at apex. *Clamp connections* present.

Material examined: **China***,* Hunan Province, Sangzhi County, Badagong Nature Reserve, on soil in angiosperm forest, 23 Sep. 2020, T. Cao, paratype, Wei 10417 (IFP 019477).

Notes: *Hydnum tenuistipitum* and *H. brevispinum* form a well-supported lineage in the tree (Fig. 4) so, we suggest subgenus *Brevispina*; the five samples in the subgenus are all collected from a subtropical forest in China. *Hydnum tenuistipitum* resembles *H. brevispinum* in the whitish and smooth pileal surface, non-decurrent to subdecurrent spines, thick-walled pileipellis hyphae and slightly thick-walled stipitipellis hyphae, but the latter species differs from *H. tenuistipitum* by the smaller pileus (less than 15 mm wide), shorter stipe (less than 25 mm wide), smaller (5–5.8 × 3.8–4.8 µm) and broadly ellipsoid basidiospores and shorter basidia (20–40 µm long). The Australasian *Hydnum treui* belongs to subtropical/tropical forest and is similar to *H. tenuistipitum* in having a whitish pileal surface, non-decurrent to subdecurrent spines and subglobose basidiospores, however it can be distinguished from the latter species by shorter stipes (15–20 mm long), and smaller basidia (35–42 × 6–7 µm) with 4 sterigmata (Niskanen *et al.* 2018).

Hydnum ventricosum T. Cao & H. S. Yuan, ***sp. nov.*** MycoBank MB 839423; Figs 1, 4, 5X–Y, 6Q, 23

Etymology: *Ventricosum* (Lat.), refers to the ventricose basidia.

Typus: **China**, Liaoning Province, Xinbin County, Gangshan Mt., on soil in angiosperm and *Pinus* sp. mixed forest, 12 Aug. 2020, H. S. Yuan, **holotype**, Yuan 14536 (IFP 019478).

Diagnosis: Differs from *Hydnum berkeleyanum* in having a smaller pileus (28–35 *vs.* up to 80 mm wide), shorter spines (1–5 mm *vs.* up to 9 mm long), shorter but broader (46 × 14 *vs.* 60 × 9 µm) ventricose basidia and slightly thick-walled pileipellis hyphae.

Description: *Basidiocarps* solitary to concrescent, fleshy and leathery when fresh, becoming soft corky and light in weight upon drying. *Pilei* 28–35 mm wide, irregularly round, plano-convex, shallowly depressed in the center. *Pileal surface* dry, subglabrous, azonate, orange (6A7) when moist, brown (6D6–6D7) upon drying. *Pileal margin* thin, entire and incurved, concolorous with the pileal surface. *Pileal context* 1–2.5 mm thick, yellowish white to orange-white (4A2–5A2). *Hymenophore* hydnoid, spines non-decurrent, crowded, evenly distributed; surface orange-white (5A2–6A2) when fresh, brownish orange (6C4-6C6) when dry, subulate, straight to somewhat flexuous, solitary, 1–5 mm long, shortest near the pileus margin, 2–4 per mm, brittle when dry. *Stipes* central or eccentric, 30–35 mm long, 10–15 mm wide, subcylindrical, solid; surface glabrous, concolorous with the spine surface, bruising brownish when handled; stipe base somewhat narrower than apex and white basal mycelium absent. *Odour* mild and fruity.

Basidiospores subglobose, (7.5–)8.2–9.0(–9.5) × (7.0–)7.5–8.5(–9.0) µm, L_m = 8.64 µm, W_m = 8.17 µm, Q = 1.05–1.09 (n = 60/2), smooth, thin-walled, IKI–, hyaline, some with granular contents; hilar appendix 0.3–1 µm long. *Basidia* fusiform to subcylindric, ventricose, 30–46 × 7.5–14 µm, sometimes with large guttules or finely granulose contents; sterigmata 2–4, up to 8 µm long, 1–3 µm wide at base, somewhat curving. *Basidioles* numerous, subclavate, smaller than basidia, 13–35 × 3–11 µm. *Cystidia* absent. *Subhymenium trama* filamentous hyphae 3–7.5 µm wide, thin- to slightly thick-walled, brownish yellow in KOH. *Hyphae of spines* 2–5 µm, thin-walled, apex cylindrical. *Pileipellis* composed of cylindrical hyphae, 5–10 µm wide, slightly thick-walled, interwoven to subparallel, rarely branched; terminal elements rounded at apex, cells 38–95 × 6–10 µm. *Stipitipellis* composed of subcylindrical hyphae, thick-walled, subparallel, 7.5–18 µm wide, terminal elements rounded at apex. *Clamp connections* present.

Material examined: **China**, Liaoning Province, Xinbin County, Gangshan Mt., on soil in angiosperm and *Pinus* sp. mixed forest, 26 Aug. 2020, H. S. Yuan, paratype, Yuan 14601 (IFP 019479).

Notes: The two samples of *Hydnum ventricosum* cluster with HKAS61795. This cluster forms a separate branch with strong support (100 % ML and 0.99 BPP) and all samples were collected from a temperate forest in China. We describe them as a new taxon.

In the phylogenetic tree, *Hydnum ventricosum* falls in subg. *Rufescentia* Niskanen & Liimat and formed a subgroup with *H. berkeleyanum*, *H. rufescens* and *H. subrufescens*.

Morphologically, the Indian species *H. berkeleyanum* is closely related to *H. ventricosum* in having a light orange pileal surface, entire pileal margin, subglobose basidiospores, 2–4 sterigmata and presence of clamps, but differs from it in having a larger pileus (up to 80 mm wide), longer spines (up to 9 mm long), longer but slenderer basidia (up to 60 μm long and less than 9 μm wide) and thin-walled pileipellis hyphae (Wang *et al.* 2018). *Hydnum rufescens* is the type species of subg. *Rufescentia*, and is similar to *H. ventricosum* in having the non-decurrent spines and presence of clamps. However, *H. rufescens* can be distinguished from the new species by the larger pileus (up to 65 mm across), deep reddish orange pileal surface, longer stipes (up to 55 mm long), slenderer basidia (less than 9 μm wide) and smaller basidiospores (7–8.5 × 6–7.2 μm) (Niskanen *et al.* 2018). *Hydnum subrufescens* is a species described from Canada and is a synonym of *H. aerostatisporum* according to Swenie *et al.* (2018). It is related to *H. ventricosum* in having an orange-tinted pileus surface and non-decurrent spines. But *H. subrufescens* can be differentiated from the latter by the larger pileus (up to 60 mm wide), longer stipes (up to 40 mm long), slenderer basidia (less than 9 μm wide) and smaller basidiospores (7.4–8.8 × 6.4–7.8 μm) (Niskanen *et al.* 2018).

Hydnum albomagnum Banker, Bull. Torrey Bot. Club 28: 207. 1901. MycoBank MB 141572.

Notes: Phylogenetic analyses based on ITS and nLSU sequences and morphological characteristics confirmed the new record. The two Chinese samples and the American *Hydnum albomagnum* formed an isolated lineage with strong support (98 % in ML and 0.99 BPP). For a detailed description of *H. albomagnum*, see Banker (1901) and Yanaga *et al.* (2015). This species was originally described from the USA and recorded in Japan by Yanaga *et al.* (2015).

Materials examined: **China**, Hunan Province, Sangzhi County, Badagong Mt. Nature Reserve, on soil in angiosperm forest, 21 Sep. 2020, W. M. Qin, Wei 10194 (IFP 019480); 23 Sep. 2020, W. M. Qin, Wei 10247 (IFP 019481).

Hydnum minum Yanaga & N. Maek., Mycoscience 56: 435. 2015. MycoBank MB 808762.

Notes: Morphological and phylogenetic analyses based on ITS and nLSU sequences confirmed the new record, which is described in detail by Yanaga *et al.* (2015). This species was originally described from Japan (Yanaga *et al.* 2015) and so far, has only been collected in two East Asian countries, China and Japan (Yanaga *et al.* 2015, Niskanen *et al.* 2018).

Materials examined: **China**, Hunan Province, Sangzhi County, Badagong Mt. Nature Reserve, on soil in angiosperm forest, 23 Sep. 2020, T. Cao, Wei 10252 (IFP 019482), 10260 (IFP 019483).

Notes on other genera phylogenetically accepted in *Hydnaceae* in this study

Bergerella Diederich & Lawrey, Bryologist 123(2): 159. 2020. MycoBank MB 835061.

Type species: *Bergerella atrofusca* Diederich & Lawrey, Bryologist 123(2): 159. 2020. MycoBank MB 835062.

Notes: *Bergerella* is a lichenicolous genus described from Austria with hosts *Physcia aipolia* and *P. stellaris*. *Bergerella atrofusca* is the single species in the genus and is characterised by dark reddish brown and hairless bulbils as well as the absence of clamps (Lawrey *et al.* 2020). Phylogenetic analysis indicated it is a member of the *Cantharellales*, with closest relatives in the genus *Minimedusa* Weresub & P.M. LeClair (Lawrey *et al.* 2020). Our phylogenetic tree (Fig. 1) shows that *Be. atrofusca* belongs to *Hydnaceae*. *Bergerella atrofusca* and *Bryoclavula phycophila* form a lineage with moderate support in our tree. The *Bergerella*-*Bryoclavula* lineage clustered with *Minimedusa* and the three genera form a subclade with 46 % support in the ML analysis. Despite the clavarioid basidiocarps and absence of a bulbil-like structure, *Br. phycophila* is a lichenised species (Masumoto & Degawa 2020a). *Minimedusa* is a bulbil-forming and lichenicolous genus like *Bergerella* (Lawrey *et al.* 2007). Thus *Bergerella, Bryoclavula* and *Minimedusa* form a distinct lichen-associated branch in the *Hydnaceae*.

Bryoclavula H. Masumoto & Y. Degawa, Mycol. Progr. 19(7): 708. 2020. MycoBank MB 833863.

Type species: *Bryoclavula phycophila* H. Masumoto & Y. Degawa, Mycol. Progr. 19(7): 708. 2020. MycoBank MB 833864.

Notes: *Bryoclavula* has a single species, *Br. phycophila*, which is characterised by small-sized, whitish to pale cream and clavate or fusiform basidiocarps, basidia with 4–6 sterigmata, narrowly ellipsoid to elongate basidiospores and slow-growing colonies with undulate margin (Masumoto & Degawa 2020a). Morphologically, *Bryoclavula* is closely related to *Multiclavula* R.H. Petersen in having clavarioid basidiocarps and 4–6 sterigmata, and both are lichenised genera. However, *Bryoclavula phycophila* does not form the globular or bulbil-like lichenised thallus like the species in *Multiclavula* (Oberwinkler 1970, Nelsen *et al.* 2007, Masumoto & Degawa 2020a, b). The two lichenised genera have a distant relationship in the phylogenetic tree according to Masumoto & Degawa (2020a) and also this study.

Bryoclavula was described from Japan and is nested in the "CHS assemblage (following the the name in the article)" in *Cantharellales* (Masumoto & Degawa 2020a). In our tree (Fig. 1), *Bryoclavula* fell in *Hydnaceae* and formed a distinct lichen-associated subclade with *Bergerella,* and *Minimedusa* in the family. Three species of the polyphyletic genus *Sistotrema, S. adnatum, S. coronilla* and *S. hypogaeum*, are also members of this subclade according to Masumoto & Degawa (2020a). The three species of *Sistotrema* differ from the taxa in the other three genera of the lichen-associated subclade in all respects and the phylogenetic relationship of *Sistotrema* spp. should be further studied.

Bulbilla Diederich, Flakus & Etayo, Lichenologist 46(3): 340. 2014. MycoBank MB 807650.

Type species: *Bulbilla applanata* Diederich, Flakus & Etayo, Lichenologist 46(3): 340. 2014. MycoBank MB 807651.

Notes: *Bulbilla* is described from South America and is strictly lichenicolous with *Peltigerales* hosts. It belongs to the *Cantharellales* and is characterised by relatively large (200–500 μm), hairless, and diverse-coloured bulbils as well as an absence of clamps (Diederich *et al.* 2014). Bulbils of the genus are slightly immersed in the thallus and often leave holes when removed which is distinctly different from the other three bulbilliferous and lichenicolous genera of *Cantharellales viz*., *Burgoa*, *Burgellopsis* and *Minimedusa*. The bulbils in these genera are often loosely attached to the substratum and do not leave conspicuous scars when removed (Goidànich 1937, Diederich & Lawrey 2007, Diederich *et al.* 2014).

The phylogeny of *Bulbilla* shows that it is a separate lineage in the *Cantharellales*, forming a group with *Clavulinaceae* Donk and is closely related to *Hydnaceae* (Diederich *et al.* 2014). Hibbett *et al.* (2014) suggested *Cantharellaceae*, *Clavulinaceae* and *Sistotremataceae* as synonyms of *Hydnaceae.* Thus, we suspect *Bulbilla* is a member of *Hydnaceae* and this has been confirmed by our phylogenetic study. In the tree (Fig. 1), the two samples of the genus type species *B. applanata* nest in *Hydnaceae* and form an unsupported group with the *Clavulina*-*Membranomyces* lineage. Ecologically, species of the *Clavulina*-*Membranomyces* lineage possess ECM nutritional modes (Smith *et al.* 2011, Argüelles-Moyao *et al.* 2017), while *Bulbilla* is strictly lichenicolous (Diederich *et al.* 2014). Morphologically, species in *Clavulina* have clavarioid to coralloid/infundibuliform, resupinate or effused basidiocarps (Henkel *et al.* 2011, Uehling *et al.* 2012a, b, Felipe 2012, He *et al.* 2016), *Membranomyces* has resupinate ones (Jülich 1975) and *Bulbilla* forms bulbils (Diederich *et al.* 2014). Thus, it can be concluded that the relationships between *Bulbilla* and the *Clavulina*-*Membranomyces* lineage are rather distant, and their generic rank seems to be appropriate. *Bulbilla* contains only one species now and the discovery of more taxa are needed for the further study of the phylogenetic relationships within the genus.

Burgella Diederich & Lawrey, Mycol. Progr. 6(2): 62. 2007. MycoBank MB 511585.

Type species: *Burgella flavoparmeliae* Diederich & Lawrey, Mycol. Progr. 6(2): 64. 2007. MycoBank MB 511586.

Notes: *Burgella* was suggested by Diederich and Lawrey to embrace the lichenicolous species with yellow to orange-coloured bulbils (Diederich & Lawrey 2007). The only two species in the genus, *Burgella flavoparmeliae* (type species) and *B. lutea*, fell within the *Cantharellales* based on molecular evidence (Diederich & Lawrey 2007, Lawrey *et al.* 2007, Diederich *et al.* 2014). *Burgella* nested in *Hydnaceae* according to our phylogeny analysis (Fig. 1); the result is similar to Lawrey *et al.* (2016). *Burgella* formed a group with *Sistotrema oblongisporum* and *S. brinkmannii* (Diederich & Lawrey 2007, Lawrey *et al.* 2007, Diederich *et al.* 2014) and it is also confirmed by our tree (Fig. 1). Bulbils occur in *Sistotrema oblongisporum* and *S. brinkmannii* (Hallenberg 1984) which also makes the two species closely related to *Burgella* spp.

Burgellopsis Diederich & Lawrey, Lichenologist 46(3): 344. 2014. MycoBank MB 807653.

Type species: *Burgellopsis nivea* Diederich & Lawrey, Lichenologist 46(3): 344. 2014. MycoBank MB 807654.

Notes: *Burgellopsis nivea* is the only species in the genus. It was described from Great Britain and the pure white bulbils and absence of clamps are distinct features of the genus *Burgellopsis* (Diederich *et al.* 2014). Only the nLSU sequence data are available for the genus at this time. Phylogenetically, the result in Diederich *et al.* (2014) shows that *Burgellopsis* belongs to *Clavulinaceae* and forms an unsupported group with the *Burgella*-*Sistotrema* lineage. The tree in Lawrey *et al.* (2016) suggests that *Burgellopsis* falls in *Hydnaceae* and groups with *Multiclavula* R.H. Petersen. In the present study, *Burgellopsis* and *Rogersiomyces* form a weakly supported (42 % in ML) group which is closely related to the *Burgella*-*Sistotrema* lineage.

Burgoa Goid., Boll. R. Staz. Patalog. Veget. Roma, N.S. 17: 354. 1937. MycoBank MB 7457.

Type species: *Burgoa verzuoliana* Goid., Boll. R. Staz. Patalog. Veget. Roma, N.S. 17: 359. 1937. MycoBank MB 255369.

Notes: *Burgoa* is one of the bulbilliferous and lichenicolous genus in *Cantharellales* (Diederich & Lawrey 2007, Lawrey *et al.* 2007, Diederich *et al.* 2014). It is typified by *B. verzuoliana* and characterised by whitish, brownish to black and hairless bulbils and the presence of clamps (Diederich & Lawrey 2007). The genus includes ten species (http://www.indexfungorum.org/) which grow on various lichens distributed worldwide (Diederich *et al.* 2018).

Schlechte and Hoffmann (2000) suggested *Burgoa turficola* Schlechte & P. Hoffmann belongs to *Athelia* Pers., but the combination has been rejected by Lawrey *et al.* (2007). Phylogenetic research shows that *Burgoa turficola* is nested in *Agaricales* (Diederich & Lawrey 2007, Lawrey *et al.* 2007). Therefore, whether *Burgoa* is monophyletic requires further research by combining phylogenetic and morphological evidence. However, we have confirmed that several samples of *Burgoa* indeed belong to the *Cantharellales* and are embedded in the *Hydnaceae*. The type species, *Burgoa verzuoliana*, and *B. angulosa* form a fully supported lineage with *Sistotrema octosporum* and *S. eximum* in our tree (Fig. 1). *S. biggsiae* Hallenb., *S. efibulatum* (J. Erikss.) Hjortstam and *S. sernanderi* (Litsch.) Donk are also members of this lineage according to Lawrey *et al.* (2007, 2016) and Masumoto & Degawa (2020a).

Clavulina J. Schröt., Krypt.-Fl. Schlesien (Breslau) 3.1(25-32): 442. 1888. MycoBank MB 17322.

Type species: *Clavulina cristata* (Holmsk.) J. Schröt., Krypt.-Fl. Schlesien (Breslau) 3.1(25-32): 442. 1888. MycoBank MB 114572.

Notes: *Clavulina* is typified by *Clavulina cristata* and comprises 88 described species from temperate or tropical ecosystems around the world (Thacker & Henkel 2004, Douanla-Meli 2007, Duhem & Buyck 2007, Trappe & Castellano 2007, Henkel *et al.* 2005, 2011, Uehling *et al.* 2012a, b, Olariaga & Salcedo 2012, Wartchow 2012, He *et al.* 2016, Tibpromma *et al.* 2017, Pérez-Pazos *et al.* 2019, Wu *et al.* 2019, Yuan *et al.* 2020). The genus is characterised by simple or branched, clavarioid to coralloid (occasionally cantharelloid, cerebriform, resupinate or effused) basidiocarps, a monomitic hyphal system and smooth, hyaline, subglobose to broadly ellipsoid basidiospores (Corner 1950, 1970, Petersen 1988, Thacker & Henkel 2004, Henkel *et al.* 2005, Uehling *et al.* 2012a). Ecologically, most *Clavulina* species have an ECM lifestyle except for a few suspected of being saprotrophic (Hobbie *et al.* 2001, 2002, Zeller *et al.* 2007, Rinaldi *et al.* 2008, Tedersoo *et al.* 2012, Hou *et al.* 2012, Tedersoo & Smith 2013, Ważny 2014). *Clavulina* was recovered as a monophyletic group in the *Cantharellales* (Thacker & Henkel 2004, Moncalvo *et al.* 2006, Olariaga *et al.* 2009). It was initially selected as the type genus of *Clavulinaceae* Donk (Donk 1961), but now belongs to *Hydnaceae* (Hibbett *et al.* 2014). *Clavulina* forms a well-supported group with *Membranomyces* Jülich in our tree (Fig. 1) and they share ECM nutritional modes.

Membranomyces Jülich, Persoonia 8(3): 296. 1975. MycoBank MB 18042.

Type species: *Membranomyces spurius* (Bourdot) Jülich, Persoonia 8(3): 296. 1975. MycoBank MB 317560.

Notes: *Membranomyces* nests in *Hydnaceae* (Larsson 2007, Hibbett *et al.* 2014) and belongs to the *Cantharellales* (Moncalvo *et al.* 2006). There are two species in the genus including the type species, *Membranomyces spurius* and *Me*. *delectabilis* (H.S. Jacks.) Kotir. & Saaren. They are both described from Europe and are also widely distributed in Asia, Middle East, Canada and the USA (Jülich 1975, Kotiranta & Saarenoksa 1993). *Membranomyces* is characterised by resupinate and effused basidiocarps with smooth hymenophore, monomitic hyphal system, and smooth, ellipsoid to subglobose basidiospores (Jülich 1975, Kotiranta & Saarenoksa 1993). Despite the different shape of their respective basidiocarps, *Membranomyces* is anatomically similar to *Clavulina* in having a monomitic hyphal system, two-spored basidia and smooth, ellipsoid to subglobose basidiospores (Corner 1950, 1970, Petersen 1988, Thacker & Henkel 2004). Ecologically, the two genera share the ECM nutritional modes (Argüelles-Moyao *et al.* 2017). Our phylogenetic analyses also indicate an apparent relationship between *Membranomyces* and *Clavulina*. The two genera form a distinct ECM lineage in the *Hydnaceae* (Fig. 1).

Minimedusa Weresub & P.M. LeClair, Can. J. Bot. 49(12): 2210. 1971. MycoBank MB 18065.

Type species: *Minimedusa polyspora* (Hotson) Weresub & P.M. LeClair, Can. J. Bot. 49(12): 2210. 1971. MycoBank MB 317759.

Notes: *Minimedusa* was recovered as a monophyletic genus in the *Cantharellales* and includes three bulbilliferous species. *Minimedusa polyspora* and *Mi*. *obcoronata* are saprophytic and grow on various substrates (Hotson 1912, Sutton *et al.* 1984, Diederich & Lawrey 2007), while *Mi*. *pubescens* Diederich, Lawrey & Heylen is a lichenicolous species (Weresub & LeClair 1971, Diederich & Lawrey 2007). The phylogenetic results of Lawrey *et al.* (2007) placed *Minimedusa* in the *Cantharellales* grouping with *Sistotrema coronilla*. In the tree of Masumoto & Degawa (2020a), *Minimedusa* setted in the “CHS assemblage” and in Lawrey *et al.* (2016) and Lawrey *et al.* (2020) the genus fell in the *Hydnaceae*. Our study confirms that *Minimedusa* indeed nests in *Hydnaceae* (with full support) and forms a subclade with *Bergerella* and *Bryoclavula* (Fig. 1).

Multiclavula R.H. Petersen, Am. Midl. Nat. 77: 207. 1967. MycoBank MB 18080.

Type species: *Multiclavula corynoides* (Peck) R.H. Petersen, Am. Midl. Nat. 77: 215. 1967. MycoBank MB 334548.

Notes: *Multiclavula* is typified by *Mu*. *corynoides* and characterised by the simple or branched small clavarioid basidiocarps and lichenised nutritional mode (Petersen 1967, Fischer *et al.* 2007, Nelsen *et al.* 2007, Masumoto & Degawa 2020b). *Multiclavula* is morphologically and ecologically similar to another lichenised genus *Bryoclavula* but it has a globular or bulbil-like structure which is lacking in *Bryoclavula* and phylogenetically it is distant from *Bryoclavula* (Masumoto & Degawa 2020a). *Multiclavula* consists of thirteen species from Asia, Europe, North America, Oceania and South America (Corner 1950, Petersen 1967, Petersen 1988, Nelsen *et al.* 2007, Masumoto & Degawa 2020b).

Multiclavula is nested in *Hydnaceae* (Hibbett *et al.* 2014) and was recovered as monophyletic with high support in several previous molecular phylogenetic studies (Nelsen *et al.* 2007, Masumoto & Degawa 2020a, b). *Multiclavula*, *Burgella*, *Clavulina* and *Membranomyces* initially belonged to the family *Clavulinaceae* (Kirk *et al.* 2008). Binder *et al.* (2005), Moncalvo *et al.* (2006) and Masumoto & Degawa (2020b) suggested *Multiclavula* as a sister group to *Clavulina* and the *S. brinkmannii-oblongisporum* clade according to molecular evidence, however, in the studies of Masumoto & Degawa (2020a) as well as Lawrey *et al.* (2020), the relationship between the two genera seems distant. Our study (Fig. 1) also confirmed that *Multiclavula* is a well-supported monophyletic group in the *Hydnaceae* and provided the evidence that *Multiclavula* is not a sister clade of *Clavulina* and *S. brinkmannii-oblongisporum*, but is a single lineage in the family. The result is similar to Masumoto & Degawa (2020a) and Lawrey *et al.* (2020). The change in the status of *Multiclavula* in different molecular analyses is probably due to the addition of several lichenicolous genera like *Bulbilla*, *Burgella* and *Burgellopsis* as well as the saprotrophic genus *Rogersiomyces* J.L. Crane & Schokn to the phylogeny.

Neoburgoa Diederich, Bryologist 119(4): 344. 2016. MycoBank MB 818611.

Type species: *Neoburgoa freyi* Diederich, Bryologist 119(4): 344. 2016. MycoBank MB 818612.

Notes: The lichenicolous *Neoburgoa* is nested within *Hydnaceae* and consists of a single species, *Neoburgoa freyi*, described from Europe (Lawrey *et al.* 2016). *Neoburgoa freyi* is characterised by immersed to superficial, yellow to orange, roundish to ellipsoid or irregular bulbils, internally composed of roundish to ellipsoid or polyhedral cells, clamps absent in bulbils but present in culture (Lawrey *et al.* 2016). Morphologically, *Neoburgoa* is closely related to another lichenicolous genus *Burgella* in having yellow to orange bulbils. However, *Neoburgoa* has a distant phylogenetic relationship with *Burgella* as well as with other lichenicolous bulbil-forming genera including *Bergerella*, *Bulbilla*, *Burgella*, *Burgellopsis*, *Burgoa* and *Minimedusa* as shown by Lawrey *et al.* (2016), Masumoto & Degawa (2020a) and this study. The two samples of *N. freyi* form a separate lineage in *Hydnaceae* in our tree (Fig. 1).

Rogersiomyces J.L. Crane & Schokn., Am. J. Bot. 65: 903. 1978. MycoBank MB 16297.

Synonym: *Hyphobasidiofera* K. Matsush. & Matsush., Matsush. Mycol. Mem. 9: 33. 1996. MycoBank MB 27665.

Type species: *Rogersiomyces okefenokeensis* J.L. Crane & Schokn., Am. J. Bot., Suppl. 65(8): 903. 1978. MycoBank MB 322867.

Notes: *Rogersiomyces* is a saprotrophic genus nested in *Hydnaceae* and characterised by gymnocarpous basidiocarps composed of fasciculate or loose synnematous holobasidia and the spores germinating directly via hyphae (Crane & Schoknecht 1978, Psurtseva *et al.* 2016). The genus consists of two species: the type species *Rogersiomyces okefenokeensis* J.L. Crane and Schokn. which was described from the USA and the Vietnamese species *R. malaysiana*. Phylogenetic analysis shows *Rogersiomyces* grouping with *Sistotrema oblongisporum* in the family. In our molecular analysis, it was recovered in *Hydnaceae* and forms a weakly supported group with the bulbilliferous and lichenicolous genus *Burgellopsis* (Fig. 1), however, there are no common morphological or ecological features that verify the phylogenetic relationship between the two genera. The status of *Rogersiomyces* in *Hydnaceae* should be further clarified.

Sistotrema Fr., Syst. Mycol. (Lundae) 1: 426. 1821. MycoBank MB 18551.

Synonym: *Galziniella* Parmasto, Consp. System. Corticiac. (Tartu): 39. 1968. MycoBank MB 17637.
Heptasporium Bref., Unters. Gesammtgeb. Mykol. (Liepzig) 14: 167. 1908. MycoBank MB 17738.
Hydnotrema Link, Handb. Erk. Gew. 3: 298. 1833. MycoBank MB 17796.

Type species: *Sistotrema confluens* Pers., Neues Mag. Bot. 1: 108. 1794. MycoBank MB 215678.

Notes: There are *ca.* 55 recognised species of *Sistotrema* with a worldwide distribution according to the notes of He *et al.* (2019). It is a morphologically, ecologically diverse, and polyphyletic genus in *Hydnaceae* (Larsson 2007, Hibbett *et al.* 2014). Only the type species, *S. confluens,* and *S. subconfluens* form stipitate basidiocarps on the ground, while other species in the genus have resupinate basidiocarps on wood (Kotiranta & Larsson 2013, Zhou & Qin 2013, Crous *et al.* 2014, Gruhn *et al.* 2017, Kaur *et al.* 2019). The hymenophore configuration in the genus also various from smooth, poroid to hydnoid (Eriksson *et al.* 1984). The genus is often characterised by the urniform basidia mostly with 6–8 sterigmata. Ecologically, species of *Sistotrema* have ectomycorrhizal, saprotrophic, or endophytic nutritional modes (Eriksson *et al.* 1984, Di Marino *et al.* 2008, Münzenberger *et al.* 2012, Hibbett *et al.* 2014).

In phylogeny, *Sistotrema* was retrieved as highly polyphyletic (Binder *et al.* 2005, Moncalvo *et al.* 2006, Nilsson *et al.* 2006). The type species, *Sistotrema confluen*s, and *S. muscicola* as well as *S. alboluteum* are closely related to the stipitate-ECM lineages *Cantharellus*, *Craterellus* and *Hydnum*, while other species of *Sistotrema* are distributed over several genera in *Hydnaceae* including *Clavulina*, *Multiclavula* and *Membranomyces* or form single lineages in the family (*e.g., S. adnatum* and *S. coronilla*) (Pine *et al.* 1999, Hibbett & Binder 2002, Larsson *et al.* 2004, Moncalvo *et al.* 2006). To avoid immoderately missed data at more loci, only six species of *Sistotrema* (including the type species and five other species) are involved in our present study. We confirmed the *Sistotrema* is a highly polyphyletic genus nested in *Hydnaceae*. The six *Sistotrema* species form three well-supported groups in the family *viz.*, *Sistotrema confluens*-*subconfluens* and *Hydnum* group, *S. brinkmannii*-*oblongisporum* and *Burgella* group, as well as the *S. eximum*-*octosporum* and *Burgoa* group (Fig. 1). We do not intend to discuss and solve the comprehensive phylogeny of the entire genus *Sistotrema* in the present paper due to insufficient samples. It should be done elsewhere pending both morphological and molecular evidences.

Sistotremella Hjortstam, Cortic. N. Eur. (Oslo) 7: 1379. 1984. MycoBank MB 25849.

Type species: *Sistotremella perpusilla* Hjortstam, Cortic. N. Eur. (Oslo) 7: 1381. 1984. MycoBank MB 115329.

Notes: *Sistotremella* is typified by *S. perpusilla* and characterised by resupinate, effuse and dry crustaceous basidiocarps, a monomitic hyphal system, basidia with 6–8 sterigmata and ellipsoid, cyanophilous basidiospores (Eriksson *et al.* 1984). There are three species in the genus, the type species, *Sistotremella perpusilla*, and *S. hauerslevii* Hjortstam and *S. paullicorticioides* Boidin & Gilles. They are all wood-decaying fungi and mainly distributed in Europe (Sweden, Denmark, and France) (Eriksson *et al.* 1984, Boidin & Gilles 1994). *Sistotremella* belongs to *Hydnaceae* according to the notes in He *et al.* (2019), however, molecular phylogenies for *Sistotremella* are rare. A phylogenetic tree based on nLSU in Masumoto & Degawa (2020a) recovered *Sistotremella* in the “CHS assemblage”. The ITS and nLSU of *S. perpusilla* (CBS 126048) is used in the present research, and our study based on multi-marker dataset presents the first phylogenetic evidence that *Sistotremella* is a member of *Hydnaceae*.

Genera traditionally recognised in *Hydnaceae* but in need of modern interpretation

Corallofungus Kobayasi, J. Jap. Bot. 58: 174. 1983. MycoBank MB 17667.

Type species: *Corallofungus hatakeyamanus* Kobayasi, J. Jap. Bot. 56(6): 174. 1983. MycoBank MB 107676.

Gloeomucro R.H. Petersen, Mycologia 72(2): 303. 1980. MycoBank MB 17667.

Type species: *Gloeomucro nodosus* (Linder) R.H. Petersen, Mycologia 72(2): 303. 1980. MycoBank MB 113838.

Ingoldiella D.E. Shaw, Trans. Br. Mycol. Soc. 59(2): 258. 1972. MycoBank MB 8631.

Type species: *Ingoldiella hamata* D.E. Shaw, Trans. Br. Mycol. Soc. 59(2): 258. 1972. MycoBank MB 315815.

Parastereopsis Corner, Nova Hedwigia 27: 331. 1976. MycoBank MB 18186.

Type species: *Parastereopsis borneensis* Corner, Nova Hedwigia 27: 331. 1976. MycoBank MB 319210.

Osteomorpha G. Arnaud ex Watling & W.B. Kendr., Naturalist (Hull), Ser. 104(no. 948): 1. 1979. MycoBank MB 517859.

Type species: *Osteomorpha fragilis* G. Arnaud ex Watling & W.B. Kendr., Naturalist (Hull), Ser. 104(no. 948): 1. 1979. MycoBank MB 302109.

Repetobasidiellum J. Erikss. & Hjortstam, Cortic. N. Eur. (Oslo) 6: 1247. 1981. MycoBank MB 25481.

Type species: *Repetobasidiellum fusisporum* J. Erikss. & Hjortstam, Cortic. N. Eur. (Oslo) 6: 1247. 1981. MycoBank MB 116023.

DISCUSSION

In the phylogenetic tree (Fig. 1), *Hydnaceae* is the sister clade of *Tulasnellaceae*. The two families together with *Botryobasidiaceae* and *Ceratobasidiaceae* form the *Cantharellales* with high support. The result provides phylogenetic evidence based on a multiple-marker dataset for the division of the *Cantharellales* as in Hibbett *et al.* (2014). *Cantharellus* is a sister clade of *Craterellus* while *Hydnum* groups with *Sistotrema confluens*-*subconfluens*. The cantharelloid and ECM genera *Cantharellus*, *Craterellus* and *Hydnum* together with *Sistotrema sensu stricto* form a well-supported subclade in the *Hydnaceae* (Fig. 1).

We suggest that *Hydnaceae* is equivalent to the “core cantharelloid clade” which was supported by Moncalvo *et al.* (2006). In that study, the family was phylogenetically delimited to include seventeen genera according to the analysis based on a five-marker combined dataset. Fifteen genera are confirmed as monophyletic lineages in our tree (Fig. 1). *Sistotrema* is confirmed as polyphyletic in accordance with Moncalvo *et al.* (2006). Although *Burgoa* species form a fully supported lineage with *Sistotrema octosporum* and *S. eximum* in the tree, whether *Burgoa* is monophyletic requires further research since *Burgoa turficola* is nested in the *Agaricales* (Diederich & Lawrey 2007, Lawrey *et al.* 2007). The six genera *Corallofungus*, *Gloeomucro*, *Ingoldiella*, *Parastereopsis*, *Osteomorpha* and *Repetobasidiellum* are traditionally recognised as members of *Hydnaceae* (He *et al.* 2019, http://www.indexfungorum.org 2021) but they all lack a modern interpretation, and their sequence data are unavailable. Thus, the status of the six genera is still unsolved. In addition, *Paullicorticium* J. Erikss. was also placed in *Hydnaceae* (http://www.indexfungorum.org 2021) though several phylogeny analyses have suggested the genus placed outside of the *Cantharellales* (Hibbett & Binder 2002, Larsson *et al.* 2004, Larsson 2007). Hibbett & Binder (2002) and Binder *et al.* (2005) show that *Sistotremastrum niveocremeum* is in the cantharelloid clade and it is closely related to *Sistotrema brinkmannii*, however, Moncalvo *et al.* (2006) deem that the sequence labeled *Sistotremastrum niveocremeum* that nested in this clade represents a misidentification; the true *Sistotremastrum niveocremeum* belongs to the trechisporoid clade. In the case of *Repetobasidium* J. Erikss., the phylogeny of Nilsson *et al.* (2006) has placed the genus in the *Rickenella* clade of the *Hymenochaetales*. Here, we follow the previous studies and consider the genera *Paullicorticium*, *Sistotremastrum* and *Repetobasidium* do not belong to *Hydnaceae*.

The morphology of the taxa in *Hydnaceae* is highly diverse. Several morphologically related lineages have been recognised in our tree. The "*Cantharellus*-*Craterellus*" lineage share the cantharelloid and colourful basidiocarps, smooth, wrinkled to veined hymenophore, relatively long basidia (sometimes up to 100 µm long) and mostly 2–6 sterigmata (Wilson *et al.* 2012, Buyck *et al.* 2014, Henkel *et al.* 2014). The "*Hydnum* and *Sistotrema confluens*-*subconfluens*" lineage share the stipitate basidiocarps and hydnoid hymenophore (Eriksson *et al.* 1984, Zhou & Qin 2013, Niskanen *et al.* 2018, Swenie *et al.* 2018); although the shape of basidiocarps in "*Clavulina*-*Membranomyces*" lineage range from clavarioid (*Clavulina*) to corticioid (*Membranomyces*), they share the monomitic hyphal system and two-spored basidia (Jülich 1975, Thacker & Henkel 2004). Species in the "*Burgella* and *S. oblongisporum*-*brinkmannii*" lineage share the feature of forming bulbils (Hallenberg 1984, Diederich *et al.* 2014). Corticioid species of *Sistotrema* and *Sistotremella*, clavarioid species of *Multiclavula* and *Bryoclavula*, bulbil-forming species *Bergerella*, *Bulbilla*, *Burgella*, *Burgellopsis*, *Minimedusa*, *Neoburgoa*, *Burgoa* as well as hypochnoid species in *Rogersiomyces* are alternately distributed in the lower middle position of the tree (Fig. 1). The result that stipitate-pileus species are placed at the top, clavarioid species in the middle and corticioid or bulbil-forming species at the bottom of the tree may intimate the morphological evolution in *Hydnaceae*.

Ecologically, there are two distinct ECM group, the "*Cantharellus*, *Craterellus*, *Hydnum* and *Sistotrema sensu stricto*" group and the "*Clavulina* and *Membranomyces*" group (clade with blue branches in Fig. 1), they are both well-supported in the tree. In addition, other genera with the lichenicolous and lichenised (green branches), saprotrophic (pink branches) nutritional modes (Table 2) are throughout the clade and there is no ecological evidence for their status in the tree of *Hydnaceae* (Fig. 1). This result is similar to the study of Lawrey *et al.* (2016) which was based on nLSU.

The phylogenetic relationships within *Hydnaceae* are partially elucidated and we have provided a more accurate delimitation in the sense of genus for the family. However, although our study contains a relatively comprehensive dataset of the genus in *Hydnaceae*, more material and additional molecular markers are necessary for more comprehensive studies of some specific clades.

KEY TO GENERA IN *HYDNACEAE*

1a.	Basidiocarps mucous to watery gelatinous	*Gloeomucro*
1b.	Basidiocarps not watery gelatinous	2
2a.	Clavarioid basidiocarps present	3
2b.	Clavarioid basidiocarps absent	6
3a.	Basidiocarps with distinct fragrance	*Corallofungus*
3b.	Basidiocarps without special odour	4
4a.	With ECM nutritional model	*Clavulina*
4b.	Lichen-associated	5
5a.	Lichenised, globular thallus present	*Multiclavula*
5b.	Lichenised, globular thallus absent	*Bryclavula*
6a.	Conidia present	7
6b.	Conidia absent	9
7a.	Conidia with subglobal form, basidiocarps tubeform	*Parastereopsis*
7b.	Conidia without subglobal form, basidiocarps unknown	8
8a.	Conidia with narrow form and often branched; conidiophores long, up to 120 µm long	*Ingoldiella*
8b.	Conidia cylindrical, conidiophores short, < 10 µm present	10
9b.	Bulbills absent	16
10a.	Clamps present	11
10b.	Clamps absent	*Burgella*
11a.	Bulbills < 110 µm wide	12
11b.	Bulbills > 300 µm wide	4
12a.	Bulbills loosely attached to the substratum	13
12b.	Bulbills tightly attached to the substratum	*Neoburgoa*
13a.	Bulbills up to 450 µm wide, whitish bulbils present	*Burgoa*
13b.	Bulbills < 300 µm wide, whitish bulbils absent	*Bryclavula*
14a.	Bulbills < 200 µm wide	15
14b.	Bulbills 200–500 µm wide	*Bulbilla*
15a.	Bulbills pure white, 100–200 µm wide	*Burgellopsis*
15b.	Bulbills dark reddish brown, 25–35 µm wide	*Bergerella*
16a.	Dendrohyphidia present	17
16b.	Dendrohyphidia absent	18
17a.	Cystidia present, spores ellipsoid	*Sistotremella*
17b.	Cystidia absent, spores subfusiform	*Repetobasidiellum*
18a.	Synnematous basidia absent	19
18b.	Synnematous basidia present	*Rogersiomyces*
19a.	Clamps present	20
19b.	Clamps absent	*Membranomyces*
20a.	Hydnoid hymenophore present	21
20b.	Hydnoid hymenophore absent	22
21a.	Corticioid basidiocarps absent	*Hydnum*
21b.	Corticioid basidiocarps present	*Sistotrema*
22a.	Pileus non-perforation, stipe often solid	*Cantharellus*
23b.	Pileus sometimes perforation, stipe often hollow	*Craterellus*

ACKNOWLEDGEMENTS

This research was financed by the National Natural Science Foundation of China (Project Nos. 31970017, 31770028 & 31470148), the Special Funds for the Young Scholars of Taxonomy of the Chinese Academy of Sciences (Project No. ZSBR-015) and the Biodiversity Investigation, Observation and Assessment Program (2019–2023) of Ministry of Ecology and Environment of China.

REFERENCES

Agerer R, Kraigher H, Javornik B (1996). Identification of ectomycorrhizae of *Hydnum rufescens* on Norway spruce and the variability if the ITS region of *H. rufescens* and *H. repandum (Basidiomycetes)*. *Nova Hedwigia* **63**: 183–194.

An DY, Liang ZQ, Jiang S, *et al.* (2017). *Cantharellus hainanensis*, a new species with a smooth hymenophore from tropical China. *Mycoscience* **58**: 438–444.

Argüelles-Moyao A, Garibay-Orijel R, Márquez-Valdelamar LM, *et al.* (2017). *Clavulina-Membranomyces* is the most important lineage within the highly diverse ectomycorrhizal fungal community of *Abies religiosa*. *Mycorrhiza* **27**: 53–65.

Bahram M, Põlme S, Kõljalg U, *et al.* (2012). Regional and local patterns of ectomycorrhizal fungal diversity and community structure along an altitudinal gradient in the Hyrcanian forests of northern Iran. *New Phytologist* **193**: 465–473.

Banker HJ (1901). A preliminary contribution to a knowledge of the *Hydnaceae*. *Bulletin of the Torrey Botanical Club* **28**: 199–222.

Berkeley MJ, Curtis MA (1860). Characters of new fungi, collected in the North Pacific exploring expedition by Charles Wright. *Proceedings of the American Academy of Arts and Sciences* **4**: 111–130.

Bi ZS, Zheng GY, Li TH (1994). *Macrofungus flora of Guangdong Province*. Guangdong Science and Technology Press, Guangdong.

Bigelow HE (1978). The cantharelloid fungi of New England and adjacent areas. *Mycologia* **70**: 707–756.

Bijeesh C, Kumar AM, Vrinda KB, *et al.* (2018). Two new species of *Craterellus (Cantharellaceae*) from tropical India. *Phytotaxa* **346**: 157–168.

Binder M, Hibbett DS, Larsson KH, *et al.* (2005). The phylogenetic distribution of resupinate forms across the major clades of mushroom-forming fungi (*Homobasidiomycetes*). *Systematics and Biodiversity* **3**: 113–157.

Boa E (2004). Wild edible fungi: a global overview of their use and importance to people. *Food and Agriculture Organization* **17**: 1–147.

Boidin J, Gilles G (1994). Contribution à la connaissance des Corticiés à basides urniformes ou suburniformes (*Basidiomycotina*). *Bulletin de la Société Mycologique de France* **110**: 185–229.

Buyck B (2014). Exploring the diversity of “smooth chanterelles” (*Cantharellus, Cantharellales*). *Cryptogamie Mycologie* **35**: 23–40.

Buyck B, Duhem B, Das K, *et al.* (2017). Fungal biodiversity profiles 21–30. *Cryptogamie Mycologie* **38**: 101–146.

Buyck B, Hofstetter V, Ryoo R, *et al.* (2020). New *Cantharellus* species from South Korea. *MycoKeys* **76**: 31–47.

Buyck B, Kauff F, Eyssartier G, *et al.* (2014). A multilocus phylogeny for worldwide *Cantharellus* (*Cantharellales, Agaricomycetidae*). *Fungal Diversity* **64**: 101–121.

Buyck B, Kauff F, Cruaud C, *et al.* (2012). Molecular evidence for novel *Cantharellus* (*Cantharellales, Basidiomycota*) from tropical African miombo woodlands and a key to all tropical African chanterelles. *Fungal Diversity* **58**: 281–298.

Buyck B, Moreau PA, Courtecuisse R, *et al.* (2016a). *Cantharellus coccolobae* sp. nov. and *Cantharellus garnieri*, two tropical members of *Cantharellus* subg. *Cinnabarinus*. *Cryptogamie Mycologie* **37**: 391–403.

Buyck B, Olariaga I, Justice J, *et al.* (2016b). The dilemma of species recognition in the field when sequence data are not in phase with phenotypic variability. *Cryptogamie Mycologie* **37**: 367–389.

Cairney JWG, Chambers SM (1999). *Ectotnycorrhizal fungi key genera in profile*. Springer-Verlag Berlin Heidelberg, New York: 253–268.

Cao T, Yu JR, Hu YP, *et al.* (2021). *Craterellus atrobrunneolus sp. nov.* from southwestern China. *Mycotaxon* **136**: 59–71.

Chen JJ, Cui BK, Dai YC (2016). Global diversity and molecular systematics of *Wrightoporia s.l. (Russulales, Basidiomycota)*. *Persoonia* **37**: 21–36.

Chiu WF (1973). Ten new species of *Agaricales* from Yunnan, China. *Acta Microbiologica Sinica* **13**: 129–135.

Contu M, Vizzini A, Carbone M, *et al.* (2009). Identity and neotypification of *Craterellus cinereus* and description of *Cantharellus atrofuscus sp. nov. Mycotaxon* **110**: 139–149.

Corner EJH (1950). A monograph of *Clavaria* and allied genera. *Annals of Botany Memoirs* **1**: 1–740.

Corner EJH (1970). Supplement to “A monograph of *Clavaria* and allied genera”. *Nova Hedwigia Beih* **47**: 22–51.

Corner EJH (1966). *A monograph of cantharelloid fungi*. Annals of Botanical Memoirs No. 2. Oxford Univ Press, Oxford, UK: 255.

Crane JL, Schoknecht JD (1978). *Rogersiomyces*, a new genus in the *Filobasidiaceae* (*Homobasidiomycetes*) from an aquatic habitat. *American Journal of Botany* **65**: 902–906.

Crous PW, Wingfield MJ, Schumacher RK, *et al.* (2014). Fungal planet description sheets: 281–319. *Persoonia* **33**: 212–289.

Gruhn G, Hallenberg N, Courtecuisse R (2017). *Sistotrema macabouense* (*Cantharellales, Hydnaceae*), a new corticioid fungus from Martinique. *Phytotaxa* **303**: 65–70.

Dahlman M, Danell E, Spatafora JW (2000). Molecular systematics of *Craterellus*: cladistic analysis of nuclear LSU rDNA sequence data. *Mycological Research* **104**: 388–394.

Dai YC, Zhou LW, Yang ZL, *et al.* (2010). A revised checklist of edible fungi in China. *Mycosystema* **29**: 1–21.

Darriba D, Taboada GL, Doallo R, *et al.* (2012). jModelTest 2: more models, new heuristics and parallel computing. *Nature Methods* **9**: 772.

Das K, Ghosh A, Chakraborty D, *et al.* (2017). Fungal biodiversity profiles 31–40. *Cryptogamie Mycologie* **38**: 353–406.

Das K, Rossi W, Leonardi M, *et al.* (2018). Fungal biodiversity profiles 61–70. *Cryptogamie Mycologie* **39**: 381–418.

De Kesel A, Amalfim M, Ngoy BKW, *et al.* (2016). New and interesting *Cantharellus* from tropical Africa. *Cryptogamie Mycologie* **37**: 283–327.

De Kesel A, Yorou NS, Buyck B (2011). *Cantharellus solidus*, a new species from Benin (West-Africa) with a smooth hymenium. *Cryptogamie Mycologie* **32**: 277–283.

Deepika K, Upadhyay RC, Reddy MS (2012). *Craterellus indicus sp. nov.*, a new species associated with *Cedrus deodara* from the western Himalayas, India. *Mycological Progress* **11**: 769–774.

Di Marino E, Scattolin L, Bodensteiner P, *et al.* (2008). *Sistotrema* is a genus with ectomycorrhizal species – confirmation of what sequence studies already suggested. *Mycological Progress* **7**: 169–176.

Diederich P, Lawrey JD (2007). New lichenicolous, muscicolous, corticolous and lignicolous taxa of *Burgoa s.l.* and *Marchandiomyces s.l.* (anamorphic *Basidiomycota*), a new genus for *Omphalina foliacea*, and a catalogue and a key to the non-lichenized, bulbilliferous basidiomycetes. *Mycological Progress* **6**: 61–80.

Diederich P, Lawrey JD, Capdet M, *et al.* (2014). New lichen-associated bulbil-forming species of *Cantharellales* (*Basidiomycetes*). *Lichenologist* **46**: 333–347.

Diederich P, Lawrey DJ, Ertz D (2018). The 2018 classification and checklist of lichenicolous fungi, with 2000 non-lichenized, obligately lichenicolous taxa. *The Bryologist* **121**: 340–425.

Donk MA (1961). Four new families of *Hymenomycetes*. *Persoonia* **1**: 405–407.

Douanla-Meli CM (2007). *Fungi* of Cameroon. *Bibliotheca Mycologica* **202**: 1–410.

Duhem B, Buyck B (2007). Edible mushrooms from Madagascar 2. *Clavulina albiramea comb. nov. (Cantharellales*), an edible clavarioid fungus shared between African miombo and Malagasy *Uapaca* woodland. *Nova Hedwigia* **85**: 317–330.

Dunham SM, O’Dell TE, Molina R (2003). Analysis of nrDNA sequences and microsatellite allele frequencies reveals a cryptic chanterelle species *Cantharellus cascadensis sp. nov.* from the American Pacific Northwest. *Mycological Research* **107**: 1163–1177.

Earle FS (1909). The genera of the North American Fungi. *Bulletin of the New York Botanical Garden* **5**: 373–451.

Eriksson J, Hjortstam K, Ryvarden L (1984). *The Corticiaceae of North Europe*: **7**: 1282–1449.

Eyssartier G, Buyck B (1999). Notes nomenclaturales et taxinomiques sur deux espèces françaises de *Cantharellus* (*Basidiomycotina*). *Cryptogamie Mycologie* **20**: 107–111.

Feibelman TP, Doudrick RL, Cibula WG, *et al.* (1997). Phylogenetic relationships within the *Cantharellaceae* inferred from sequence analysis of the nuclear large subunit rDNA. *Mycological Research* **101**: 423–430.

Felipe W (2012). *Clavulina incrustata*, a new species from Pernambuco, Brazil. *Cryptogamie Mycologie* **33**: 105–114.

Feng B, Wang XH, Ratkowsky D, *et al.* (2016). Multilocus phylogenetic analyses reveal unexpected abundant diversity and significant disjunct distribution pattern of the hedgehog mushrooms (*Hydnum* L.). *Scientific Reports* **6**: 55–86.

Fischer E, Ertz D, Killmann D, *et al.* (2007). Two new species of *Multiclavula* (lichenized basidiomycetes) from savanna soils in Rwanda (East Africa). *Botanical Journal of the Linnean Society* **155**: 457–465.

Fries EM (1821). *Systema Mycologicum*. Ex Officina Berlingiana, Lundae: 1–318.

Goidànich G (1937). Studi sulla microflora fungina della pasta di legno destinata alla fabbricazione della carte. *Bolletino della Stazione di Patologia Vegetale di Roma* **17**: 305–399.

Grebenc T, Martín MP, Kraigher H (2009). Ribosomal ITS diversity among the European species of the genus *Hydnum* (*Hydnaceae*). *Anales del Jardín Botanico de Madrid* **66S1**: 121–132.

Gulden G, Høiland K (1989). *Craterellus konradii* and an intermediate form between *C. cornucopioides* and *C. konradii*. *Opera Botanica* **100**: 85–91.

Hall T (2005). *BioEdit: biological sequence alignment editor for Win95/98/NT/2K/XP*. Ibis Therapeutic, Carlsbad, CA.

Hallenberg NA (1984). A taxonomic analysis of the *Sistotrema brinkmannii* complex (*Corticiaceae, Basidiomycetes*). *Mycotaxon* **21**: 389–411.

Hansen L, Knudsen H (1997). *Nordic macromycetes*: **Vol. 3**. Nordsvamp, Copenhagen.

He G, Chen SL, Yan SZ (2016). Morphological and molecular evidence for a new species in *Clavulina* from southwestern China. *Mycoscience* **57**: 255–263.

He MQ, ZhaoRL, Hyde KD, *et al*. (2019). Notes, outline and divergence times of *Basidiomycota*. *Fungal Diversity* **99**: 105–367.

Heinemann P (1958). Champignons recoltes au Congo Belgepar Madame Goossens-Fontana III. *Cantharellineae*. *Bulletin du Jardin botanique de l'État a Bruxelles* **28**: 335–438.

Hembrom ME, Das K, Adhikari S, *et al*. (2017). First report of *Pterygellus* from Rajmahal hills of Jharkhand (India) and its relation to *Craterellus (Hydnaceae, Cantharellales)*. *Phytotaxa* **306**: 201–210.

Henkel TW, Aime MC, Mehl HK (2009). *Craterellus excelsus sp. nov.* from Guyana. *Mycotaxon* **107**: 201–208.

Henkel TW, Aime MC, Mehl HK, *et al*. (2006). *Cantharellus pleurotoides*, a new and unusual basidiomycete from Guyana. *Mycological Research* **110**: 1409–1412.

Henkel TW, Aime MC, Uehling JK, *et al*. (2011). New species and distribution records of *Clavulina* (*Cantharellales, Basidiomycota*) from the Guiana Shield. *Mycologia* **103**: 883–894.

Henkel TW, Meszaros R, Aime MC, *et al*. (2005). New *Clavulina* species from the Pakaraima Mountains of Guyana. *Mycological Progress* **4**: 343–350.

Henkel TW, Wilson AW, Amie MC, *et al*. (2014). *Cantharellaceae* of Guyana II: New species of *Craterellus*, new South American distribution records for *Cantharellus guyanensis* and *Craterellus excelsus*, and a key to the neotropical taxa. *Mycologia* **106**: 307–322.

Hibbett DS, Bauer R, Binder M, *et al*. (2014). Agaricomycetes. In: *The mycota VII part A* (McLaughlin DJ, Spatafora JW, eds). Springer-Verlag, Berlin: 373–412.

Hibbett DS, Binder M (2002). Evolution of complex fruiting-body morphologies in homobasidiomycetes. *Proceedings of the Royal Society B-Biological Sciences* **269**: 1963–1969.

Hobbie E, Weber N, Trappe J (2001). Mycorrhizal *vs*. saprotrophic status of fungi: the isotopic evidence. *New Phytologist* **150**: 601–610.

Hobbie E, Weber N, Trappe J, *et al*. (2002). Using radiocarbon to determine the mycorrhizal status of fungi. *New Phytologist* **156**: 129–136.

Hotson JW (1912). Culture studies of fungi producing bulbils and similar propagative bodies. *Proceedings of the American Academy of Arts and Sciences* **48**: 227–306.

Hou W, Lian B, Dong H, *et al*. (2012). Distinguishing ectomycorrhizal and saprophytic fungi using carbon and nitrogen isotopic compositions. *Geoscience Frontiers* **3**: 351–356.

Hyde KD, Tennakoon SD, Jeewon R, *et al*. (2019). Fungal diversity notes 1036–1150: taxonomic and phylogenetic contributions on genera and species of fungal taxa. *Fungal Diversity* **96**: 1–242.

Jian SP, Dai R, Gao J, *et al*. (2020). *Cantharellus albus*, a striking new species from southwest China. *Phytotaxa* **470**: 133–144.

Jülich W (1975). Studies in resupinate basidiomycetes–III. *Persoonia* **8**: 291–305.

Katoh K, Rozewicki J, Yamada KD (2019). MAFFT online service: multiple sequence alignment, interactive sequence choice and visualization. *Briefings in Bioinformatics* **20**: 1160–1166.

Kaur M, Kaur R, Singh AP, *et al*. (2019). *Sistotrema macrosporum sp. nov.* from India. *Mycotaxon* **133**: 675–680.

Kirk PM, Cannon PF, Minter DW, *et al*. (2008). *Ainsworth & Bisby's dictionary of the fungi*, 10th edn. CABI, Wallingford.

Kirk PM, Larsson KH (2013). A without-prejudice list of generic names of fungi for protection under the International Code of Nomenclature for algae, fungi, and plants. *IMA Fungus* **4**: 381–443.

Kornerup A, Wanscher J (1981). *Methuen handbook of colour Fletcher*: 252. Norwich.

Kotiranta H, Larsson KH (2013). *Sistotrema luteoviride sp. nov. (Cantharellales, Basidiomycota*) from Finland. *Acta Mycologica* **48**: 219–225.

Kotiranta H, Saarenoksa R (1993). Rare Finnish *Aphyllophorales* (*Basidiomycetes*) plus two new combinations in Efibula. *Annales Botanici Fennici* **30**: 211–249.

Kreisel H (1969). *Grundzüge eines natürlichen systems der Pilze*. Gustav Fischer Verlag/Cramer, Jena.

Kumari D, Upadhyay RC, Reddy MS (2011). *Cantharellus pseudoformosus*, a new species associated with *Cedrus deodara* from India. *Mycoscience* **52**: 147–151.

Lao DT, TN K, Ngo VT, *et al*. (2019). First record of *Cantharellus minor* from Vietnam with identification support from a combination of nrLSU and nrSSU phylogenetic analysis. *Advancements in Life Sciences*, 125–130.

Larsson KH (2007). Re-thinking the classification of corticioid fungi. *Mycological Research* **111**: 1040–1063.

Larsson KH, Larsson E, Kõljalg U (2004). High phylogenetic diversity among corticioid homobasidiomycetes. *Mycological Research* **108**: 983–1002.

Lawrey JD, Binder M, Diederich P, *et al*. (2007). Phylogenetic diversity of lichen-associated homobasidiomycetes. *Molecular Phylogenetics and Evolution* **44**: 778–789.

Lawrey JD, Sikaroodi M, Gillevet PM, *et al*. (2020). A new species of bulbil-forming lichenicolous fungi represents an isolated clade in the *Cantharellales*. *Bryologist* **123**: 155–162.

Lawrey JD, Zimmermann E, Sikaroodi M, *et al*. (2016). Phylogenetic diversity of bulbil-forming lichenicolous fungi in *Cantharellales* including a new genus and species. *The Bryologist* **119**: 341–349.

Leacock PR, Riddell J, Wilson AW, *et al*. (2016). *Cantharellus chicagoensis sp. nov.* is supported by molecular and morphological analysis as a new yellow chanterelle in midwestern United States. *Mycologia* **108**: 765–772.

Le JZ, Hu XW, Peng YB, *et al*. (1993). *The macrofungus flora of Hunan Province*. Hunan Normal University Press, Changsha.

Lee SS, Watling R, Noraini-Sikin Y (2002). Ectomycorrhizal basidiomata fruiting in lowland forests of Peninsular Malaysia. *Bois et Forêts des Tropiques* **274**: 33–43.

Masumoto H, Degawa Y (2020a). *Bryoclavula phycophila gen. et sp. nov.* belonging to a novel lichenised lineage in *Cantharelles* (*Basidiomycota*). *Mycological Progress* **19**: 705–714.

Masumoto H, Degawa Y (2020b). *Multiclavula petricola sp. nov.* (*Cantharellales, Basidiomycota*), a new clavarioid and lichenised fungus growing on rocks. *Mycoscience* **61**: 155–159.

Matheny PB (2005). Improving phylogenetic inference of mushrooms with *RPB1* and *RPB2* nucleotide sequences (*Inocybe; Agaricales*). *Molecular Phylogenetics and Evolution* **3**: 1–20.

Matheny PB, Austin EA, Birkebak JM, *et al*. (2010). *Craterellus fallax*, a black trumpet mushroom from eastern North America with a broad host range. *Mycorrhiza* **20**: 569–575.

Matheny PB, Wang Z, Binder M, *et al*. (2007). Contributions of *rpb2* and *tef1* to the phylogeny of mushrooms and allies (*Basidiomycota, Fungi*). *Molecular Phylogenetics and Evolution* **43**: 430–451.

McNabb RFR (1971). Some new and revised taxa of New Zealand *Basidiomycetes* (*Fungi*). *New Zealand Journal of Botany* **9**: 355–370.

Mel'nik V, Alexandrova A, Zmitrovich I, *et al*. (2015). First record of *Hyphobasidiofera malaysiana* (*Basidiomycota*) from Vietnam. *Mycobiota* **5**: 1–5.

Miller LW (1933). The genera of *Hydnaceae*. *Mycologia* **25**: 286–302.

Moncalvo JM, Nilsson RH, Koster B, *et al*. (2006). The cantharelloid clade: dealing with incongruent gene trees and phylogenetic reconstruction methods. *Mycologia* **98**: 937–948.

Morehouse EA, James TY, Ganley ARD, *et al*. (2003). Multilocus sequence typing suggests the chytrid pathogen of amphibians is a recently emerged clone. *Molecular Ecology* **12**: 395–403.

Münzenberger B, Schneider B, Nilsson RH, *et al*. (2012). Morphology, anatomy, and molecular studies of the ectomycorrhiza formed axenically by the fungus *Sistotrema* sp. (*Basidiomycota*). *Mycological Progress* **11**: 817–826.

Nelsen MP, Lücking R, Umaña L, *et al*. (2007). *Multiclavula ichthyiformis (Fungi: Basidiomycota: Cantharellales: Clavulinaceae*), a remarkable new basidiolichen from Costa Rica. *American Journal of Botany* **94**: 1289–1296.

Nilsson RH, Larsson KH, Larsson E, *et al*. (2006). Fruiting body guided molecular identification of root-tip mantle mycelia provides strong indications of ectomycorrhizal associations in two species of *Sistotrema* (*Basidiomycota*). *Mycological Research* **110**: 1426–1432.

Nilsson RH, Tedersoo L, Abarenkov K, *et al*. (2012). Five simple guidelines for establishing basic authenticity and reliability of newly generated fungal ITS sequences. *MycoKeys* **4**: 37–63.

Niskanen T, Liimatainen K, Nuytinck J, *et al.* (2018). Identifying and naming the currently known diversity of the genus *Hydnum*, with an emphasis on European and North American taxa. *Mycologia* **110**: 890–918.

Oberwinkler F (1970). Die gattungen der basidiolichenen. *Berichte der Deutschen Botanischen Gesellschaft* **4**: 139–169.

Ogawa W, Endo N, Fukuda M, *et al.* (2018). Phylogenetic analyses of Japanese golden chanterelles and a new species description, *Cantharellus anzutake sp. nov. Mycoscience* **59**: 153–165.

Olariaga I, Grebenc T, Salcedo I, *et al.* (2012). Two new species of *Hydnum* with ovoid basidiospores: *H. ovoideisporum* and *H. vesterholtii*. *Mycologia* **104**: 1443–1455.

Olariaga I, Jugo B, García-Etxebarria K, *et al.* (2009). Species delimitation in the European species of *Clavulina* (*Cantharellales, Basidiomycota*) inferred from phylogenetic analyses of ITS region and morphological data. *Mycological Research* **113**: 1261–1270.

Olariaga I, Salcedo I (2012). New combinations and notes in clavarioid fungi. *Mycotaxon* **121**: 37–44.

Osmundson TW, Robert VA, Schoch CL, *et al.* (2013). Filling gaps in biodiversity knowledge for macrofungi: contributions and assessment of a herbarium collection DNA barcode sequencing project. *PLoS One* **8**: e62419.

Parad GA, Ghobad-Nejhad M, Tabari M, *et al.* (2018). *Cantharellus alborufescens* and *C. ferruginascens (Cantharellaceae, Basidiomycota*) new to Iran. *Cryptogamie Mycologie* **39**: 1–12.

Peck CH (1873). Report of the Botanist (1869). *Annual Report on the New York State Museum of Natural History* **23**: 27–135.

Persoon CH (1825). *Mycologia Europaea* **2**: 1–214.

Petersen RH (1967). Notes on clavarioid fungi. VII. Redefinition of the *Clavaria vernalis – C. mucida* complex. *American Midland Naturalist* **77**: 205–221.

Petersen RH (1969). Notes on cantharelloid fungi. II. Some new taxa, and notes on *Pseudocraterellus*. *Persoonia* **5**: 211–223.

Petersen RH (1975). Notes on cantharelloid fungi. VI. New species of *Craterellus* and infrageneric rearrangement. *Ceska mykologie* **29**: 199–204.

Petersen RH (1979a). Notes on cantharelloid fungi. IX. Illustrations of new or poorly understood taxa. *Nova Hedwigia* **31**: 1–23.

Petersen RH (1979b). Notes on cantharelloid fungi. X. *Cantharellus confluens* and *C. lateritius, Craterellus odoratus* and *C. aureus*. *Sydowia* **32**: 198–208.

Petersen RH (1988). The clavarioid fungi of New Zealand. *Mycologia* **80**: 571–576.

Pérez-Pazos E, Villegas-Ríos M, Garibay-Orijel R, *et al.* (2019). Two new species of *Clavulina* and the first record of *Clavulina reae* from temperate *Abies religiosa* forests in central Mexico. *Mycological Progress* **18**: 1187–1200.

Pine EM, Hibbett DS, Donoghue MJ (1999). Phylogenetic relationships of cantharelloid and clavaroid *Homobasidiomycetes* based on mitochondrial and nuclear rDNA sequences. *Mycologia* **91**: 944–963.

Porter TM, Skillman JE, Moncalvo JM (2008). Fruiting body and soil rDNA sampling detects complementary assemblage of *Agaricomycotina* (*Basidiomycota, Fungi*) in a hemlock dominated forest plot in southern Ontario. *Molecular Ecology* **17**: 3037–3050.

Psurtseva NV, Zmitrovich IV, Malysheva VF (2016). Taxonomy and developmental morphology of *Rogersiomyces malaysianus comb. nov.* (*Cantharellales, Agaricomycetes*). *Botany* **94**: 579–592.

Raja HA, Baker TR, Little JG, *et al.* (2017). DNA barcoding for identification of consumer-relevant mushrooms: a partial solution for product certification? *Food Chemistry* **214**: 383–392.

Rambaut A (2012). *FigTree version 1.4.0*. http://tree.bio.ed.ac.uk/software/figtree.

Redhead SA, Norvell LL, Danell E, *et al.* (2002). Proposals to conserve the names *Cantharellus lutescens* Fr.: Fr. and *C. tubaeformis* Fr.: Fr. (*Basidiomycota*) with conserved types. *Taxon* **51**: 559–562.

Reid DA (1962). Notes on fungi which have been referred to the *Thelephoraceae senso lato*. *Persoonia* **2**: 109–170.

Rinaldi C, Comandini O, Kuyper T (2008). Ectomycorrhizal fungal diversity: separating the wheat from the chaff. *Fungal Diversity* **33**: 1–45.

Ronquist F, Teslenko M, van der Mark P, *et al.* (2012). MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* **61**: 539–542.

Sayers EW, Cavanaugh M, Clark K, *et al.* (2020). GenBank. *Nucleic Acids Research* **48**: 84–86.

Schlechte GB, Hoffmann P (2000). Der Torfhäutchenpilz, *Athelia turficola sp. nov.* (Nebenfruchtform: *Burgoa turficola* anam. *nov.*), eine neue Art auf gärtnerischen Kultursubstraten. *Gartenbauwissenschaft* **65**: 144–146.

Shao SC (2011). *Taxonomy and Phylogeny of the genus Cantharellus from Southwestern China with screening primers on Population Genetics of C. tuberculosporus*. Ph.D. dissertation. Kunming Institute of Botany, Chinese Academy of Sciences, China.

Shao SC, Buyck B, Hofstetter V, *et al.* (2014). *Cantharellus hygrophorus*, a new species in subgenus *Afrocantharellus* from tropical southwestern China. *Cryptogamie Mycologie* **35**: 283–291.

Shao SC, Buyck B, Tian XF, *et al.* (2016a). *Cantharellus phloginus*, a new pink-colored species from southwestern China. *Mycoscience* **57**: 144–149.

Shao SC, Liu PG, Tian XF, *et al.* (2016b). A new species of *Cantharellus* (*Cantharellales, Basidiomycota, Fungi*) from subalpine forest in Yunnan, China. *Phytotaxa* **252**: 273–279.

Shao SC, Liu PG, Wei TZ, *et al.* (2021). New insights into the taxonomy of the genus *Cantharellus* in China: epityfication of *C. yunnanensis* W.F. Chiu and the first record of *C. cibarius* Fr. *Cryptogamie Mycologie* **42**: 25–37.

Shao SC, Tian XF, Liu PG (2011). *Cantharellus* in southwestern China: a new species and a new record. *Mycotaxon* **116**: 437–446.

Smith AH (1968). The *Cantharellaceae* of Michigan. *The Michigan Botanist* **7**: 143–183.

Smith AH, Smith HV, Weber NS (1979). *How to know the non-gilled mushrooms*. Wm. C. Brown, Dubuque: 324.

Smith ME, Henkel TW, Aime MC, *et al.* (2011). Ectomycorrhizal fungal diversity and community structure on three co-occurring leguminous canopy tree species in a Neotropical rainforest. *New Phytologist* **192**: 699–712.

Stamatakis A (2014). RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* **30**: 1312–1313.

Stamatakis A, Hoover P, Rougemont J (2008). A rapid bootstrap algorithm for the RAxML web-servers. *Systematic Biology* **75**: 758–771.

Stöger A, Schaffer J, Ruppitsch W (2006). A rapid and sensitive method for direct detection of *Erwinia amylovora* in symptomatic and asymptomatic plant tissues by polymerase chain reaction. *Journal of Phytopathology* **154**: 469–473.

Sutton BC, Kuthubutheen AJ, Muid S (1984). *Pneumatospora obcoronata gen. et sp. nov.* from Malaysia. *Transactions of the British Mycological Society* **83**: 423–429.

Swenie RA, Baroni TJ, Matheny PB (2018). Six new species and reports of *Hydnum* (*Cantharellales*) from eastern North America. *MycoKeys* **42**: 35–72.

Tedersoo L, Naadel T, Bahram M, *et al.* (2012). Enzymatic activities and stable isotope patterns of ectomycorrhizal fungi in relation to phylogeny and exploration types in an afro-tropical rain forest. *New Phytologist* **195**: 832–843.

Tedersoo L, Smith ME (2013). Lineages of ectomycorrhizal fungi revisited: foraging strategies and novel lineages revealed by sequences from belowground. *Fungal Biology Reviews* **27**: 83–99.

Thacker JR, Henkel TW (2004). New species of *Clavulina* from Guyana. *Mycologia* **96**: 650–657.

Thorn RG, Kim JI, Lebeuf R, *et al.* (2017). The golden chanterelles of Newfoundland and Labrador: a new species, a new record for North America, and a lost species rediscovered. *Botany* **95**: 547–560.

Tian XF, Buyck B, Shao SC, *et al.* (2012). *Cantharellus zangii*, a new subalpine basidiomycete from southwestern China. *Mycotaxon* **120**: 99–103.

Tibpromma S, Hyde J, Jeewon R, *et al.* (2017). Fungal diversity notes 111-252: taxonomic and phylogenetic contributions to fungal taxa. *Fungal Diversity* **83**: 1–261.

Tibuhwa DD (2018). Inventory of the genus *Craterellus* Persoon from Kigoma Region, Tanzania. *Tanzania Journal of Science* **44**: 24–36.

Trappe JM, Castellano MA (2007). *Clavulina lilliputiana*, a diminutive new species from Tasmania. *Australasian Mycologist* **25**: 87–89.

Uehling JK, Henkel TW, Aime MC, *et al.* (2012a). New species and distribution records for *Clavulina* (*Cantharellales, Basidiomycota*) from the Guiana Shield, with a key to the lowland neotropical taxa. *Fungal Biology* **116**: 1263–1274.

Uehling JK, Henkel TW, Aime MC, *et al.* (2012b). New species of *Clavulina* (*Cantharellales, Basidiomycota*) with resupinate and effused basidiomata from the Guiana Shield. *Mycologia* **104**: 547–556.

Veldre V, Abarenkov K, Bahram M, *et al.* (2013). Evolution of nutritional modes of *Ceratobasidiaceae* (*Cantharellales, Basidiomycota*) as revealed from publicly available ITS sequences. *Fungal Ecology* **6**: 256–268.

Vilgalys R, Hester M (1990). Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several *Cryptococcus* species. *Journal of Bacteriology* **172**: 4238–4246.

Vizzini A, Picillo B, Ercole E, *et al.* (2013). Detecting the variability of *Hydnum ovoideisporum (Agaricomycetes, Cantharellales*) on the basis of Italian collections, and *H. magnorufescens sp. nov. Mycosphere* **4**: 32–44.

Wang XH, Das K, Horman J, *et al*. (2018). Fungal biodiversity profiles 51–60. *Cryptogamie Mycologie* **39**: 211–257.

Wartchow F (2012). *Clavulina incrustata*, a new species from Pernambuco, Brazil. *Cryptogamie Mycologie* **33**: 105–113.

Ważny R (2014). Ectomycorrhizal communities associated with silver fir seedlings (*Abies alba* Mill.) differ largely in mature silver fir stands and in Scots pine forecrops. *Annals of Forest Science* **71**: 801–810.

Weresub LK, LeClair PM (1971). On *Papulaspora* and bulbilliferous basidiomycetes *Burgoa* and *Minimedusa*. *Canadian Journal of Botany* **49**: 2203–2213.

White TJ, Bruns T, Lee S, Taylor J (1990). Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: *PCR protocols, a guide to methods and applications* (Innis MA, Gelfand DH, Sninsky JJ, White TJ, eds). Academic, San Diego.

Wilson AM, Aime MC, Dierks J, Mueller GM, Henkel TW (2012). *Cantharellaceae* of Guyana I: new species, combinations and distribution records of *Craterellus* and a synopsis of known taxa. *Mycologia* **104**: 1466–1477.

Wright SH, Berch SM, Berbee ML (2009). The effect of fertilization on the belowground diversity and community composition of ectomycorrhizal fungi associated with western hemlock (*Tsuga heterophylla*). *Mycorrhiza* **19**: 267–276.

Wu CL, He Y, Yan J, *et al*. (2019). Two new species of *Clavulina* (*Cantharellales*) from southwestern China based on morphological and molecular evidence. *Mycological Progress* **18**: 1071–1078.

Yanaga K, Sotome K, Ushijima S, *et al*. (2015). *Hydnum* species producing whitish basidiomata in Japan. *Mycoscience* **56**: 434–442.

Yomyart S, Watling R, Phosri C, *et al*. (2012). Two interesting cantharelloids from Nan and Kanchanaburi provinces, Thailand. *Mycotaxon* **122**: 413–420.

Yuan HS, Lu X, Dai YC, *et al*. (2020). Fungal diversity notes 1277–1386: taxonomic and phylogenetic contributions to fungal taxa. *Fungal Diversity* **104**: 1–266.

Zang M (1980). Some new species of *Basidiomycetes* from the Xizang autonomous region of China. *Acta Microbiologica Sinica* **20**: 29–34.

Zang M, Li B, Xi JX, The Comprehensive Scientific Expedition to the Qinghai-Xizang Plateau, Chinese Academy of Sciences (1996). *Fungi of Hengduan Mountains*. Science Press, Beijing.

Zeller B, Brechet C, Maurice JP, *et al*. (2007). 13C and 15N isotopic fractionation in trees, soils and fungi in a natural forest stand and a Norway spruce plantation. *Annals of Forest Science* **64**: 419–429.

Zhang J, Wu D, Deng CY, *et al*. (2020). A new species of *Craterellus* (*Cantharellales, Hydnaceae*) from Guizhou Province, China. *Phytotaxa* **472**: 259–268.

Zhong XR, Li TH, Jiang ZD, *et al*. (2018). A new yellow species of *Craterellus (Cantharellales, Hydnaceae*) from China. *Phytotaxa* **360**: 35–44.

Zhou LW, Qin WM (2013). *Sistotrema subconfluens sp. nov.* (*Cantharellales, Basidiomycota*) from Changbaishan Nature Reserve, northeastern China. *Mycoscience* **54**: 178–182.

Zhurbenko MP, Pino-Bodas R (2017). A revision of lichenicolous fungi growing on *Cladonia*, mainly from the Northern Hemisphere, with a worldwide key to the known species. *Opuscula Philolichenum* **16**: 188–266.