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

Ting Cao1, Ya-Ping Hu3, Jia-Rui Yu1-2, Tie-Zheng Wei4, and Hai-Sheng Yuan1,2*

1CAS Key Laboratory of Forest Ecology and Management, Institute of Applied Ecology, Chinese Academy of Sciences, Shenyang 110164, PR China; 2University of the Chinese Academy of Sciences, Beijing 100049, PR China; 3Nanjing Institute of Environmental Sciences, MEE/State Environmental Protection Scientific Observation and Research Station for Ecological Environment of Wuyi Mountains, Nanjing 210042, PR China; 4State 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 Sistotremaaceae 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 infer 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 Carisi, Craterellus subgenus Imperforati, subg. Lamelles, subg. Longibasidios, subg. Ovoidei, and Hydnum subgenus Brevispina); seventeen new species (Ca. laevihymeninus, Ca. magnus, subm. Cr. badiogriseus, Cr. crocelebatus, Cr. macrosporus, Cr. squamatus, H. brevispina, H. flabellatum, H. flavidocanum, H. longibasidium, H. pallidocroceum, H. pallidomarginatum, H. sphaericum, H. tenuistipitum and H. ventricosum); two synonyms (Ca. anztutake and Ca. tuberculoporus as Ca. yunnanensis), and two newly recorded species (H. albomagnus and H. minum). The delimitation of the 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 Carisi T. Cao & H.S. Yuan, subg. Craterellus, subg. Imperforati T. Cao & H.S. Yuan, subg. Lamelles T. Cao & H.S. Yuan, subg. Longibasidios 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 Cr. badiogriseus, Cr. crocelebatus T. Cao & H.S. Yuan, Cr. macrosporus T. Cao & H.S. Yuan, Cr. squamatus T. Cao & H.S. Yuan, Hydnum brevispina 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, T. Cao & H.S. Yuan, H. tenuistipitum T. Cao & H.S. Yuan, H. ventricosum T. Cao & H.S. Yuan; New synonyms: Cantharellus anztutake W. Ogawa, N. Endo, M. Fukuda and A. Yamada and Ca. tuberculoporus M. Zang as Ca. yunnanensis W.F. Chiu; Species new to China: Hydnum albomagnus Banker, Hydnum minum Yanga & N. Maek.

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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 Adams and Craterellus Pers. of Cantharellaceae J. Schröt., Clavulinaceae 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 Sistotremaaceae were synonyms of the family Hydnaceae. The new combined Hydnaceae comprised nine genera and was characterised by having stichic basidia and septa with perforate p parishones (Hibbett et al. 2014, Lawrey et al. 2016) did the first phylogenetic 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).
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 Multiclavaula) (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 & Saarenkoski 1993), two to six (e.g. Cantharellus) (Buyck et al. 2014) or eight (e.g. Sistotrema and Sistotrema) (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 Sistotrema are saprotrophic (Eriksson et al. 1984, Boidin & Gilles 1994, Nilsson et al. 2006, Hibbett et al. 2014). Besides, some genera with lichenicicolous or lichenised nutritional modes (e.g. Multiclavaula 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 addition, 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; Lm = mean spore length (arithmetic average of all spores); Wm = mean spore width (arithmetic average of all spores); Q = variation in the ratios of Lm/Wm 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 465 compound microscope. Colour codes are from Kermerup & 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-TcCanth (Buyck et al. 2014) for RPB2 of Cantharellus and RRPB2-5F/bRRPB2-7.1R (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 H₂O (ddH₂O), and 0.9 μL template DNA. PCR amplification was confirmed on 1 % agarose
| Species                        | GenBank No.                | Specimen/culture voucher | Country   |
|-------------------------------|----------------------------|--------------------------|-----------|
|                              | nLSU | ITS       | mtSSU | RPB2 | TEF1 |                      |            |
| **Cantharellales**            |      |           |       |      |      |                      |            |
| Hydnaceae                     |      |           |       |      |      |                      |            |
| Bergerella atrofusca Diederich & Lawrey | -    | MN902070  | -     | -    | -    | Berger 34240 (T)    | Austria    |
| Bryoclavula phyocphila H. Masumoto & Y. Degawa | LC508118 | NR169921  | -     | -    | -    | TNS F-79667 (T)     | Japan      |
| Bulbilla applanata Diederich, Flakus & Etayo | LC544110 | LC544109  | -     | -    | -    | S-287-FB3           | Japan      |
|                              | -    | KC336078  | -     | -    | -    | Flakus 16422 (T)    | Bolivia    |
| Burgella flavoparmeliae Diederich & Lawrey (T) | DQ915469 | -        | -     | -    | -    | JL162-01 (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         |
| Burgosia angulosa Diederich, Lawrey & Etayo | DQ915471 | DQ915480  | -     | -    | -    | JL146-00 (T)        | Spain      |
| B. verzuliiana Gold. (T)      | NG058614 | NR145334  | -     | -    | -    | CBS 131.38 (T)      | Japan      |
| Cantharellus addalaensis Henn. | KF294667 | -        | KF294592 | KF294745 | JX192992 | BB 98.033 (neotype) | Tanzania   |
|                              | KF294621 | -        | KF294550 | KF294695 | JX192976 | BB 98.057           | Tanzania   |
| Ca. africabarius Buyck & V. Hofstetter | KF294668 | -        | KF294593 | KF294746 | JX192993 | BB 96.235 (T)       | Zambia     |
|                              | KF294669 | -        | KF294594 | KF294747 | JX192994 | BB 96.236           | Zambia     |
| Ca. albidoletescens Buyck, Eyssart. & V. Hofst. | KF294646 | KF981365 | KF294577 | KF294723 | JX192982 | BB 08.070 (T)       | Madagascar |
|                              | KF294645 | -        | KF294576 | KF294722 | KF294752 | BB 08.057           | Madagascar |
| Ca. alborefulescens (Malengo) Papetti & S. Alberti | KR677531 | KR677493 | -     | KX907235 | KX907216 | AH44223             | Spain      |
| Ca. albovenosus Buyck, Antonin & Ryoo | KX929161 | KX907209 | -     | KX907232 | KX907243 | BB 12.075           | Switzerland |
|                              | -    | -        | -     | -    | -    | MW124387            | Korea      |
|                              | -    | -        | -     | -    | -    | KY271942            | Korea      |
| Ca. albus S.P. Jian & B. Feng | MT782540 | -        | -     | MT776012 | MT776015 | MT776017            | China      |
|                              | MT782542 | -        | -     | MT776014 | MT776017 | MT776017            | China      |
| Ca. altipes Buyck & V. Hofst. | KF294636 | -        | KF294567 | KF294713 | GQ914945 | BB 07.162           | USA        |
|                              | KF294627 | -        | KF294556 | KF294702 | GQ914939 | BB 07.019 (T)       | USA        |

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| Species | GenBank No. | Specimen/culture voucher | Country |
|---------|-------------|--------------------------|---------|
| **Ca. ambohitantelyensis Buyck & V. Hofst.** | KF294656 | BB 08.336 (T) | Madagascar |
| **Ca. amethystus (Quel.) Sacc.** | KF294639 JN944020 KF294570 KF294716 GQ914953 | BB 07.284 | Slovakia |
| **Ca. anzutake W. Ogawa, N. Endo, M. Fukuda and A. Yamada** | LC085415 LC085359 | TNS-F-61925 (T) | Japan |
| **Ca. appalachiensis R.H. Petersen** | KF294635 - KF294565 KF294711 GQ914979 | BB 07.123 | USA |
| **Ca. brunneopallidus Buyck, Randrianj. & V. Hofst.** | MK422941 - MT002300 MT004809 MK422925 | BB 11.116 | Madagascar |
| **Ca. californiaus D. Arora & J.S. Dunham** | KF294635 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 | PRL8916 | USA |
| **Ca. cerinoalbus Eyssart. & Walleyn** | KP639214 KP639200 - | PRL8332 | USA |
| **Ca. cinnabarinus (Schwein.) Schwein.** | KF294630 - KF294530 KF294705 GQ914984 | BB 07.053 | USA |
| **Ca. citrinus Buyck, R. Ryoo & Antonín** | - - - | MW124385 | Korea |
| **Ca. congoensis Beeli** | KF294609 - KF294542 1GQ914984 | BB 98.039 | Tanzania |
| **Ca. conspicus Eyssart., Buyck & Verbeken** | - - | GE 99.560 | Zimbabwe |
| **Ca. curvatus Buyck, R. Ryoo & Antonín** | - - | MW124390 | Korea |
| **Ca. cyphelloides Suhara & S. Kurogi** | NG058027 NR154853 - | TNS-F-61721 (T) | Japan |
| **Ca. decolorans Eyssart. & Buyck** | KF294654 NR154788 - KF294731 GQ914968 | 469/BB 08.278 | Madagascar |
| **Ca. dentatilus Heinem.** | KF294616 - KF294690 | BB 98.013 | Tanzania |
| **Ca. ferruginascens P.D. Orton** | KR677524 KR677486 - KX828750 KX828829 | BIO-Fungi 11700 | Spain |
| **Ca. ferruginascens P.D. Orton** | KF294638 - KF294569 KF294715 GQ914952 | BB 07.283 | Slovakia |
| Species | GenBank No. | Specimen/culture voucher | Country |
|---------|-------------|--------------------------|---------|
| Ca. flavolateritius Buyck & V. Hofst. | KX896783 | VH 1076 | USA |
| Ca. gracilis Buyck & V. Hofst. | KF294612, KX857095, KX857094 | VH 1078 (T), BB 98.234 (T) | USA, Tanzania |
| Ca. guyanensis Mont. | KX857095, KX857094 | 1517/1501/MRG07 | Guyana |
| Ca. hainanensis N.K. Zeng, Zhi Q. Liang & S. Jiang | KY407524, KY407521 | FH MU 1931 (T), BB 98.036 (T) | China, Tanzania |
| Ca. humidicolus Buyck & V. Hofst. | KF294666, KJ004002 | BB 98.036 (T) | Tanzania |
| Ca. hygrophorus Shao, Buyck & Yu | KF294633, KF294650, KF294613 | BB 98.036, KY407524, JX192971 | Tanzania, China, Tanzania |
| Ca. ibityensis Buyck, Randrianj. & V. Hofst. | KF294651 | BB 08.203 | Madagascar |
| Ca. lateritius (Berk.) Singer | KF294650, KF294628, KF294663 | BB 08.196 (T) | Madagascar |
| Ca. laevihymeninus MW979520, MW979521 | MW980543, MW980544 | Yuan 13900, Yuan 13902 | China |
| Ca. lewisii Buyck & V. Hofst. | JN940597, KF294623 | BB 07.003 (T) | USA |
| Ca. magnus MW979516, MW979517 | MW980524, MW980525 | Wei 10319, Wei 10244 | China |
| Ca. minor Peck | KF294632, KF294625 | BB 07.057 | USA |
| Ca. miomboensis Buyck & V. Hofst. | KF294613, KF294608 | BB 98.021 (T), BB 96.197 (T) | Tanzania, Madagascar |
| Ca. nigrescens Buyc, Randrianj. & V. Hofst. | KF294614, KF294611 | BB 101095, BB 98.037 | Tanzania, China |
| Ca. pellens Pilat | KX907215, KX907178 | BB 09.409 | Italy |
| Ca. parvisporus (Eyssart. & Buyck) Buyck & V. Hofst. | KF294614 | BB 08.020 | Tanzania |
| Ca. parvisporus Eyssart. & Buyck | KF294611 | BB 08.037 | Tanzania |
| Ca. phloginus S.C. Shao & P.G. Liu | KF801100, KF801101 | SSC99 (T) | China |

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| Species                          | GenBank No.                  | Specimen/culture voucher | Country   |
|---------------------------------|------------------------------|--------------------------|-----------|
| **Ca. phloginus**               | MW979518, MW979519           | Yuan 14468               | China     |
|                                 | MW999424, MW999425           |                          |           |
| **Ca. platyphyllus Heinem.**    | KF294620, KF294617           | BB 98.126 (T), BB 98.012 | Tanzania  |
|                                 | MW979519, MW999424           |                          |           |
| **Ca. platyphyllus subsp. Bojerensis Eyssart. & Buyck** | KF294648                  | BB 08.160                | Madagascar|
| **Ca. romagnesianus Eyssart. & Buyck** | KX828806, KX828807          | PC0085043 (T)            | France    |
| **Ca. roseocanus (Redhead, Norvell & Danelli) Redhead, Norvell & Moncalvo** | KX828810                  | AH44218                  | Spain     |
| **Ca. sebosus Buyck, Randrianj. & V. Hofst.** | KF294652                  | BB 08.234 (T)            | Madagascar|
| **Ca. splendens Buyck**         | KF294649, KF294671           | BB 96.199, BB 96.306     | Zambia    |
|                                 | KF294618, KF294670           |                          |           |
| **Ca. subalbidus A.H. Sm. & Morse** | AY041149, AY041179         | OSC 75937                | USA       |
| **Ca. subamethysteus Eyssart. & D. Stubbe** | KX828814                  | OSC 81782                | USA       |
| **Ca. subincarnatus Eyssart. & Buyck** | KF294661                  | DS 06.218 (T)            | Malaysia  |
| **Ca. subminor**                | MW979522, MW979523, MW979524 | Yuan 13917, Yuan 13925, Yuan 13926 | China, China, China |
| **Ca. subpruinosus Eyssart. & Buyck** | MW979530                  |                             |           |
| **Ca. symoensii Heinem.**       | KF294619, KF294618           | BB 98.113 (epitype), BB 98.011 | Tanzania, Tanzania |
|                                 | KF294629, KF294622           |                          |           |
| **Ca. tabernensis Feib. & Cibula** | JN940608, JN940609         | BB 07.064, BB 07.040     | USA, USA  |
| **Ca. tanzanicus Buyck & V. Hofst.** | JN940600                  | BB 07.125 (T)            | USA       |
| **Ca. tenuithrix Buyck & V. Hofstetter** | JN940600, KF294629          | BB 07.035 (T)            | USA       |
| Species | GenBank No. | Specimen/culture voucher | Country |
|---------|-------------|--------------------------|---------|
| Ca. texensis Buyck & V. Hofst | JN940601 | KF294964 | BB 07.120 | USA |
| | KF294626 | KF294555 | BB 07.018 (T) | USA |
| Ca. tomentosoides Buyck & V. Hofst. | MK422937 | MT002295 | BB16.007 (T) | Central African Republic |
| Ca. tomentosus Eyssart. & Buyck | KF294672 | KF294597 | BB 88.060 (T) | Tanzania |
| | KF294610 | KF294543 | BB 88.038 | Tanzania |
| Ca. tuberculosporus M. Zang | KU720305 | - | - | China |
| | KU720306 | - | - | China |
| Ca. vaginatus S.C. Shao, X.F. Tian & P.G. Liu | HM594681 | HO416692 | SSC 6 | China |
| Ca. versicolor S.C. Shao & P.G. Liu | MW979525 | MW980531 | MW999458 | Yuan 13640 | China |
| | MW979526 | MW980532 | MW999459 | MW999427 | Yuan 13681 | China |
| Ca. yunnanensis W.F. Chiu | KU720333 | - | - | XieXD174 | China |
| | MW979527 | - | - | MW999428 | Yuan 13983 | China |
| Ca. yunnanensis “as Cantharellus anzutake” | MW979514 | MW980541 | - | MW999422 | Yuan 14539 | 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 albicus Fr. | MT921161 | - | - | - | HGASMF01-3581 (T) | China |
| | MT921162 | - | - | - | HGASMF01-10046 | China |
| Cr. albostrigosus C.K. Pradeep & K.B. Vrinda | MG593194 | - | - | - | TBGT16577 (T) | India |
| Cr. atratoxides T.W. Henkel, Aime & A.W. Wilson | JQ915129 | JQ915103 | - | - | TH8473 | Guyana |
| | NG042660 | JQ915111 | - | - | TH9232 (T) | Guyana |

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| Species                          | GenBank No.                      | Specimen/culture voucher | Country       |
|---------------------------------|----------------------------------|--------------------------|---------------|
| **Cr. atratus** (Corner) Yomyart, Watling, Phosri, Piap. & Shian. | JQ915118 JQ915092 - - - - | MCA1070 Guyana          |
| **Cr. atrobrunneolus** T. Cao & H.S. Yuan | MN894058 MN902353 - - - - | Yuan 13878 China        |
| **Cr. badiogriseus**            | MW979532 MW980548 - - - MW999432 | Yuan 14776 China        |
| **Cr. caeruleofuscus** A.H. Sm. | MW979533 MW980549 - - - MW999433 | Yuan 14779 China        |
| **Cr. carolinensis** R.H. Petersen | - GU590930 - - | ADW00122 USA           |
| **Cr. cinereoacinereus** T.W. Henkel & A.W. Wilson | JQ915130 JQ915104 - - - - | TH8999 Guyana          |
| **Cr. cinereus** (Pers.) Pers.   | JF412278 - - - - | isolate 107-08 (T) India |
| **Cr. cornucopioides** (L.) Pers. | - UDB000053 - - | KF01-46 Denmark         |
| **Cr. crocealis**               | MW979529 MW980572 - MW999460 MW999430 | Yuan 14623 China        |
| **Cr. crocealis** T.W. Henkel & Aime | MW979530 MW980573 - MW999461 MW999431 | Yuan 14647 China        |
| **Cr. excelsus** T.W. Henkel & Aime | JQ915127 JQ915101 - - - | TH7515 Guyana          |
| **Cr. fallax** A.H. Sm.         | AY700188 DG205680 - - | AFOTL-ID 286 USA        |
| **Cr. hasleri** R.H. Petersen   | - GU590931 - - | RHP55560 USA            |
| **Cr. ignicolor** (R.H. Petersen) Dahlan, Danell & Spatafora | AF105314 - - - | UPSF 11794 USA          |
| **Cr. indicus** D. Kumari, Ram. Upadhyay & Mod.S. Reddy | NG060387 NR119831 - - | PUN 3884 (T) India     |
| **Cr. inusitatus** C.K. Pradeep & K.B. Vrinda | MG593195 - | MSR6 India              |
| **Cr. lutescens** (Fr.) Fr.     | MG701171 MG727896 - - | GDMG48105 (T) China     |
| **Cr. lutescens** T.H. Li & X.R. Zhong | MG727898 MG727899 - | GDMG46532 China        |
|                                | - AY082606 - - | taxon:104198 Ireland    |
|                                | - GU373513 - - | H 6005875 Finland       |
| Species                          | GenBank No.               | Specimen/culture voucher | Country   |
|---------------------------------|---------------------------|--------------------------|-----------|
| **Cr. macroporus**              | MW979531                  | Yuan 14782               | China     |
|                                  | MW980574                  |                          |           |
| **Cr. melanoxeros**             | JQ976983                  | SS576                    | Sweden    |
| (Desm.) Pérez-De-Greg.          |                           |                          |           |
| **Cr. odoratus** (Schwein.) Fr. | AF105306                  | UPSF 11794               | USA       |
| **Cr. olivaceoluteus** T.W. Henkel, Aime & A.W. Wilson | JQ915124 | MCA3186                  | Guyana    |
|                                  | JQ915098                  |                          |           |
| **Cr. parvogriseus** U. Singh, K. Das & Buyck | JQ915135 | THB205 (T)               | Guyana    |
|                                  | JQ915109                  |                          |           |
| **Cr. pleuroboïdes** T.W. Henkel, Aime & S.L. Mill.) A.W. Wilson | JQ915123 | MCA3124                  | Guyana    |
|                                  | JQ915097                  |                          |           |
| **Cr. shoreae** Hembrom, K. Das, A. Panhar & Buyck | JQ915136 | THB220                   | Guyana    |
|                                  | KY290585                  | CAL 1396 (T)             | India     |
| **Cr. squamatus**               | MW979534                  | Yuan 14520               | China     |
|                                  | MW980571                  |                         |           |
| **Cr. strigous T.W. Henkel, Aime & A.W. Wilson** | MW979535 | Yuan 14721               | China     |
|                                  | MW980570                  |                         |           |
| **Cr. tubaeformis** (Fr.) Quel. | JQ915120                  | MCA1750                  | Guyana    |
|                                  | JQ915094                  |                          |           |
| **Hydnum albertense** Niskanen & Liimat. | JQ915134 | THB204 (T)               | Guyana    |
|                                  | JQ915108                  |                          |           |
| **Hy. albomagnum** Banker       | DQ898741                  | TM 0268                  | Canada    |
|                                  | -                         |                            |           |
| **Hy. berkeleyanum** K. Das, Hembrom, A. Baghela & Vizzini | DQ218305 | AFTOL-ID 471             | USA       |
|                                  | DQ234553                  |                            |           |
| **Hy. boreorepandum** Niskanen, Liimat. & Nemela | MW979536 | AFC234568                | USA       |
|                                  | -                         |                            |           |
|                                  | NR158533                  | CAL 1656 (T)             | India     |
| **Hy. boreorepandum** Niskanen, Liimat. & Nemela | NG070500 |                          |           |
|                                  | KU612667                  | H KAS77834                | China     |
| **Hy. boreorepandum** Niskanen, Liimat. & Nemela | MW979538 | Wei 10375                | China     |
|                                  | KU812525                  |                            |           |
| **Hy. boreorepandum** Niskanen, Liimat. & Nemela | - | HTN 1679                 | Finland   |
|                                  | KX388657                  |                            |           |
| **Hy. boreorepandum** Niskanen, Liimat. & Nemela | - | H 6003711 (T)            | Finland   |

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| Species                              | GenBank No.          | Specimen/culture voucher | Country |
|--------------------------------------|----------------------|--------------------------|---------|
| **nLSU**                             | **ITS**              | **mtSSU**                | **RPB2**| **TEF1** |
| Hy. brevispinum                      | MW979559            | MW980578                 | -       | -        | Wei 10214 | China |
| Hy. canadense Niskanen & Liimat.     | MW979560            | MW980579                 | -       | -        | Wei 10258 | China |
| Hy. cremeoalbum Liimat. & Niskanen   | KX388681            | -                        | -       | -        | HTN 09-006 (T) | Canada |
| Hy. ellipsosporum Ostrow & Beenken  | AB906674            | AB906678                 | -       | -        | TUMH 40462 | Japan |
| Hy. ellipsosporum Ostrow & Beenken  | KU612676            | KU612619                 | -       | -        | HKAS92345 | China |
| Hy. cremeoalbum Liimat. & Niskanen   | HY379944            | HY379936                 | -       | -        | RAS 246 (T) | USA |
| Hy. ellipsosporum Ostrow & Beenken  | HY8117158           | HY8117157                | -       | -        | HY5579 (T) | Germany |
| Hy. ferruginescens Swenie & Matheny  | HY3799155           | HY379942                 | -       | -        | HY16005 (T) | USA |
| Hy. flabellatum                      | HY90556             | HY90575                  | -       | -        | Yuan 14708 | China |
| Hy. flavidocanum                     | MW979545            | MW980545                 | MW980533| MW999466| MW999440 | Yuan 13903a | China |
| Hy. flavidocanum                     | MW979546            | MW980560                 | MW980536| MW999467| MW999441 | Yuan 13900a | China |
| Hy. ibericum Olaniga, Liimat. & Niskanen | HY547879         | HY547845                 | -       | -        | HY547845 | Spain |
| Hy. jussii Niskanen, Liimat. & Kytov | HY388655            | HY388655                 | HY388655| HY999436| HY999437 | HY999437 | Finland |
| Hy. longibasidium                    | MW979539            | MW980533                 | MW999464| MW999438| MW999439 | Wei 10383 | China |
| Hy. magnorufescens Vizzini, Picillo & Contu | KU612669          | KU612659                 | -       | -        | voucher 161209 | Slovenia |
| Hy. melitosarx Ruots., Huhtinen, Olaniga, Niskanen, Liimat. & Ammirati | KC293545 | KC293545 | - | - | HG2818 (T) | Italy |
| Hy. melitocephalidum Kranab., Liimat. & Niskanen | KC388683 | KC388683 | - | - | H 7043937 (T) | USA |
| Hy. melitocephalidum Kranab., Liimat. & Niskanen | KC388685 | KC388685 | - | - | K 176869 | UK |
| Hy. melitocephalidum Kranab., Liimat. & Niskanen | FJ845406 | FJ845406 | - | - | SMI356 (T) | Canada |
| Species                        | GenBank No.          | Specimen/culture   | Country |
|-------------------------------|----------------------|--------------------|---------|
|                               | nLSU | ITS | mtSSU | RPB2 | TEF1 | voucher                  |                     |
| **Hy. minum Yanaga & N. Maek.** |      |     |       |      |     | TUMH60737 (T)       | Japan               |
|                               | KY407528 | -   | -     | -    | -    | N.K.Zeng2819          | China               |
|                               | MW979543 | MW980557 | - | - | - | Wei 10252 | China |
|                               | MW979544 | MW980558 | - | - | - | Wei 10260 | China |
| **Hy. multiscolor Liimat. & Niskanen** |       |     |       |      |     | LJU GIS 1336 (T) | Slovenia |
|                               | - | AJ547885 | - | - | - | REB 341 | USA |
| **Hy. neorespandum Niskanen & Liimat.** |       |     |       |      |     | HTN10-095 (T) | Canada |
|                               | - | KX388659 | - | - | - | HTN 10-086 | Canada |
| **Hy. olympicum Niskanen, Liimat. & Ammirati** |       |     |       |      |     | 09-134 (T) | USA |
|                               | - | KX388661 | - | - | - | - | - |
| **Hy. oregonense Norvell, Liimat. & Niskanen** |       |     |       |      |     | SAT-10-208-05 | USA |
|                               | - | MT955159 | - | - | - | HVM61 | USA |
| **Hy. ovoidesporum Olariaga, Grebenc, Salcedo & M.P. Martin** |       |     |       |      |     | PNW-MS g2010502h1-09 (T) | USA |
|                               | - | AJ534972 | - | - | - | voucher 71106 | Slovenia |
| **Hy. pallidocroceum** | MW979554 | MW980568 | - | - | MW999449 | BIO Fungi 12683 (T) | Spain |
|                               | MW979555 | MW980569 | - | - | MW999450 | Yuan 14023 | China |
| **Hy. pallidomarginatum** | MW979552 | MW980566 | MW980539 | MW999473 | MW999447 | Yuan 13928a | China |
|                               | MW979553 | MW980567 | MW980540 | MW999474 | MW999448 | Yuan 13940a | China |
| **Hy. quebecense Niskanen & Liimat.** |       |     |       |      |     | HTN 10-064 (T) | Canada |
|                               | - | KX388662 | - | - | - | CN9 | USA |
| **Hy. repandum L.** | - | NR164553 | - | - | - | H6003710 (T) | Finland |
| **Hy. repando-orientale Liimat. & Niskanen** |       |     |       |      |     | TUMH60745 (HT) | Japan |
|                               | - | AB906684 | - | - | - | TUMH60743 | Japan |
| **Hy. rufescens Pers.** | - | KX388688 | - | - | - | H 6003708 (epitype) | Finland |
|                               | - | KX388656 | - | - | - | HTN 7839 | Estonia |
| **Hy. slovenicum Liimat. & Niskanen** |       |     |       |      |     | LJU GIS 1338 (T) | Slovenia |
|                               | - | AJ547870 | - | - | - | LJU GIS 1340 | Slovenia |
|                               | - | AJ547884 | - | - | - | - | - |
| Species                  | nLSU     | ITS     | mtSSU | RPB2 | TEF1 | Specimen/culture voucher | Country            |
|-------------------------|----------|---------|-------|------|------|--------------------------|--------------------|
| Hydnum sp.              | KU612668 | KU612607| -     | -    | -    | HKAS82411                | Taiwan-Island      |
|                         | KU612644 | KU612597| -     | -    | -    | HKA61337                 | China              |
| Hydnum sp.2             | KU61261  | KU612543| -     | -    | -    | HKAS92340                | China              |
| Hydnum sp.3             | KU612605 | KU612531| -     | -    | -    | HKAS61795                | China              |
| Hydnum sp.6             | KU612617 | KU612541| -     | -    | -    | HKAS51070                | China              |
| Hydnum sp.7             | KU612654 | KU612562| -     | -    | -    | HKAS55410                | China              |
| Hydnum sp.10            | KU612681 | KU612567| -     | -    | -    | HKAS92361                | China              |
| Hydnum sp.13            | KU612617 | KU612541| -     | -    | -    | HKAS55305                | China              |
| Hydnum sp.15            | KU612617 | KU612541| -     | -    | -    | HKAS92336                | China              |
| Hydnum sp.16            | KU612617 | KU612541| -     | -    | -    | HKAS92350                | China              |
| Hy. sphaericum          | MW979549 | MW980563| MW999470| MW999444 | Wei 10243 | China                      |
| Hy. subconnatum Swenie & Matheny | - | MH379930 | -     | -    | -    | RAS235 (T) | USA                |
| Hy. subcremeoalbum Tedersoo, Limat. & Niskanen | - | MH379930 | -     | -    | -    | RAS235 (T) | USA                |
| Hy. submulsicolor Niskanen & Limat. | - | UDB013289 | -     | -    | -    | TU110668 (T) | Papua New Guinea  |
| Hy. subolympicum Limat. & Niskanen | KU612653 | KU612541| -     | -    | -    | HTN 10-132 (T) | Canada            |
| Hy. subovoidesporum Niskanen & Limat. | KU612653 | KU612541| -     | -    | -    | F1188765 | USA                |
| Hy. subovoidesporum Niskanen & Limat. | - | NR158494 | -     | -    | -    | H 800370 (T) | Finland            |
| Hy. subrufescens Niskanen & Limat. | KU612663 | KU612535| -     | -    | -    | HTN 10-154 (T) | Canada            |
Table 1. (Continued).

| Species                  | GenBank No.          | Specimen/culture voucher | Country     |
|--------------------------|----------------------|--------------------------|-------------|
|                          | nLSU | ITS | mtSSU | RPB2 | TEF1 |                      |
| **Hy. subtilior** Svenie & 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** Svenie, Ovrebo & Matheny |     | MH379909 | -     | -    | -    | CLO4985 (T) USA      |
|                          | -    | MH379949 | -     | -    | -    | 10762TJB USA         |
| **Hy. ventricosum**      | MW979547 | MW980561 | MW980537 | MW999468 | MW999442 | Yuan 14536 China      |
|                          | MW979548 | MW980562 | MW980538 | MW999469 | MW999443 | Yuan 14601 China      |
| **Hy. vesterholti** Olariaga, Grebenc, Salcedo & M.P. Martin |     | 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 obscurata (B. Sutton, Kuthub. & Muid) Diederich, Lawrey & Heylen |     | GQ303309 | GQ303278 | - | - | CBS 120605 Thailand |
| Mi. polyspora (Hotson) Weresub & P.M. LeClair |     | MH866167 | MH854646 | - | - | CBS 113.18 (T) USA |
| Multiclavula corynoides (Peck) R.H. Petersen |     | MG833798 | MG833806 | - | - | SH-Ecto-3 China |
| Mu. mucida (Pers.) R.H. Petersen |     | EU909345 | EU909345 | - | - | TUB 011734 Germany |
| Mu. petricola H. Masumoto & Y. Degawa |     | LC516465 | LC516464 | - | - | 356 ex-type (T) Japan |

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| Species                                           | GenBank No.          | Specimen/culture voucher | Country     |
|--------------------------------------------------|----------------------|--------------------------|-------------|
| **Tulasnelliaceae**                               |                      |                          |             |
| Tulasnella asymmetrica Warcup & P.H.B. Talbot     | DQ520101             | AFTOL-ID 1678            | Germany     |
| T. irregularis Warcup & P.H.B. Talbot             |                       |                          |             |
| T. pruinosa Bourdot & Galzin                      |                       |                          |             |
| Tulasnella sp.                                    | DQ520097             | AFTOL-ID 1879            | Germany     |
| T. violea (Quel.) Bourdot & Galzin                |                       |                          |             |
| Species                        | GenBank No.                        | Specimen/culture voucher | Country |
|-------------------------------|-----------------------------------|--------------------------|---------|
| **Ceratobasidiaceae**         |                                   |                          |         |
| Ceratobasidium globisporum Warcup & P.H.B. Talbot | MH873365 DQ278942 - DQ301723 DQ301644 | CBS 569.83 | Australia |
| Ceratobasidium sp.            | AY293171 AF354083 AF354083 | GEL 5602 | USA |
| Ceratorhiza hydrophila (Sacc. & P. Syd.) Z.H. Xu, T.C. Harr., M.L. Gleason & Batzer | MT381951 MT381956 | E14504F | Ecuador |
| Rhizoctonia endophytica H.K. Saksena & Vaartaja | KP171655 KP171640 | DAOM 138188 | Canada |
| Rh. solani J.G. Kühn         | MN078809 MK481078 | BRS17 | India |
| Thanatephorus cucumeris (A.B. Frank) Donk | MH873283 DQ278946 | CBS 700.82 | Panama |
| Uthatobasidium fusisorum (J. Schröt.) Donk | AF518655 | IMI-34886 | USA |
| Uthatobasidium sp.            | AF518664 | HNB-102155 | USA |
| **Botryobasidiaceae**         |                                   |                          |         |
| Botryobasidium obtusisporum J. Erikss. | DQ898729 DQ898733 DQ898769 | GEL3030 | Canada |
| Bo. simile Hol.-Jech.        | DQ898730 KP171641 DQ898770 | GEL2348 | Canada |
| Bo. subcoronatum (Höhn. & Litsch.) Donk | AY647212 DQ301727 DQ301680 | CBS 700.82 | Panama |
| Haplotrichum conspersum (Link) Hol.-Jech. | DQ521414 DQ911612 - DQ521420 | AFTOL-ID 1766 | USA |
| **Oliveoniacae**              |                                   |                          |         |
| 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 coniformis Kobayasi | NG057658 NR154050 | CBS 6979 (T) | Japan |

(continued on next page)
Table 1. (Continued).

| Species | GenBank No. | Specimen/culture voucher | Country |
|---------|-------------|--------------------------|---------|
| Holtermanniella festucosa (Golubev & J.P. Samp.) Libkind, Wuczk., Turchetti & Boekhout | KY107040 KY102693 - KF036779 KF037052 | CBS10162 (T) | Russia |
| Ho. nyarowii (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 Lopandi, 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 + mSSU + 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.
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 *Hydnium* 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 + I + G for RPB2 1st, 2nd, and 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 + G for mtSSU, GTR + I + G for RPB2 1st, 2nd, and 3rd, and TEF1 1st, JC for TEF1 2nd and 3rd, and TEF2 1st + TIM1ef + I + G for TEF1 3rd; the third (*Craterellus*) was divided into four: TIM1 + I + G for nLSU, TrN + I for ITS1, JC

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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.
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. 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.

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Fig. 4. (continued).

Hydnus repando-orientale TUMH60743 Japan
Hydnus repando-orientale TUMH60745 Japan
Hydnus boreorepando HTN 1679 Finland
Hydnus boreorepando H 6003711 Finland
Hydnus repando H 6003710 Finland
Hydnus neorepando HTN10-095 Canada
Hydnus neorepando HTN10-086 Canada
Hydnus washingtonianum UBC F-32538 Canada
Hydnus washingtonianum strain 214 USA

Sect. Hydnus

Hydnus sphacericum Wei 10300 China
Hydnus sphacericum Wei 10262 China
Hydnus sphacericum Wei 10243 China
Hydnus sp.7 HKAS51070 China

Hydnus sp.8 HKAS55410 China

Hydnus vagabundum CLO4985 USA
Hydnus vagabundum 10782TJB USA

Hydnus olympicum 09-134 USA
Hydnus olympicum SAT-10-208-05 USA
Hydnus subolympicum F1188765 USA

Hydnus subolympicum DAO744368 Canada

Hydnus slovenicus LJIU GIS 1338 Slovenia
Hydnus slovenicus LJIU GIS 1340 Slovenia

Sect. Olympica

Hydnus subtilior RAS180 USA
Hydnus subtilior TENNO73034 USA

Hydnus ibericum MA-fungi 3457 Spain
Hydnus ibericum BIO:Fungi:12330 Spain

Hydnus pallidomarginatum Yuan 13940a China
Hydnus pallidomarginatum Yuan 13928a China

Hydnus flabellatum Yuan 14708 China

Hydnus tenuistipitum Wei 10410 China
Hydnus tenuistipitum Wei 10417 China

Hydnus sp.10 HKAS93261 China

Hydnus brevispinum Wei 10214 China
Hydnus brevispinum Wei 10258 China

Hydnus cremealbum TUMH 40462 Japan
Hydnus cremealbum TUMH 60740 Japan
Hydnus cremealbum HKAS92345 China

Hydnus subcremecrum TU110688 Papua New Guinea

Hydnus albomagnum Wei 10194 China
Hydnus albomagnum Wei 10247 China
Hydnus albomagnum AFTOL-ID 471 USA
Hydnus albomagnum RAS231 USA

Hydnus sp.13 HKAS57714 China
Hydnus sp.13 HKAS58838 China

Hydnus treuil TU110403 Papua New Guinea
Hydnus zongloicense GO-2010-142a Mexico

Hydnus minum Wei 10260 China
Hydnus minum N.K.Zeng2819 China
Hydnus minum Wei 10252 China
Hydnus minum TUMH60737 Japan

Hydnus flavidocanum Yuan 13900a China
Hydnus flavidocanum Yuan 13903a China

Hydnus sp. HKAS61337 China
Hydnus sp.15 HKAS55325 China
Hydnus sp.15 HKAS92336 China

Hydnus sp.16 HKAS52807 China
Hydnus sp.16 HKAS92350 China

Subgen. Alba

Sistotrema muscicola taxon:154757 Finland
Sistotrema muscicola KHL 11721 Finland

Outgroup
by performing 1000 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 *Tulasnellaeeae*. Seventeen genera were confirmed in *Hydnaceae*. 

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

| Genera          | Morphology of basidiocarps | Nutritional modes               | Distribution                  | Number of species¹ | 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) |
| Burgeilla       | Bulbil-forming              | Lichenicolous                   | North and South America       | 2                  | Diederich & Lawrey (2007), Diederich et al. (2014) |
| Burgeillopsis   | Bulbil-forming              | Lichenicolous                   | Scotland                      | 1                  | Diederich et al. (2014) |
| Burgoa          | Bulbil-forming              | Lichenicolous                   | Asia, Europe                  | 10                 | Diederich & Lawrey (2007) |
| Cantharellus    | Cantharellloid              | Ectomycoorrhizal                | Worldwide                     | 328                | Buyck et al. (2014) |
| Clavulina       | Clavarioi coralloid/ infundibuliform, resupinate, or effused | Ectomycoorrhizal                | Worldwide                     | 88                 | Smith et al. (2011), Tibpromma et al. (2017) |
| Corallofungus   | Clavarioid                  | -                               | Japan                         | 2                  | He et al. (2019) |
| Craterellus     | Cantharellloid, Tuberiform  | Ectomycoorrhizal                | 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           | Ectomycoorrhizal                | Worldwide                     | 49                 | Feng et al. (2016) |
| Inogoldiella    | -                           | Saprotrophic                    | Australia, Canada, Malaysia   | 3                  | He et al. (2019) |
| Membranomyces   | Resupinate                  | Ectomycoorrhizal                | Asia, Middle East, Europe, Canada, USA | 2 | Argüelles-Moyas et al. (2017), Jülich (1975), Kotiranta & Saarenkoska (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   | Hypochroid                  | Saprotrophic                    | USA, Asia                     | 2                  | Mel’nik et al. (2015), Psurtseva et al. (2016) |
| Sistotrema      | Resupinate, stipitate       | Saprotrophic, Ectomycoorrhizal, Endophyte | Worldwide                     | 55                 | Kirk & Larsson (2013), Hibbett et al. (2014) |
| Sistotremella   | Resupinate                  | Saprotrophic                    | Europe                        | 3                  | Eriksson et al. (1984), Boidin & Gilles (1994) |

¹The number of the species based on the http://www.indexfungorum.org/; and He et al. 2019 (Note and outline of *Basidiomycota*).
The Cantharellus dataset comprises 113 samples i.e., 111 from 61 Cantharellus species and 2 as outgroups (Craterellus tubaeformis and C. comucopioides). The data matrix comprised 385 sequences and had an aligned length of 2675 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, Cantharellus laevihymeninus and Cantharellus subminor are revealed, and two synonyms, Cantharellus anzutake and Cantharellus tuberculosporus as Cantharellus 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. Cinna-barinus, 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 ellipso sporum and Sistotrema muscicola). The data matrix comprised 81 sequences and had an aligned length of 1701 bases. The BI

![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 badogresseus (IFP 019452). G. Craterellus croceaflor (IFP 019454). H. Craterellus macrosporus (IFP 019456). I. Craterellus squamatus (IFP 019457). J. Hydnum brevispinum (IFP 019464). K–L. Hydnum flabilatum (IFP 019459). M–N. Hydnum flavocanum (IFP 019460). O. Hydnum longibasidium (IFP 019462). P–Q. Hydnum pallidocrocus (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.](image_url)
Fig. 6. Microscopic structures of basidiospores. A. Cantharellus laevithymeninus (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 squamosus (IFP 019457). H. Hydnum brevispinum (IFP 019464). I. Hydnum flabelatum (IFP 019459). J. Hydnum flavidocanum (IFP 019460). K. Hydnum longibasidium (IFP 019462). L. Hydnum pallidocrocum (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.
analysis resulted in an average standard deviation of split frequencies = 0.002033. Six subgenera including subgen. Carlosi, 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 1460 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.
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. 9. Microscopic structures of *Cantharellus subminor* (IFP 019445). 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) 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.
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.)
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.
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,
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.
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

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

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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 *Cantharellus 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 (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 sterrig mata and longer terminal cells (up to 70 μm long) of the pileipellis (Buyck et al. 2016b).

*Cantherallus 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 sterrig mata. 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).

**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 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, *Lm* = 7.87 μm, *Wm* = 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* subcylindrical, subclavate to clavate, 22.5–75 × 6.5–10 μm, sometimes with large guttules or finely granulose contents; sterrigma 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. *Slitipellis* 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, *Cantherallus 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).
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 (Buijck 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).
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, Lm = 8.38 μm, Wm = 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 sub-clavate, 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. 18. Microscopic structures of *Hydnum pallidocroceum* (IFP 019466). A. Hymenium and subhymenium. B. Basidiospores. C. Pileipellis. Scale bar = 10 μm.
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, Huangngu 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 stigmata, ellipsoid basidiospores and presence of clamps, but *C. minor* differs by the non-intercurrent 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 stigmata (Evansartier & Buyck 1999). *Cantharellus albus* is another Chinese species embedded 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 (50–69 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 show that four samples (Yuan 13983, 13985, 14539, 14636) which were collected from Liaoning Province, group with *C. yunnanensis* (XieXD 174). *C. tuberculosporus* (HKAS85195 and HKAS85196) 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 KUT20337 (XieXD 174), KM893834 (HKAS85195), KM893835 (HKAS85196) 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.
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* are well-supported clades within the genus *Craterellus* that may also be much reduced (Petersen 1979a). The species in the genus often possess an ectomycorrhizal nutritional mode and are distributed worldwide. Most of the species in the genus *Craterellus* are edible and show diversity in colour (Dahlman 2013, Henkel et al. 2018). Up to now, there are only four species described from China (Berkeley & Curtis 1860, Zhong et al. 2013, Cao et al. 2020). 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. croceilabus*, *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 wrinkled 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. *lavicanus* Sacc., *C. cornucopioides* var. *mediosporus* Corn., *C. cornucopioides* var. *parvisporus* Heinem., *C. cornucopioides* var. *roseus* R. Heim, *C. philippinensis* Bres. and *C. verrucosus* Mass.) 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 & Håland 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. albidos*, *C. albostrigosus*, *C. carolinensis*, *C. hesteri*, *C. indicus*, *C. insulatus*, *C. parvogriseus*, *C. shoreae* and *Pseudocraterellus sinusus* (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 wrinkled 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, Bijesh 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...
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, Myco-taxon 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., Epirc. Syst. Mycol. (Upsal.): 532. 1838. MycoBank MB 190345.

**Notes:** Craterellus luteus and C. odoratus constitute a genus 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 (SB2), lighter than pileal surface. *Pileal context* 0.3–0.5 mm thick, orange-grey to brownish orange (SB2–5C3). *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.

*Basidiocarps* broadly ellipsoid, (7.5–) 8.0–10.5(–11.0) × (6.5–)6.8–8.2(–8.0) μm, Lm = 9.35 μm, Wm = 7.33 μm, Q = 1.25–1.28 (n = 60/2), smooth, thin-walled, IKI–, hyaline, some with granular contents, inamylloid; 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 badiogriseus*, 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 basidiocarps, 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 surface, broadly ellipsoid basidiocarps 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 basidiocarps (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 (6F3–7F3). *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 3–6 mm wide, subconic, hollow; surface glabrous, concolorous with the hymenophore; stipe base equal or slightly enlarged and rarely covered with basal mycelium. Odour fruity.

**Basidiocarps** ellipsoid, (9.0–)10.0–12.0(–12.5) × (6.5–)6.8–8.0(–8.2) μm, Lm = 10.31 μm, Wm = 7.33 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

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Fig. 21. Microscopic structures of *Hydnum tangerinum* (IFP 019473). A. Hymenium and subhymenium. B. Basidiospores. C. Pileipellis. Scale bar = 10 μm.
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, Liao Ning Province, Fushun City, Xinbin County, Gang Shan 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 stigmata 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). The large (up to 15 μm long) spores of Craterellus macrosporus are like those of C. konradi. The European Craterellus konradi has the habit of C. cornucopioides and may be a member of the C. cornucopioides complex. However, Craterellus konradi has yellowish basidiospores (Gulden & Høiland 1989). Craterellus cornucopioides var. parvisporus Heinem. 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 stigmata.

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, Lm = 13.46 μm, Wm = 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, subcylindric 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 stigmata, 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 type (large (up to 15 μm long) spores of Craterellus macrosporus are like those of C. konradi. The European Craterellus konradi has the habit of C. cornucopioides and may be a member of the C. cornucopioides complex. However, Craterellus konradi has yellowish basidiospores (Gulden & Høiland 1989). Craterellus cornucopioides var. parvisporus Heinem. 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 stigmata.

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 stigmata.

Description: Basidiocarps solitary to concrecent, 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, Lm = 13.03 μm, Wm = 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,
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 & Hailand 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, except 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. medioporous* 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 μm) than *C. squamatus* (Heinemann 1958).

*Craterellus croceialbus*, *C. squamatus*, *C. macrosorus*, 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 macrosorus* and *C. squamatus* form a well-supported lineage (Fig. 3). The similarity of the ITS sequences between *C. squamatus* and *C. macrosorus* 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. macrosorus* differs *C. squamatus* by having a larger pleus (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 macrosorus* 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 obvovoid-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* lineage 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 (Grebenč 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. berkelyanum*, *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

**Etyymology:** *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 conccrescent, 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. *Palida* and subg. *Rufescensia* 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, Sanxhi 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/B6). *Pileal margin* thin, entire and slightly decurved, concolorous with the pileal surface. *Pileal context* 1–3 mm thick, pure white. *Hymenophore* hydroid, 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 mm 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 subcylindrical, ventricose, 20–40 × 3–10 μm, sometimes with large guttules or finely granulate contents; sterigmata 4–6, up to 7 μm long, 1.5 mm 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. albium* 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. albium* 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 semi-circular pileus.

**Typus:** *China*, Liaoning Province, Xinxing 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* hydroid, spines non-decurrent or subdecurrent, crowded, evenly distributed; surface orange-white (4A2/B6). *Spines* short, 1–6 mm long, 0.2–0.5 mm thick, concolorous with the pileal surface. *Stipes* central or eccentric, up to 25 mm long, 1–2 mm thick, pure 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). *Pileal margin* thin, entire and straight, concolorous with the pileal surface. *Pileal context* 1–5 mm thick, yellowish white (4A2). *Hymenophore* hydroid, 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 mm per mm, brittle when dry. *Stipe* 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.
**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*, 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 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 mm wide, brittle when dry.

**Notes:** *Hydnum flavidocanum* was collected from a temperate forest in northeast China. It is embedded in the subgenus *Palida* and shares the small to medium basidiocarps, cream-coloured to ochraceous with very pale orange pleiur, 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 flavidocanum* can be differentiated from *H. ibericum* 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. flavidocanum* 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 Pythelotia* differs from *Hydnum flavidocanum* in having one-spored basidia (sometimes), thin-walled pileipellis hyphae with yellowish content and thin-walled and slenderer stipitipellis hyphae (4–8 μm wide) (Oliari et al. 2012).

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

**Diagnosis:** Differs from *Hydnum ferruginescens* in having a subzonate to zonate pileal surface, smaller basidiocarps, larger basidiospores (8.5–11 × 7.8–9.8 μm) and slenderer pileipellis hyphae (up to 5 μm long), 1–3 μm wide at base, 1–3 mm in width, somewhat curving. *Basidiospores* numerous, subcilindrical 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. *Hymenophore* orange to orange-yellow (5B6) when dry; *Pileal margin* subglabrous and smooth, subulate, 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. *Hymenophore* orange to orange-yellow (5B6) when dry; *Pileal context* incurved, concolorous with the pileal surface. *Clamp connections* present. **Notes:** Moist with pilei, 25–40 mm long, 8–10 mm wide, subcilindrical, 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 × 6.8–8.9) × (5.2–5.5–6.5) μm, Lm = 7.75 μm, Wm = 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 subcilindric, subclavate to clavate, 33.5–55 × 5–10 μm, sometimes with large gulletes or finely granulose contents; sterigmata 2–5, up to 5 μm long, 1–3 μm wide at base, somewhat curving. *Basidiospores* numerous, subcilindrical 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. *Hymenophore* orange to orange-yellow (5B6) when dry; *Pileal margin* subglabrous and smooth, subulate, 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. *Hymenophore* orange to orange-yellow (5B6) when dry; *Pileal context* incurved, concolorous with the pileal surface. *Clamp connections* present. **Notes:** Moist with pilei, 25–40 mm long, 8–10 mm wide, subcilindrical, 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.
glabrous, white, staining pale yellow when handled; stipe base enlarged and white basal mycelium absent. Odour mild and fruity.

**Basidiocarps** broadly ellipsoid to subglobose, (8.0–) 8.5–11.0(–11.5) × (7.5–)7.8–9.8(–10.0) μm, Lm = 9.81 μm, Wm = 9.03 μm, Q = 1.08–1.13 (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 gullates 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** filamentosus, 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, Sangzh’i County, Badagong Mt. Nature Reserve, on soil in angiosperm forest, 24 Sep. 2020, T. Cao, paratype, Wei 10367 (IFP 019469).

**Notes:** **Hydnum longibasidium** falls in subg. *Rufescintia* and is closely related to *Hydnum pallidocroceum* (HKAS824411) (Taiwan Island), *H. ferruginascens* (southeastern US) and *H. magnorufescens* (Italian) (Feng et al. 2016, Niskanen et al. 2018). In terms of molecular and morphological characteristics, *Hydnum ferruginascens* 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 ferruginascens* 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. ferruginascens*, 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 140023 (IFP 019466).

**Diagnosis:** Differ 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.

**Basidiocarps** broadly ellipsoid, (7.5–) 7.8–9.5(–10.0) × (5.5–)6.0–7.5(–8.0) μm, Lm = 9.09 μm, Wm = 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 gullates 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** filamentosus, 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. mellceopalidum* as well as *H. albertense*. *Hydnum mellceopalidum* 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 μm vs. 7.5–8.5 × 6–7 μm).

**Description:** Basidiocarps solitary to concrescent, sometimes multiplepilose, 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 color 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, spores 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 mm wide, 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, *Lm* = 8.75 μm, *Wm* = 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* subcylindrical, 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 filamentosa,* 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 embedded 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 (Sweenie 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, We10243 (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 mm per mm, brittle when dry. Stipe central or eccentric, 15–25 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.

**Basidiocarps** broadly ellipsoid, (7.5–)8.0–8.8(–)9.0 × (6.0–)6.5–7.5(–)8.0 μm, Lm = 8.36 μm, Wm = 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 gills or finely granulose contents; sterrigmates 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. **Stipurpellis** 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 HKASS1070 and were all collected from subtropical China. Although the coverage between the ITS sequences of Wei 10243 (holotype of H. sphaericum, 647 bp) and HKASS1070 (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 share the small to medium basidiocarps, orange-tinted pileal surface and non-decurrent spines with presence of clamps, but **H. melitosarx** in having subglobose basidiospores. The genus type species Hydnum tangerinum 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, 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 basidiocarps 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 sterrigmates, and presence of puleurocystidia (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 basidiocarps and basidia with 3–6 sterrigmates.

**Description:** Basidiocarps solitary or concrescent, fleshy and leathery when fresh, becoming soft Cory 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, velutinicate, 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 toward 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, greish 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.

**Basidiocarps** broadly ellipsoid, (7–)7.2–8.8(–)9 × (5.5–)5.8–7(–)7.5 μm, Lm = 8.11 μm, Wm = 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 gills or finely granulose contents; sterrigmates 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. **Stipurpellis** composed of subcylindrical hyphae, slightly thick-walled, interwoven, 3.5–13 μm wide, terminal elements rounded at apex. **Clamp connections** present.

**Materials 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 basidiocarps, 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 basidiocarps (Q avg. = 1.11) and basidia with 3 sterrigmates (Niskanen et al. 2018). **Hydnum muliscolor** and H. submuliscolor both share medium basidiocarps, orange-tinted pileal surface and non-decurrent spines with H. tangerinum, however, H. muliscolor can be differentiated from H. tangerinum by having shorter basidiocarps (Lm = 7.5); H. submuliscolor differs from H. tangerinum in having subglobose basidiocarps (Q avg. = 1.13) and basidia with 3–4 sterrigmates (Niskanen et al. 2018).
**Hydnum tenuistipitum** T. Cao & H. S. Yuan, sp. nov. Myco-Bank MB 839422; Figs 4, 5W, 6Q, 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 (up 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 (5A3) when handled; *stipe* 60 mm long, 2–6 mm wide, subcylindrical, solid; *pore 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, Lm = 7.08 μm, Wm = 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 *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. Myco-Bank MB 839423; Figs 1, 4, 5X–Y, 6Q, 23

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

**Typus:** China. Liaoning Province, Xinkou 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 (25–35 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, glabrous, azonate, orange (6A7) when moist, brown (6D6–6D7) upon drying. *Pilear 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* hydronym, 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, 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, (7.5–)8.2–9.0(−9.5) × (7.0–)7.5–8.5(−9.0) μm, Lm = 8.64 μm, Wm = 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 subcylindrical, 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, Xinkou 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 & Läitum 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. *Rufescantia*, and is similar to *H. ventricosum* in having the non-recurved 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 (7.8–7.2 μm) (Niskanen et al. 2018). *Hydnum subrufescens* is a species described from Canada and is a synonym of *H. aerostatisporum* according to Svenie et al. (2018). It is related to *H. ventricosum* in having an orange-tinted pileus surface and non-recurved 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., Mycosenwie 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 atrofuscus* 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 atrofuscus* 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. atrofuscus* belongs to *Hydnaceae*. *Bergerella atrofuscus* and *Bryoclavula phyophila* form a lineage with moderate support in our tree. The *Bergerella*-*Bryoclavula* lineage clustered with *Minimedusa* and the three genera form a clade with 46 % support in the ML analysis. Despite the clavarioid basidiocarps and absence of a bulbil-like structure, *Br. phyophila* is a lichenised species (Masumoto & Degawa 2020a). *Minimedusa* is a bulb-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 phyophila* H. Masumoto & Y. Degawa, Mycol. Progr. 19(7): 708. 2020. MycoBank MB 833864.

Notes: *Bryoclavula* has a single species, *Br. phyophila*, 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 phyophila* 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 clade 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 clade according to Masumoto & Degawa (2020a). The three species of *Sistotrema* differ from the taxa in the other three genera of the lichen-associated clade 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 planulata* 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 (Goitánich 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 Sistotremaecae 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-Moyoa et al. 2017), while Bulbilla is strictly lichenicolous (Diederich et al. 2014). Morphologically, species in Clavulina have clavarianoid to coralloid/infundibuliform, resupinate or effused basidiocarps (Henkel et al., 2011, Uehling et al. 2012, a, b, Felipe 2012, He et al. 2016). Membranomyces has resupinate ones (Jülich 1975) and Bulbilla forms bulblasts (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). Bulblasts 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 bulbiliferous 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 *Atheia* 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. eximium* in our tree (Fig. 1). *S. biggsiae* Hallennb., *S. efibulatum* (J. Eriks.). Hjortstam and *S. serendissima* (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* (Holm.) 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, Felipe 2012, He et al. 2016). Membranomyces has resupinate ones (Jülich 1975) and Bulbilla forms bulbils (Diederich et al. 2007). Burgoa turficola (Donk 1961), but now belongs to Hydnaceae (Hibbett et al. 2014). Clavulina was recovered as a monophyletic group in the Cantharellales (Thacker & Henkel 2004, Moncalvo et al. 2006, Oliariga et al. 2009). It was initially selected as the type genus of Clavulinaeae Donk (Donk 1961) and some authors do not agree to this classification. The genus is characterised by simple or branched, clavarianoid to coralloid (occasionally cantharelloid, cerebriform, resupinate or effused) basidiocarps, a monomitic hyphal system and smooth, hyaline, 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, Ważyń 2014). Clavulina was recovered as a monophyletic group in the Cantharellales (Thacker & Henkel 2004, Moncalvo et al. 2006, Oliariga et al. 2009). It was initially selected as the type genus of Clavulinaeae 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 spori us and Me. detectabilis (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 & Saarenkoska 1993). Membranomyces is characterised by resupinate and effused basidiocarps with smooth hymenophore, monomitic hyphal system, and smooth, ellipsoid to subglobose basidiospores (Jülich 1975, Kotiranta & Saarenkoska 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).

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

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

Notes: Minimediuma was recovered as a monophyletic genus in the Cantharellales and includes three bulbiliferous species. Minimediuma polyspora and Mi. obconorata 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 Minimediuma in the Cantharellales grouping with Sistotrema coronilla. In the tree of Masumoto & Degawa (2020a), Minimediuma settled 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 Minimediuma 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 Muc. 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 2020a). 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, Bergeella, 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, Burgeilla and Burgellopsis as well as the saprotrophic genus Rogersiomycy 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 ellipsoidal or irregular bulbs, internally composed of roundish to ellipsoidal or polyhedral cells, clamps absent in bulbs but present in culture (Lawrey et al. 2016). Morphologically, Neoburgoa is closely related to another lichenicolous genus Burgeilla in having yellow to orange bulbs. However, Neoburgoa has a distant phylogenetic relationship with Burgeilla as well as with other lichenicolous bulbil-forming genera including Bergearella, Bulbilla, Burgeilla, Burgellopsis, Burgoa and Minimediuma 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).

Rogersiomycy J.L. Crane & Schokn., Am. J. Bot. 65: 903. 1978. MycoBank MB 16287.

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

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

Notes: Rogersiomycy is a saprotrophic genus nested in Hydnaceae and characterised by gymnocarpaceous basidiocarps composed of fuscate or loose synnematous holobasidia and the spores germinating directly via hyphae (Crane & Schoknchet 1978, Psurtseva et al. 2016). The genus consists of two species: the type species Rogersiomycy okefeokeenesis J.L. Crane and Schokn. which was described from the USA and the Vietnamese species R. malaysiana. Phylogenetic analysis shows Rogersiomycy grouping with Sistotrema oblongisporum in the family. In our molecular analysis, it was recovered in Hydnaceae and forms a weakly supported group with the bulbiliferous 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 Rogersiomycy in Hydnaceae should be further clarified.
Sistotrema Fr., Syst. Mycol. (Lundae) 1: 426. 1821. MycoBank MB 18551.

Synonym: Galziniella Parmasto, Conspl. System. Corticiac. (Tartu): 39. 1968. MycoBank MB 17637.

Heptasporium Bref., Unters. Gesammtgeb. Mykol. (Leipzig) 14: 167. 1908. MycoBank MB 17738.

Hydnотrema 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 varies from smooth, poroid to hydnoid (Eriksson et al. 1984). The genus is often characterised by the uniform basidium 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 confluens, and S. muscicola as well as S. aboluteum 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, Multiclava 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 immediately 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. eximium-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.

Sistotrema Hjarstam, Cortic. N. Eur. (Oslo) 7: 1379. 1984. MycoBank MB 25849.

Type species: Sistotrema perpusilla Hjarstam, Cortic. N. Eur. (Oslo) 7: 1381. 1984. MycoBank MB 115329.

Notes: Sistotrema is typified by S. perpusilla and characterised by resupinate, effuse and dry crustaceous basidiocarps, a monomitic hyphal system, basidium with 6–8 sterigmata and ellipsoid, cyanophilous basidiospores (Eriksson et al. 1984). There are three species in the genus, the type species, Sistotrema perpusilla, and S. hauerslevii Hjarstam and S. paulii-corticioides Boidin & Gilles. They are all wood-decaying fungi and mainly distributed in Europe (Sweden, Denmark, and France) (Eriksson et al. 1984, Boidin & Gilles 1994). Sistotrema belongs to Hydnaceae according to the notes in He et al. (2019), however, molecular phylogenies for Sistotrema are rare. A phylogenetic tree based on nLSU in Masumoto & Degawa (2020a) recovered Sistotrema 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 Sistotrema 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.

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

Type species: Gloeomuco 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. Erkiss. & Hjortstam, Cortic. N. Eur. (Oslo) 6: 1247. 1981. MycoBank MB 25481.

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

DISCUSSION

In the phylogenetic tree (Fig. 1), Hydnaceae is the sister clade of Tulasiellaceae. The two families together with Botryobasidaceae and Ceratobasidaceae 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 cantharellloid 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 cantharellloid 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. eximium in the tree, whether Burgoa is monophyletic requires further research since Burgoa turicola is nested in the Agaricales (Diederich & Lawrey 2007, Lawrey et al. 2007). The six genera Corallofungus, Gloeomuco, Ingridiella, Parasteropsis, 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, Paullioticium J. Erikss. was also placed in Hydnaceae (http://www.indexfungorum.org 2021) though several phylogeny analyses have suggested the genus placed outside of the Cantharelles (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 Rickereilla clade of the Hymenochaetales. Here, we follow the previous studies and consider the genera Paullioticium, 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 confluentus-subconfluents” 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 “Clavulinia-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 Sistotremastrum, clavarioid species of Multiclavula and Bryoclavula, bulb-forming species Bergerella, Bulbilla, Burgeila, Burgellina, Minimedusa, Neoburgoa, Burgoa as well as hypochonid species in Rogersiomycetes 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 bulb-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), saprotrrophic (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 | Gloeomuco | 2 |
| 1b | Basidiocarps not watery gelatinous | 3 |
| 2a | Clavarioid basidiocarps present | 3 |
| 2b | Clavarioid basidiocarps absent | 6 |
| 3a | Basidiocarps with distinct fragrance | Corallofungus | 4 |
| 3b | Basidiocarps without special odour | 4 |
| 4a | With ECM nutritional model | Clavulina | 5 |
| 4b | Lichen-associated | 5 |
| 5a | Lichenised, globose thallus present | Multiclavula | 6b |
| 5b | Lichenised, globose thallus absent | 6a |
| 6a | Conidia present | 7 |
| 6b | Conidia absent | 7 |
| 7a | Conidia with subglobal form, basidiocarps tubiform | Parasteropsis | 8 |
| 7b | Conidia without subglobal form, basidiocarps unknown | 8 |
| 8a | Conidia with narrow form and often branched; conidiophores long, up to 120 μm long | Ingridiella | 9 |
| 8b | Conidia cylindrical, conidiophores short, < 10 μm present | 9 |
| 9a | Bulbills absent | 10 |
| 9b | Bulbills present | 11 |
| 10a | Clamps present | 11 |
| 10b | Clamps absent | Burgeila |
| 11a | Bulbills < 110 μm wide | 12 |
| 11b | Bulbills > 300 μm wide | 13 |
| 12a | Bulbills loosely attached to the substratum | 13 |
| 12b | Bulbills tightly attached to the substratum | Neoburgoa |
| 13a | Bulbills up to 450 μm wide, whitish bulbills present | Burgoa |
| 13b | Bulbills < 300 μm wide, whitish bulbills absent | 15 |
| 14a | Bulbills < 200 μm wide | 16 |
| 14b | Bulbills 200–500 μm wide | Bulbilla |
| 15a | Bulbills pure white, 100–200 μm wide | Burgeilliosis |
| 15b | Bulbills dark reddish brown, 25–35 μm wide | Bergerella |
| 16a | Dendrohyphidia present | 17 |
| 16b | Dendrohyphidia absent | 18 |
| 17a | Cystidia present, spores ellipsoid | Sistotremastrum |
| 17b | Cystidia absent, spores subfusiform | Repetobasidiellum |
| 18a | Synnematous basidia absent | 19 |
| 18b | Synnematous basidia present | Rogersiomycetes |
| 19a | Clamps present | 20 |
| 19b | Clamps absent | Membranomyces |
| 20a | Hydnoid hymenophore present | 21 |
| 20b | Hydnoid hymenophore absent | 22 |
| 21a | Corticioid basidiocarps absent | Hydnstrombium |
| 21b | Corticioid basidiocarps present | Sistotrema |
| 22a | Pileus non-perforation, stipe often solid | 23b |
| 22b | Pileus sometimes perforation, stipe often hollow | Craterellus |

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