Multi-Gene Phylogeny and Taxonomy of *Hydnellum* (Bankeraceae, Basidiomycota) from China

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Abstract: The genus *Hydnellum* is an important group of stipitate hydnaceous fungi which can form ectomycorrhiza with many species of woody plants. In recent decades, the frequency and number of basidiocarps observed in China have been declining significantly. So far, however, we know little about the species diversity of *Hydnellum* in China. In this study, we conducted molecular phylogenetic analyses based on sections of multiple loci, including the large subunit of nuclear ribosomal RNA gene (nLSU), the internal transcribed spacer regions (ITS), the small subunit of nuclear ribosomal RNA gene (SSU) and the second-largest subunit of RNA polymerase II gene (RPB2), as well as morphological studies, of collected samples of *Hydnellum* from China. We also inferred Maximum Likelihood and Bayesian phylogenies for the order Thelephorales from the dataset of the combined nLSU and ITS. This study has revealed the phylogenetic position of *Hydnellum* in the order Thelephorales, and phylogenetically confirmed ten major clades in Thelephorales; Twenty-nine taxa are proposed, described or reported, including 10 new subgenera (*Hydnellum* subgenus *Hydnellum*, subg. *Caesipinsum*, subg. *Croceum*, subg. *Infatum*, subg. *Rhizomorphum*, subg. *Scabrosum*, subg. *Spongiosum*, subg. *Subindufibulatum*, subg. *Violaceum* and subg. *Zonatum*), 11 new species (*Hydnellum atrorubrum*, *H. atrospinosum*, *H. bomiense*, *H. brunneo-rubrum*, *H. fibulatum*, *H. granulosum*, *H. infatum*, *H. rubidofuscum*, *H. squamulosum*, *H. salcatum* and *H. yunnanense*), 3 newly recorded species (*H. caeruleum*, *H. peckii* and *H. spongiosipes*) and 5 notable specimens (*Hydnellum* sp 1, *H. sp 2, H. sp 3, *H. sp 4 and H. sp 5). A classification system based on the morphological characteristics (especially the hyphal structure types) and molecular analyses is proposed to accommodate most species in *Hydnellum*. The distinguishing characters of the subgenera and the new species with their closely related taxa are discussed. A key to the species of *Hydnellum* from China is provided.

Keywords: nLSU + ITS + SSU + RPB2; stipitate hydnoid fungi; taxonomy; new taxa; Thelephorales

1. Introduction

The genus *Hydnellum*, together with *Bankera*, *Phellodon* and *Sarcodon*, are a homogenous group of soil-inhabiting Basidiomycota (with the common characteristic of a hymenophore with a spinulose hymenium) that belongs to the Bankeraceae, Thelephorales [1,2].

All species of Bankeraceae are considered ectomycorrhizal and are associated with woody plants, mainly members of Pinaceae and Fagaceae [3–7], and colonize natural or relatively undisturbed forests [8]. These fungi can absorb organic substances from host plants and also transport nutrients and water from the soil to the plants, which improves the stability of forest ecosystems [9,10]. In addition, some species of *Hydnellum* have important medicinal functions, including cholesterol-lowering, antioxidant, anti-inflammatory, anti-tumor, immune enhancement, etc. [11]. For instance, Lee et al. [12] suggested that *H. concrencres* extracts prevents the expression of NDV-HN glycoprotein on the cell surface by...
inhibiting the activity of α-glucosidase, thus exhibiting anti-viral function. This can be on par with the health benefit potentials of herbal plant infusions [13].

Due to substantial declines in abundance, they have become the focus of increasing conservation concern [14–16]. This is mainly attributed to the effect of habitat loss, aerial pollution, nitrogen deposition and soil acidification [17–21]. Stipitate hydnoid fungi, as symbols for the recent decline of ectomycorrhizal fungi, have been redlisted in, e.g., Norway, Poland, Germany, and the Netherlands [7,14,18,19,22–24]. Furthermore, an action plan for 14 rare species of hydnoid fungi has been announced to provide strategic management for their future conservation in the UK [25].

The genus Hydnellum is characterized by single to gregarious or coalescent pileate, stipitate basidiocarps, spinous hymenophore, corky to woody, not duplex to duplex, azonate to zonate context, uninflated to inflated generative hyphae, with or without clamp connections, and brown, irregularly ellipsoid to globose, tuberculate basidiospores. Some species display olivaceous or blue-green colours with KOH [1,2,5,26,27]. However, differentiation between closely related species within Hydnellum becomes significantly difficult on account of their macromorphological polymorphism caused by growing around obstacles or fusing to other adjacent basidiocarps [2,27]. Therefore, molecular sequence data are very important in identifying them. Molecular evidence has confirmed that Hydnellum has a close phylogenetic affiliation with the genus Sarcodon, and both genera aggregated in the same clade, named the “Hydnellum-Sarcodon lineage” [28–30]. Furthermore, the phylogenetic analysis of Hydnellum and Sarcodon according to Baird et al. [27] suggested that the generic limits need reassessment. To revise the generic limits and make genera monophyletic, Larsson et al. [31] moved 12 species from Sarcodon to Hydnellum, resulting in the generic circumscription of Hydnellum being amended. Morphologically, basidiospore size appears to separate the genera in most cases.

Most of the described species of Hydnellum are distributed to North America [2,27,32–34] and Europe [1,6,35,36], with a few species reported from Singapore, India, Australia, and New Guinea [26]. About 61 species have been described and transferred to the genus according to Index Fungorum (http://www.indexfungorum.org/ (accessed on 1 August 2021)) and MycoBank; however, only three taxa have been previously reported from China, and detailed molecular studies have not been performed [37]. Some specimens of this genus collected from China were identified as H. aurantiacum, H. ferrugineum and H. suaveolens based solely on morphological characteristics. However, molecular methods revealed that these specimens are misidentified, and the specimens need to be re-identified.

Numerous Hydnellum specimens have been collected from field investigations on stipitate hydnoid fungi in China during the past two decades. During the study of these specimens, twenty-nine new taxa have been identified using morphological characters and phylogenetic analyses of nuc rDNA ITS1-5.8S-ITS2 combined with nuc 28S rDNA, nuc 18S rDNA and nuc RPB2 rDNA sequences. In this paper, we present these taxa with illustrated morphological descriptions, phylogeny and comparison with related and/or similar taxa, a key and classification system.

The aims of this study are: (1) To describe the new taxa of Hydnellum from China and confirm or propose infrageneric subdivision (new subgenera, new species and newly recorded species) based on morphological and phylogenetic analyses; (2) To provide a classification system using hyphal structure types, molecularly supported clades and morphological characteristics within Hydnellum and Sarcodon; and (3) To confirm the phylogenetic position of Hydnellum within the Thelephorales.

2. Materials and Methods
2.1. Morphological Studies

Specimens were deposited at the herbarium of the Institute of Applied Ecology, Chinese Academy of Sciences (IFP). Microscopic procedures followed Mu et al. [38]. Structures were examined microscopically from sections mounted in Cotton Blue (CB): 0.1 mg aniline blue dissolved in 60 g pure lactic acid; CB+ = cyanophilous, CB− = acyanophilous. Amy-
loid and dextrinoid reactions were tested in Melzer’s reagent (IKI): 1.5 g KI (potassium iodide), 0.5 g I (crystalline iodine), 22 g chloral hydrate, 20 mL distilled water; IKI− = neither amyloid nor dextrinoid reaction. Sections were mounted in 5% KOH and studied at magnifications up to 1000× using a Nikon Eclipse E600 microscope (Tokyo, Japan) with phase contrast illumination. Dimensions were measured by the ruler in the eyepiece, with accuracy within 0.1 µm. In presenting basidiospore size ranges, 5% of the measurements at each end of the range are given in parentheses. The following abbreviations are used in the text: Lm = mean spore length, Wm = mean spore width, Q = range of length/width ratios for specimens studied, and n = total number of basidiospores measured from a given number of specimens. The surface morphology for the basidiospores was observed with a Phenom Prox scanning electron microscope (ESEM, Phenom Prox, FEI, The Netherlands) at an accelerating voltage of 20 kV. A thin layer of gold was coated on the samples to avoid charging. Special color terms are from Rayner [39] and Munsell [40].

2.2. Molecular Procedures and Phylogenetic Analyses

Fungal taxa and strains used in this study are listed in Table 1. Phire Plant Direct PCR Kit (Thermo Fisher Scientific, Waltham, MA, USA) procedures were used to extract total genomic DNA from the basidiocarps. Polymerase chain reactions (PCR) was performed on a Bio-Rad T100™ Thermal cycler (Bio-RAD Inc., Hercules, CA, USA). Amplification reactions were performed in a 30 µL reaction mixture using the following final concentrations or total amounts: 0.9 µL template DNA, 15 µL of 2× Phire Plant PCR buffer, 1.5 µL of each primer, 0.6 µL Phire HS II DNA Polymerase, and 10.5 µL ddH2O (double distilled water). Primer sequences for the used genes are provided in Table 2. The PCR lthermal cycling program condition was set as follows: initial denaturation at 98 °C for 5 min, followed by 39 cycles at 98 °C for 30 s, × °C (the annealing temperatures for LROR/LR7, ITS1-F/ITS4, NS1/NS4, and bRPB2-6F/bRPB2-7.1R were 47.2 °C, 57.2 °C, 48 °C and 57.2 °C, respectively) for 30 s, 72 °C for 30 s, and a final extension at 72 °C for 1 min. PCR amplification was confirmed on 1% agarose electrophoresis gels stained with ethidium bromide [41]. DNA sequencing was performed at the Beijing Genomics Institute (BGI). All newly generated sequences were submitted to GenBank. Additional LSU rDNA, ITS rDNA, SSU rDNA and RPB2 rDNA sequences in the dataset used to establish phylogenetic relationships were downloaded from GenBank (http://www.ncbi.nlm.nih.gov/genbank/php (accessed on 10 August 2021)) and UNITE (https://unite.ut.ee/index.php (accessed on 10 August 2021)) (Table 1). Nuclear ribosomal RNA genes were used to determine the phylogenetic position of the new species. After PCR amplification, the products were sequenced in both directions and the sequences were assembled using DNAMAN 8.0. DNA sequences were aligned using MAFFT 7.110 [42]. To ensure the repeatability of the results, alignments were not manually adjusted. The best-fit evolutionary models selected by jmodeltest-2.1.10 for genes were GTR+I+G (nLSU), K80+G (ITS1), K80 (5.8S), JC+G (ITS2), TrN+I+G (SSU), K80+G (RPB2) in the first dataset (Hydnellum and Sarcodon dataset) and GTR+I+G (nLSU), K80+G (ITS1), K80+G (ITS2), K80 (5.8S), K80+G (ITS2) in the second dataset (Thelephorales dataset). These models were applied in Bayesian analyses. All gaps were treated as missing data. Maximum Likelihood (ML) analysis was performed in RAXML v8.2.4 with GTR+I+G model [43]. The best tree was obtained by executing 100 rapid bootstrap inferences and thereafter a thorough search for the most likely tree using one distinct model/data partition with joint branch length optimization [44]. Bayesian analyses with MrBayes 3.2.4 [45] implementing the Markov Chain Monte Carlo (MCMC) technique and parameters pre-determined with MrMODELTEST2.3 [46,47] were performed. Four simultaneous Markov chains were run starting from random trees, 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 were obtained from the 50% majority rule consensus of the trees kept. Then the FigTree v1.3.1 were used to visualize the resulting trees.
Table 1. Voucher numbers, geographic origins and GenBank accession numbers for the specimens included; sequences produced in this study are in bold.

| Species                           | Geographic Origin | Voucher Number        | GenBank Accessions No.               |
|-----------------------------------|-------------------|-----------------------|--------------------------------------|
|                                   |                   |                       | SSU | ITS | nLSU | RPB2 |
| Amaurodon aquicoeruleus Agerer    | Australia         | UK452                 | –   | –   | –    | –    |
| A. sumatranus Miettinen & Köljalg | Indonesia         | O. Miettinen5877      | –   | –   | –    | –    |
| A. viridis (Alb. & Schwein.) J. Schröt. | Norway | KHLarsson14947b       | –   | –   | –    | –    |
| A. viridis (J.C. Schmidt)         | Russia            | TAA149664             | –   | –   | AM490942 | AM490944 |
| Bankera fuligineola tus (J.C. Schmidt) | Sweden     | Larson14947-10        | –   | –   | –    | –    |
| Coker & Beers ex Pouzar           | Estonia           | TAA152454             | –   | –   | AM490942 | AM490944 |
| B. violascens (Alb. & Schwein.) Pouzar | Finland | MVijanen130902       | –   | –   | –    | –    |
| B. violascens                      | Norway            | KHLarsson149664       | –   | –   | –    | –    |
| Boletopsis grisea (Peck) Bondartsev & Singer | Sweden     | UPS F-120382         | –   | –   | –    | –    |
| B. grisea                          | Spain             | AH 4297               | –   | –   | –    | –    |
| Bankera fuligineoalba              | Sweden            | ELarsson400-13        | –   | –   | –    | –    |
| B. fuligineoalba                   | Estonia           | TAA152454             | –   | –   | –    | –    |
| B. violascens                      | Norway            | KHLarsson149664       | –   | –   | –    | –    |
| Boletopsis grisea (Peck) Bondartsev & Singer | Finland | MVijanen130902       | –   | –   | –    | –    |
| B. grisea                          | Sweden            | UPS F-120382         | –   | –   | –    | –    |
| Hydnellum amygdaliolens            | Iberian Peninsula | SC-2011               | –   | –   | –    | –    |
| H. atrorubrum                      | China             | Wei8315               | –   | –   | –    | –    |
| H. aurantiacum (Batsch) P. Karst.  | Norway            | EBendiksen77-07       | –   | –   | –    | –    |
| H. auraticuli (Bretzelm.) Maas Geest. | Norway   | OF29502               | –   | –   | –    | –    |
| H. auraticulix                      | Norway            | OF242763              | –   | –   | –    | –    |
| H. bomiense                        | China             | Yuan13759             | –   | –   | –    | –    |
| H. biforme                         | China             | Yuan13767             | –   | –   | –    | –    |
| H. brownii                         | China             | Yuan13767             | –   | –   | –    | –    |
| H. caeruleum (Hornem.) P. Karst.   | Norway            | EBendiksen584-11      | –   | –   | –    | –    |
| H. cernuum                          | China             | Wei1474a              | –   | –   | –    | –    |
| H. chlorogenum K.A. Harrison       | China             | Wei8094               | –   | –   | –    | –    |
| H. coactatum Y.H. Mu & H.S. Yuan   | China             | Shi181                | –   | –   | –    | –    |
| H. complicatum Banker              | USA               | REB-71                | –   | –   | –    | –    |
| H. complicatum                     | USA               | REB-329               | –   | –   | –    | –    |
| H. ferrugineum (Fr.) P. Karst.     | Sweden            | Larson197-14          | –   | –   | –    | –    |
| H. ferrugipes Coker                | USA               | RPB2-16               | –   | –   | –    | –    |
| H. fibulatum                       | China             | Yuan14646             | –   | –   | –    | –    |
| H. fuscus                          | Australia         | GB-019562             | –   | –   | –    | –    |
| H. fuscosulcatus                   | Sweden            | GB-019562             | –   | –   | –    | –    |
| H. fuscusulcatus                   | Norway            | OF242833              | –   | –   | –    | –    |
| H. fuscusulcatus                   | Norway            | OF24087               | –   | –   | –    | –    |
| H. ferrugineum                     | Sweden            | Larson197-14          | –   | –   | –    | –    |
| H. ferrugipes                      | USA               | RPB2-16               | –   | –   | –    | –    |
| H. fibulatum                       | China             | Yuan14656             | –   | –   | –    | –    |
| H. fibulatum                       | China             | Yuan14656             | –   | –   | –    | –    |
| H. fibulatum                       | China             | Yuan14656             | –   | –   | –    | –    |
| H. fuligineoalgidae                | Norway            | OF242833              | –   | –   | –    | –    |
| H. fuligineoalgidae                | Norway            | OF24087               | –   | –   | –    | –    |
| H. fuscosulcatus                   | Sweden            | Larson197-14          | –   | –   | –    | –    |
| H. fuscosulcatus                   | Norway            | OF24087               | –   | –   | –    | –    |
| H. fuscosulcatus                   | Norway            | OF24087               | –   | –   | –    | –    |
| H. glaucescens                     | Sweden            | BNyleen130918         | –   | –   | –    | –    |
| H. glaucescens                     | Sweden            | LA120818              | –   | –   | –    | –    |
| H. fuscosulcatus                   | USA               | OSC 113641            | –   | –   | –    | –    |
| H. fuscosulcatus                   | USA               | OSC 113641            | –   | –   | –    | –    |
| H. glaucescens                     | USA               | OSC 113641            | –   | –   | –    | –    |
| H. glaucescens                     | USA               | OSC 113641            | –   | –   | –    | –    |
| H. glaucescens                     | USA               | OSC 113641            | –   | –   | –    | –    |
| H. glaucescens                     | USA               | OSC 113641            | –   | –   | –    | –    |
Table 1. Cont.

| Species               | Geographic Origin | Voucher Number | GenBank Accessions No. |
|-----------------------|-------------------|----------------|------------------------|
|                       |                   |                | SSU        | ITS       | nLSU    | RPB2     |
| **H. glaucopus**      | Sweden            | Edvinson110926 | –          | MK602745  | MK602745| –        |
| **H. geogenium**      | –                 | AFOTL-ID 680   | AY752971   | DQ218304  | AY631900| DQ408133|
| **H. geogenium**      | Norway            | OF296213       | –          | MK602724  | MK602724| –        |
| **H. graciipes**      | Sweden            | ELarsson219-11 | –          | MK602726  | MK602726| –        |
| **H. graciipes**      | Sweden            | GB-013779      | –          | MK602727  | MK602727| –        |
| **H. granulosum**     | China             | Yuan12213a     | MW579921   | MW579948  | MW579893| OK254213|
| **H. granulosum**     | China             | Yuan12213b     | MW579920   | MW579947  | MW579892| OK254212|
| **H. grosselepidotum**| China             | Wei8120        | –          | MN846274  | MN846283| –        |
| **H. grosselepidotum**| China             | Wei8075        | –          | MN846276  | MN846285| –        |
| **H. illudens**       | Sweden            | GB-015819      | –          | MW144341  | MW144341| –        |
| **H. illudens**       | Norway            | O-F-242769     | –          | MW144335  | MW144335| –        |
| **H. inflatum**       | China             | Wang80         | MW579922   | MW579949  | MW579894| OK254210|
| **H. inflatum**       | China             | Shi506         | MW579923   | MW579950  | MW579895| OK254211|
| **H. joeides**        | Sweden            | KHjortstam17589| –          | MK602750  | MK602750| –        |
| **H. joeides**        | China             | Nitare110829   | –          | MK602751  | MK602751| –        |
| **H. lepidum**        | Sweden            | Nitare110829   | –          | MK602754  | MK602754| –        |
| **H. lepidum**        | China             | RGCarlsson10-065| –         | MK602752  | MK602752| –        |
| **H. lidongensis**    | China             | We8365         | –          | MN846280  | MN846289| –        |
| **H. lidongensis**    | China             | We8329         | –          | MN846281  | MN846290| –        |
| **H. Lundellii**      | Norway            | OF242639       | –          | MK602759  | MK602759| –        |
| **H. Lundellii**      | Norway            | OF295814       | –          | MK602760  | MK602760| –        |
| **H. martioflacatum** | Norway            | OF242435       | –          | MK602762  | MK602762| –        |
| **H. martioflacatum** | Norway            | OF242872       | –          | MK602761  | MK602761| –        |
| **H. mirabile**       | Sweden            | SLund140912    | –          | MK602730  | MK602730| –        |
| **H. mirabile**       | Sweden            | ELarsson170-14 | –          | MK602729  | MK602729| –        |
| **H. nemorosum**      | Norway            | OF-242352      | –          | MW144372  | MW144372| –        |
| **H. nemorosum**      | Sweden            | GB-0195631     | –          | MW144373  | MW144373| –        |
| **H. parvum**         | USA               | REB-131        | –          | JN135187  | –        | –        |
| **H. parvum**         | USA               | REB-392        | –          | KC571717  | –        | –        |
| **H. peckii**         | Norway            | SSvantesson328 | –          | MK602731  | MK602731| –        |
| **H. peckii**         | Sweden            | ELarsson174-14 | –          | MK602732  | MK602732| –        |
| **H. peckii**         | China             | Yuan13708      | MW579931   | MW579966  | MW579905| OK254214|
| **H. peckii**         | China             | Yuan13720      | MW579932   | MW579967  | MW579906| OK254215|
| **H. pineticola**     | USA               | REB-49         | –          | KC571733  | –        | –        |
| **H. pineticola**     | USA               | REB-43         | –          | JN135175  | –        | –        |
| **H. piperatum**      | USA               | REB-332        | –          | JN135173  | –        | –        |
| **H. piperatum**      | USA               | REB-304        | –          | KC571723  | –        | –        |
| **H. richardi**       | USA               | SEW 93         | –          | AY569031  | –        | –        |
| **H. roseoliacum**    | Sweden            | GB-0195936     | –          | MW144373  | MW144374| –        |
| **H. roseoliacum**    | Sweden            | GB-0195687     | –          | MW144375  | MW144375| –        |
| **H. rubidofuscin**   | China             | Yuan14561      | MW579924   | MW579951  | MW579896| OK254207|
| **H. rubidofuscin**   | China             | Yuan14587      | MW579925   | MW579952  | MW579897| OK254208|
| **H. rubidofuscin**   | China             | Yuan14654      | –          | MW579953  | MW579898| OK254209|
| **H. scabrosum**      | Norway            | OF360777       | –          | MK602765  | MK602765| –        |
| **H. scabrosum**      | Norway            | OF292320       | –          | MK602766  | MK602766| –        |
| **H. scabrosum**      | Sweden            | GB-0195792     | –          | MW144380  | MW144380| –        |
| **H. scabrosum**      | Sweden            | GB-0195807     | –          | MW144381  | MW144381| –        |
| **H. scleropodium**  | USA               | REB-3          | –          | JN135186  | –        | –        |
| Species                        | Geographic Origin | Voucher Number | SSU | ITS | nLSU | RPB2 |
|-------------------------------|-------------------|----------------|-----|-----|------|------|
| H. scleropodium              | USA               | REB-352        | –   | –   | –    | –    |
| H. scrobiculatum (Fr.) P. Karst. | USA             | REB-78         | –   | –   | JN135181 | –   |
| H. spongiosipes (Peck) Pouzar | USA               | REB-107        | –   | –   | KC571743 | –   |
| H. spongiosipes              | USA               | REB-52         | –   | –   | JN135184 | –   |
| H. spongiosipes              | China             | Yuan14517      | MW579933 | MW579968 | MW579907 | OK254219 |
| H. squamulosum               | China             | Yuan13615      | MW579954 | –   | –   | –   |
| H. squamulosum               | China             | Yuan13625      | MW579956 | MW579899 | OK254204 | –   |
| H. squamulosum               | China             | Yuan13743      | MW579955 | –   | OK254203 | –   |
| H. suaveolens (Scop.) P. Karst. | Sweden         | ELarsson8-14   | –   | –   | MK602735 | MK602736 |
| H. suaveolens                | Norway            | SSvantesson877 | –   | –   | MK602736 | –   |
| H. subsuccosum K.A. Harrison | USA               | SEW 55         | –   | –   | AY569033 | –   |
| H. subsuccosum               | USA               | REB-10         | –   | –   | JN135178 | –   |
| H. suaveolii (Banker) E. Larss., K.H. Larss. & Kõljalg | USA           | REB-119        | –   | –   | KC571782 | –   |
| H. versipelle (Fr.) E. Larss., K.H. Larss. & Kõljalg | Sweden         | RGCarlsson13-057 | –   | –   | MK602771 | MK602771 |
| H. versipelle                 | Sweden            | RGCarlsson11-08 | –   | –   | MK602772 | MK602772 |
| Hydnellum sp 1               | China             | Shi164         | –   | –   | MW579969 | –   |
| Hydnellum sp 2               | China             | Yuan14387      | MW579934 | MW579970 | MW579908 | –   |
| Hydnellum sp 3               | China             | Yuan14388      | MW579971 | –   | –   | –   |
| Hydnellum sp 4               | China             | Wang295        | –   | –   | MW579972 | –   |
| Hydnellum sp 5               | China             | Yuan14594      | MW579935 | MW579973 | MW579909 | OK254205 |
| Lenzitopsis dairi L.W. Zhou & Kõljalg | China       | Yuan 2959   | –   | –   | JN169799 | JN169795 |
| L. dairi                      | China             | Yuan2952       | –   | –   | JN169798 | JN169794 |
| L. oxycedri Malençon & Bertault | Spain        | KHLarsson15304 | –   | –   | MK602774 | MK602774 |
| L. oxycedri                   | UK                | 635            | –   | –   | JN169800 | JN169796 |
| Odontia fibrosa (Berk. & M.A. Curtis) Kõljalg | China | TU115028        | –   | –   | MK602775 | MK602775 |
| O. fibrosa                    | China             | LL_17          | –   | –   | MT678878 | –   |
| O. sparsa Yuan, Y.C. Dai & H.S. Yuan | China | Yuan10718       | –   | –   | MG719980 | –   |
| O. sparsa                     | China             | Yuan10780      | –   | –   | MG719979 | –   |
| Phellodon cf. niger           | Sweden            | ELarsson35-14  | –   | –   | MK602782 | MK602782 |
| P. tomentosus (L.) Banker     | Norway            | EBendiksen11-810 | –   | –   | MK602781 | MK602781 |
| P. tomentosus                 | –                 | BG Thesis      | –   | –   | AF518637 | –   |
| Polyozellus mariae Voitk & Kõljalg | Canada  | TU117235     | –   | –   | MF100826 | –   |
| P. mariae                     | Canada            | TU117235       | –   | –   | MF100826 | –   |
| P. multiplex (Underw.) Murrill | USA               | TU117230       | –   | –   | MF100830 | MF100830 |
| P. multiplex                  | China             | TU115049       | –   | –   | MF100812 | MF100812 |
| Pseudotomentella abundiloba  | Norway            | OF110312       | MK290731 | –   | –   | –   |
| Sarcodon aspratus (Berk.) S. Ito | –                 | –             | DQ448877 | –   | –   | –   |
| Sarcodon aspratus             | Finland           | KHLarsson16190 | MK602780 | MK602780 | –   | –   |
Table 1. Cont.

| Species                        | Geographic Origin | Voucher Number       | GenBank Accessions No.         |
|--------------------------------|-------------------|---------------------|-------------------------------|
|                                |                   |                     | SSU  | ITS  | nLSU  | RPB2  |
| *S. aspratus*                  | Norway            | Svantesson355       | –    | –    | AF335110| –    | –    |
| *S. imbricatus* (L.) P. Karst. | Norway            | Einarsson384-10     | –    | –    | MK602748| MK602748| –    |
| *S. leucopus* (Pers.) Maas Geest & Nannf. | Norway       | OF296099            | –    | –    | MK602755| MK602755| –    |
| *S. quercinofibulatus* Perez-De-Greg., Maas Geest & J. Carbó | Norway | OF296099            | –    | –    | MK602755| MK602755| –    |
| *S. scabripes* (Peck) Banker | Mexico            | FCME:23240          | –    | –    | EU293829| –    | –    |
| *S. squamosus* (Schaeff.) P. Karst. | Sweden       | OF295554            | –    | –    | MK602769| MK602769| –    |
| *S. scabripes* (Peck) Banker | USA               | REB-351             | –    | –    | JN135191| –    | –    |
| *T. ganbajun*                  | China             | GDGM 48899          | –    | –    | MF593267| MF620355| –    |
| *T. iqbali* Nasir & Hanif      | Pakistan          | MH810               | –    | –    | JX241471| –    | –    |
| *T. terrestris* Ehrh.          | Denmark           | DMS-932794          | –    | –    | MT644883| MT644883| –    |
| *T. terrestris*                | Norway            | Einarsson295-13     | –    | –    | MK602777| MK602777| –    |
| *Tomentella fuscocrustosa* H.S. Yuan, X. Lu & Y.C. Dai | China           | Yuan111399          | –    | –    | MK211712| MK446366| –    |
| *T. fuscocrustosa*             | China             | Yuan111420          | –    | –    | MK211713| MK446367| –    |
| *T. patagonica* Kuhar & Rajchenb. | Argentina      | BAF52373            | –    | –    | KT032090| KT032102| –    |
| *T. patagonica*                | Argentina         | BAF52373            | –    | –    | KT032091| KT032103| –    |
| *Tomentellopsis bresadolina* (Sacc. & Trotter) Jülich & Stalpers | Sweden          | JEH 031011          | –    | –    | EU118674| EU118674| –    |
| *T. pulchella* Köljalg & Bernicchia | Norway       | KHlarsson16366      | –    | –    | MK602779| MK602779| –    |

Newly generated sequences in this study are in bold.

Table 2. The gene fragments, their corresponding primers and primer sequences used in this study.

| Genes   | Primers | Primer Sequences (5'-3') | References |
|---------|---------|--------------------------|------------|
| nLSU    | LROR    | ACCCGCTGAACCTAAGC         | Vigalys & Hester 1990 [48] |
|         | LR7     | TACGCACCACCAAGATCT        | Vigalys & Hester 1990 [48] |
| ITS     | ITS1-F  | CTTGCGTATTAGGAAGTAA       | White et al. 1990 [49] |
|         | ITS4    | TCCTCCGCTTATGATGC         | White et al. 1990 [49] |
| nSSU    | NS1     | GATGTGATATTGTCCTC         | White et al. 1990 [49] |
|         | NS4     | CTCCGCTAATTCCTTGAAG       | White et al. 1990 [49] |
| RPB2    | bRPB2-6F| TGGGGATAGGNTGGCYYC       | Liu et al. 1999 [50] |
|         | bRPB2-7.1R| CCCATRGCGYTTMCCATDGC   | Liu et al. 1999 [50] |

3. Results

Phylogenetic Analyses

In the first dataset, 272 sequences derived from four gene loci (nLSU, ITS, SSU and RPB2) were used to build phylogenetic trees; 108 of them were newly generated, including 25 of nLSU, 37 sequences of ITS, 25 of SSU and 21 of RPB2. The phylogenetic construction performed with maximum likelihood and Bayesian Inference (BI) analyses for two combined datasets showed similar topology. The combined LSU-ITS-SSU-RPB2 dataset represented 70 taxa and 3629 characters after being trimmed. *Polyozellus mariae* and *P. multiplex* were used as the outgroups according to phylogenetic analysis of Thelephorales. Bayesian analysis ran for 8 million generations and resulted in an average standard deviation of split frequencies of 0.005062. The same dataset and alignment were analysed
using the ML method. The Maximum Likelihood tree is shown in Figure 1. In the phyloge-netic tree, ten clades which correspond to subgenus Hydnellum, subg. Caesispinosum, subg. Croceum, subg. Inflatum, subg. Rhizomorphum, subg. Scabrosum, subg. Spongiosum, subg. Subindufibulatum, subg. Violaceum and subg. Zonatum were revealed. Twenty-eight sampled specimens formed 11 new species (Hydnellum atrorubrum, H. atrospinosum, H. bomiense, H. brunneorubrum, H. fibulatum, H. granulosum, H. inflatum, H. rubidofuscum, H. squamulosum, H. sulcatum and H. yunnanense) and clustered in a clade that comprised most species of Hydnellum. Four sampled specimens (Wei1474a, Yuan13708 and Yuan13720, Yuan14517) that were confirmed as new records from China clustered with Hydnellum caeruleum, H. peckii and H. spongiosipes with strong support. In addition, five notable specimens, Hydnellum sp 1, Hydnellum sp 2, Hydnellum sp 3, Hydnellum sp 4 and Hydnellum sp 5, formed five separate clades, and need further verification. In the second dataset, the combined ITS and nLSU gene also included sequences from 129 specimens representing 58 taxa of Thelephorales, as well as Stecherinum ochraceum and S. murashkinskyi, which were chosen as outgroups according to previous study [31]. The average standard deviation of split frequencies in the Bayesian analyses reached 0.007357 after running for 8 million generations. The calculated values based on the dataset analysed using the ML method. The Maximum Likelihood tree is shown in Figure 2. It revealed that the Hydnellum clade occupies an independent phylogenetic position. The Hydnellum clade is sister to the Sarcodon clade. According to the phylogenetic tree, ten major clades, Amaurodon clade, Boletopsis clade, Hydnellum clade, Lenzitopsis clade, Odontia clade, Phellodon/Bankera clade, Pseudotomentella/Polyozellus clade, Sarcodon clade, Thelephora/Tomentella clade and Tomentellopsis clade, were identified within the Thelephorales (Figure 2). Therefore, in order to use the maximum amount of genetic information when defining new species, we conducted the first dataset. Meanwhile, ITS trees of Hydnellum and Sarcodon were constructed and produced a topology similar to that generated by the first dataset (see Supplementary, Figure S1). The purpose of executing the second dataset was to demonstrate the phylogenetic position of Hydnellum species in the Thelephorales.
Figure 1. Cont.
Figure 1. Maximum likelihood tree illustrating the phylogeny of *Hydnellum* and *Sarcodon* based on nLSU, ITS, SSU and RPB2 sequence datasets. Branches are labeled with maximum likelihood bootstrap support greater than 50% and Bayesian posterior probabilities greater than 0.95. Newly sequenced collections are in bold.
Figure 2. Cont.
Figure 2. Maximum likelihood phylogenetic analysis based on the nLSU and ITS sequences of Thelephorales. Branches are labeled with maximum likelihood bootstrap support greater than 50% and Bayesian posterior probabilities greater than 0.95. Newly sequenced collections are in bold.

4. Taxonomy

*Hydnellum* subg. *Hydnellum*

MycoBank MB841191

*Etymology.* *Hydnellum* (Latin), refers to the subgenus in which the type species of the genus is located.

Included species: *Hydnellum atrospinosum*, *H. suaveolens*

Type species: *Hydnellum suaveolens* (Scop.) P. Karst.

Notes: This subgenus consists of the genus type *Hydnellum suaveolens* and our new species *H. atrospinosum*; they share the characteristics of dark blue context, decurrent and dark spines, clamped generative hyphae in the context and the spines trama and irregularly oblong, tuberculate basidiospores of similar size. Furthermore, both species occur in coniferous forests [27,34].

*Hydnellum atrospinosum* Y.H. Mu & H.S. Yuan, *sp. nov.* (Figure 3)
Figure 3. *Hydnellum atrospinosum*. (a): Basidiocarps; (b,c): SEM of basidiospores; (d–f): Microscopic structures (drawn from IFP 018516); (d): Section of hymenophore trama with basidia; (e): Hyphae from pileus context; (f): Basidiospores. —Scale bars: (a) = 1 cm; (b) = 3 μm; (c) = 1 μm; (d,e) = 10 μm; (f) = 5 μm.

MycoBank MB839034

Etymology. *Atrospinosum* (Latin), refers to the dark violet spines.
Type: CHINA, Qinghai Province, Qilian County, Binggou Forest Park, ground in Picea forest, 8 September 2012, H. S. Yuan, Yuan 6520 (holotype IFP 018516).

Basidiocarps annual, solitary to gregarious or concrescent, leathery when fresh, becoming hard and light in weight upon drying; taste mild, odor fragrant when dry. *Pileus* irregularly ellipsoid to circular, later flabelliform or semicircular and applanate with age, up to 75 mm diam and 6–11 mm thick at center. *Pileal surface* light orange (5A4) to yellowish brown (5F6), concentrically zonate, scrobiculate when fresh, becoming glabrescent, rugose when dry; margin white (5A1) when fresh, brownish orange (5C6) when dry, even. *Spine surface* dark violet (15F4) when fresh, violet-gray (15F2) when dry; spines up to 2.5 mm long, base up to 0.4 mm diam, conical, 3–4 per mm, decurrent on stipe, without spines at pileus margin, brittle when dry. *Context* not duplex, up to 11 mm thick, light yellow (4A4), brownish gray (7F2) to violet (16F5) or dark blue (20E6), woody. *Stipe* lateral, up to 4 cm long and 3 cm diam, sometimes connate, leathery when fresh, woody upon drying, brown (6E6) to violet gray (15F2), glabrous, inside solid, cylindrical to flatted or broadened below with bulbous base when old. *Hyphal structure*: hyphal system monomitic; generative hyphae with clamp-connections, CB+ in slightly thick-walled hyphae, IKI–; tissues olivaceous in KOH. *Context*: generative hyphae hyaline, thin- to slightly thick-walled, moderately branched, clamped, straight, regularly arranged, sometimes flexuous and collapsed, mostly 3–6 µm diam. *Spines*: generative hyphae hyaline, thin- to slightly thick-walled, moderately branched, more or less parallel along spines, clamped, straight, 2–3 µm diam. *Cystidia* and cystidioles absent. *Basidia* clavate, thin-walled, with four sterigmata (2.1–4.2 µm long), clamped at base, 17–45 × 3–6 µm; basidioides similar to basidia. *Basidiospores* irregular oblong or triangular, brown, thin-walled, tuberculate CB–, IKI–, (4–)4.1–5.1(–5.5) × (3–)3.1–3.9(–4) µm, Lm = 4.6 µm, Wm = 3.2 µm, Q = 1.34–1.44 (n = 60/2); tuberculi isolated, sometimes in groups of two or more, then bi- to trifurcate in shape, up to 1 µm long.

Additional specimens (paratypes) examined: CHINA, Qinghai Province, Qilian County, Binggou Forest Park, ground in *Picea* forest, 8 September 2012, H. S. Yuan, Yuan 6495 (IFP 018495, paratype); Yuan 6514 (IFP 018510, paratype).

Notes: *Hydnellum atrospinosum* and *H. suaveolens* have a close phylogenetic relationship with full support (100% in ML and 1.00 BPP). Morphologically, they both have single to gregarious basidiocarps with glabrous to rugose pileal surface, woody and dark blue context, an eccentric and terete stipe with a bulbous base, conical, decurrent and dark spines, clamped generative hyphae and irregularly oblong, tuberculate basidiocarpes of similar size. However, *H. suaveolens* differs from *H. atrospinosum* by longer spines (up to 6 mm vs. 2.5 mm in *H. atrospinosum*), context tissues turning light blue to green in KOH and presence of inflated hyphae in the context [27,34]. A special characteristic of *H. atrospinosum* is that the clamped generative hyphae are present in all parts of the basidiocarp; this trait can also be observed in *H. cruentum*, *H. cyanopodium*, *H. geogenium* and *H. scleropodium*. *H. cruentum* differs from *H. atrospinosum* by plushy to tomentose pileal surface, grayish blue and slightly longer spines (up to 3.5 mm vs. 2.5 mm in *H. atrospinosum*) and subglobose basidiocarpes [26,27,51]. *H. cyanopodium* and *H. scleropodium* obviously differs in blue spines [27,33,51]. *H. geogenium* differs in reflexed-multiplex and yellow basidiocarps, pale yellow to brown spines and subglobose basidiocarpes [1,27,34].

*Hydnellum* subg. *Caesispinosum* Y.H. Mu & H.S. Yuan, subgen. nov.

*MycoBank* MB841195

**Etymology.** Caesispinosum (Latin), refers to the blue spines.

**Included species:** *Hydnellum cyanopodium*, *H. scleropodium*

**Type species:** *Hydnellum cyanopodium* K.A. Harrison

Notes: The subgenus is composed of two American species, *Hydnellum cyanopodium* and *H. scleropodium*. Blue spines and context and fully clamped hyphae in all parts of basidiocarps are their distinctly common features. In addition, the two species both have rugose and pitted pileal surface and clamped basidia of similar size [33,34,51].

*Hydnellum* subg. *Croceum* Y.H. Mu & H.S. Yuan, subgen. nov.
MycoBank MB841196

Etymology. Croceum (Latin), refers to the orange basidiocarps.

Included species: Hydnellum aurantiacum, H. auratile, H. brunneorubrum, H. chrysinum, H. earlianum

Type species: Hydnellum aurantiacum (Batsch) P. Karst.

Notes: This subgenus includes five species, Hydnellum aurantiacum, H. auratile, H. brunneorubrum, H. chrysinum and H. earlianum. They often have orange basidiocarps, tomentose to matted pileal surface, yellow to orange spines and context, the monomitic hyphal system with uninflated and unclamped hyphae, clavate basidia with simple-septate at base and irregularly subglobose basidiospores [2,26,27,33,34,51].

Hydnellum brunneorubrum Y.H. Mu & H.S. Yuan, sp. nov. (Figure 4)

MycoBank MB839036

Type: CHINA, Liaoning Province, Xinbin County, Gangshan Nature Reserve, on the ground in Fagaceous forest, 30 August 2018, H. S. Yuan, Yuan 12997 (holotype IFP 019384).

Basidiocarps annual, solitary to gregarious or multiple pilei overlapping and fused to form a compound cluster, soft and leathery when fresh, becoming woody and light in weight upon drying; taste mild, odor none when dry. Pileus applanate and ellipsoid to irregularly circular when young, later depressed or infundibuliform to flabelliform with age, up to 40 mm diam and 5–10 mm thick at center. Pileal surface brownish orange (6C8) to brownish red (10D8), azonate, pubescent to floccose when fresh, becoming matted or fibrillose to glabrous when dry; margin white (6A1) to light orange (6A5) when fresh, light orange (5A4) when dry, involute and wavy, sometimes lobed with age. Spine surface golden yellow (5B6) to light brown (7D8) when fresh, light brown (6D7) to dark brown (7F8) when dry; spines up to 4 mm long, base up to 0.3 mm diam, conical, 3–5 per mm, more or less decurrent on stipe, without spines at pileus margin, brittle when dry. Context not duplex, up to 5 mm thick, grayish orange (5B5), woody. Stipe central to lateral, up to 3 cm long and 1 cm diam, sometimes connate, leathery when fresh, woody upon drying, brownish orange (6C8) to light brown (6D7), tomentose, solid inner, cylindrical to flat or attenuate downwards with bulbous base when old. Hyphal structure: hyphal system monomitic; generative hyphae with simple-septa, occasionally encrusted, CB+ in slightly thick-walled hyphae, IKI–; tissues olivaceous in KOH. Context: generative hyphae hyaline, thin- to slightly thick-walled, frequently branched, simple-septate, straight, regularly arranged, sometimes flexuosus and collapsed, mostly 4–6 µm diam. Spines: generative hyphae hyaline, thin-walled, frequently branched, more or less parallel along spines, frequently simple-septate, straight, 2–5 µm diam. Cystidia and cystidioles absent. Basidia clavate, thin-walled, with four sterigmata (2.5–5 µm long), simple-septate at base, 12–50 × 3–7 µm; basidioles similar to basidia. Basidiospores irregularly ellipsoid to subglobose, brown, thin-walled, tuberculate, CB–, IKI–, (4–)4.1–5.1(–5.2) × (3.1–)3.2–4.6(–4.8) µm, Lm = 4.9 µm, Wm = 3.9 µm, Q = 1.23–1.26 (n = 60/2); tuberculi usually isolated, sometimes in groups of two or more, then bi- to trifurcate in shape, up to 0.8 µm long.

Additional specimens (paratypes) examined: CHINA, Liaoning Province, Xinbin County, Gangshan Nature Reserve, on the ground in mixed forest, 30 August 2018, H. S. Yuan, Yuan 12999 (IFP 019385, paratype); Yuan 13004 (IFP 019386, paratype); 2 September 2019, H. S. Yuan, Yuan 14339 (IFP 019387, paratype); Yuan 14340 (IFP 019388, paratype); Yuan 14341 (IFP 019389, paratype); 12 August 2020, H. S. Yuan, Yuan 14562 (IFP 019390, paratype); 26 August 2020, H. S. Yuan, Yuan 14585 (IFP 019391, paratype); 12 September 2020, H. S. Yuan, Yuan 14796 (IFP 019392, paratype); Yuan 14798 (IFP 019393, paratype); Yuan 14799 (IFP 019394, paratype); Benxi County, Guanmenshan National Forest Park, on the ground in mixed forest, 29 August 2020, H. S. Yuan, Yuan 14642 (IFP 019395, paratype); Xinbin County, Qingsongling Forest Park, on the ground in mixed forest, 5 September 2020, H. S. Yuan, Yuan 14668 (IFP 019396, paratype); Yuan 14688 (IFP 019397, paratype).
Figure 4. *Hydnellum brunneorubrum*. (a,b): Basidiocarps; (c,d): SEM of basidiospores; (e-g): Microscopic structures (drawn from IFP 019384); (e): Section of hymenophore trama with basidia; (f): Hyphae from pileus context; (g): Basidiospores. —Scale bars: (a,b) = 1 cm; (c) = 3 µm; (d) = 1 µm; (e,f) = 10 µm; (g) = 5 µm.

Notes: The orange basidiocarps make *Hydnellum brunneorubrum* similar to *H. aurantiacum*, *H. auratile*, *H. chrysinum* and *H. earlianum*. *H. aurantiacum* differs from *H. brunneorubrum* in bigger pileus (up to 100 mm vs. 40 mm in *H. brunneorubrum*) with colliculose and wrinkled pileal surface, longer spines (up to 5 mm vs. up to 4 mm in *H. brunneorubrum*) and longer basidiospores (6–6.7 µm vs. 4.1–5.1 µm in *H. brunneorubrum*) [1]. *H. auratile*
differs in squamulose, concentrically zoned and occasionally black stained pileal surface, duplex stipe context with black lines in the centre and longer basidiospores (4.9–5.8 µm vs. 4.1–5.1 µm in *H. brunneorubrum*); in addition, *H. auratile* usually grows in coniferous forests [1,26]. *H. chrysinum* is differentiated by having duplex, slightly zonate context, context tissue turning dark olive or blackish in KOH and slightly longer basidia sterigmata (up to 6 µm vs. up to 5 µm in *H. brunneorubrum*) [2,33,51]. *H. earlianum* is differentiated by a larger pileus (up to 90 mm vs. 40 mm in *H. brunneorubrum*), duplex context, dark brown or black context tissues in KOH and longer basidiospores (5–6 µm vs. 4.1–5.1 µm in *H. brunneorubrum*) [27,32,34].

**Hydnellum subg. Inflatum** Y.H. Mu & H.S. Yuan, *subgen. nov.*

MycoBank MB841197

*Etymology.* *Inflatum* (Latin), refers to the presence of inflated generative hyphae.

*Included species:* *Hydnellum cristatum, H. granulosum, H. inflatum, H. mirabile, H. piperatum*

*Type species:* *Hydnellum mirabile* (Fr.) P. Karst.

*Notes:* There are five species in the subgenus *Inflatum, Hydnellum cristatum, H. granulosum, H. inflatum, H. mirabile* and *H. piperatum.* The presence of inflated generative hyphae in the context of the pileus is an important feature they share. As well as, they often have yellow to brown and depressed pileus, cylindrical stipe and unclamped generative hyphae in the context and the spine trama [1,27,34].

**Hydnellum granulosum** Y.H. Mu & H.S. Yuan, *sp. nov.* (Figure 5)

MycoBank MB839038

*Etymology.* *Granulosum* (Latin), refers to the granulose pileal surface when dry.

*Type:* CHINA, Sichuan Province, Guangyuan County, Tianzhaoshan National Forest Park, on the ground in *Acer* and *Cryptomeria* mixed forest, 13 August 2017, H. S. Yuan, Yuan 12213b (holotype IFP 019400).

*Basidiocarps* annual, solitary to gregarious or two to three pilei fused to form a complex pileus, soft and leathery when fresh, becoming hard and light in weight upon drying; taste acrid, odor fragrant when dry. *Pileus* aplanate, irregularly ellipsoid when young, later irregularly flabelliform with age, up to 50 mm diam and 5–10 mm thick at center. *Pileal surface* light yellow (4A4), light brown to grayish brown (9F3), azonate, granulose when dry; margin yellowish white (4A2), involute and wavy, sometimes lobed. *Spine surface* grayish orange (5B4) to dark brown (8F7) when dry; spines up to 2 mm long, base up to 0.3 mm diam, conical, 3–6 per mm, more or less decurrent on stipe, without spines at pileus margin, brittle when dry. *Context* not duplex, up to 9 mm thick, grayish orange (5B4), woody. *Stipe* central to lateral, up to 4 cm long and 3 cm diam, sometimes connate, hard upon drying, golden brown (5D6) to brown (6E6), rugose, solid inner, terete or attenuate or broadening downwards with bulbous base when old. *Hyphal structure:* hyphal system monomitic; generative hyphae with simple-septa, CB+ in slightly thick-walled hyphae, IKI–; tissues olivaceous in KOH. *Context:* generative hyphae hyaline, mostly slightly thick-walled, rarely thin-walled, occasionally branched, simple-septate, occasionally inflated, interwoven, mostly 4–7 µm diam. *Spines:* generative hyphae hyaline, thin- to slightly thick-walled, moderately branched, more or less parallel along spines, frequently simple-septate, straight, 3–4 µm diam. *Cystidia* and cystidioles absent. *Basidia* clavate, thin-walled, with four sterigmata (3–5 µm long), simple-septate at base, 15–30 × 5–9 µm; basidioles similar to basidia. *Basidiospores* irregularly ellipsoid to globose, brown, thin-walled, tuberculate, CB–, IKI–, (4–)4.1–5.1(–5.3) × (3.2–)3.4–4.7(–4.9) µm, Lm = 4.6 µm, Wm = 4.1 µm, Q = 1.12–1.13 (n = 60/2); tuberculi usually isolated, sometimes in groups of two or more, then bi- to trifurcate in shape, up to 1.2 µm long.

*Additional specimens (paratypes) examined:* CHINA, Sichuan Province, Guangyuan County, Tianzhaoshan National Forest Park, on the ground in *Acer* and *Cryptomeria* mixed forest, 12 August 2017, H. S. Yuan, Yuan 12213a (IFP 019401, paratype); 13 August 2017, H. S. Yuan, Yuan 12213c (IFP 019402, paratype).
Figure 5. Hydnellum granulosum. (a, b): Basidiocarps; (c, d): SEM of basidiospores; (e–g): Microscopic structures (drawn from IFP 019400); (e): Section of hymenophore trama with basidia; (f): Hyphae from pileus context; (g): Basidiospores. —Scale bars: (a, b) = 1 cm; (c) = 3 µm; (d) = 1 µm; (e, f) = 10 µm; (g) = 5 µm.

Notes: Hydnellum granulosum has a close phylogenetic relationship with H. piperatum. In morphology, H. piperatum resembles H. granulosum in having single to gregarious or concrescent basidiocarps, with lobed pileal margin from fused pilei or indeterminate growth, a single to fused, central to eccentric and terete to attenuate downwards stipe,
context tissue turning olivaceous in KOH, absence of clamp-connections and the presence of inflated hyphae. However, *H. piperatum* is distinguishable from *H. granulosum* by having a comparatively broader pileus (up to 150 mm vs. 50 mm in *H. granulosum*) with a scaly or squamulose and zonate pileal surface and strongly decurrent and longer spines (up to 5 mm vs. 2 mm in *H. granulosum*) [27]. The presence of inflated generative hyphae is a shared feature in *H. granulosum* and *H. mirabile*. They also have simple or concrescent basidiocarps with light yellow to brown pilei, and hard and cylindrical stipes. However, *H. mirabile* differs from *H. granulosum* by the plano-convex to depressed and larger pileus (up to 90 mm vs. 50 mm in *H. granulosum*), yellowish to purplish brown and longer spines (up to 5.6–5.8 µm vs. 4.1–5.1 µm in *H. granulosum*) [1].

*Hydnellum inflatum* Y.H. Mu, X.H. Wang & H.S. Yuan, sp. nov. (Figure 6)

MycoBank MB839040

*Etymology.* *Inflatum* (Latin), refers to the mostly inflated generative hyphae in the context of the pileus.

*Type:* CHINA, Yunnan Province, Maguan County, Dalishu Township, on the ground in Fagaceous forest, 14 October 2017, S. F. Shi, Shi 506 (holotype IFP 019403).

*Basidiocarps* annual, solitary to gregarious, soft and leathery when fresh, becoming corky and light in weight upon drying; taste acrid, odor fragrant when dry. *Pileus* depressed to aplanate and irregularly circular when young, later flabelliform with age, up to 75 mm diam and 3–8 mm thick at center. *Pileal surface* grayish orange (5B5) to brown (7E7), azonate, fibrous to colliculose when fresh, becoming scrobiculate when dry; margin light yellow (4A4) when fresh, orange-white (5A2) when dry, involute and wavy, often lobed with age. *Spine surface* white (5A1) to golden brown (5D7) when fresh, yellowish brown (5D5) to dark brown (7F8) when dry; spines up to 4 mm long, base up to 0.25 mm diam, conical, 4–5 per mm, strongly decurrent on stipe, without spines at pileus margin, brittle when dry. *Context* duplex, upper layer grayish yellow (4B5), loose and soft, up to 2 mm thick; lower layer pale yellow (4A3), woody, up to 3 mm thick; a dark line present between upper and lower cortical layers. *Stipe* central to lateral, up to 5 cm long and 2 cm diam, occasionally connate, fleshy when fresh, woody upon drying, light brown (6D7), smooth to rugose, inside solid, context with a dark line present at centre, cylindrical or attenuate downwards with bulbous base when old. *Hyphal structure:* hyphal system monomitic; generative hyphae with simple-septa, CB+ in slightly thick-walled hyphae, IKI−; tissues slightly olivaceous in KOH. *Context:* generative hyphae hyaline, thin- to slightly thick-walled, occasionally branched, simple-septate, mostly inflated, interwoven, mostly 4–8 µm diam. *Spines:* generative hyphae hyaline, thin- to slightly thick-walled, moderately branched, more or less parallel along spines, frequently simple-septate, straight, 2–5 µm diam. *Cystidia* and cystidioles absent. *Basidia* clavate, thin-walled, with four sterigmata (3–5 µm long), simple-septate at base, 19–33 × 4–6 µm; basidioles similar to basidia. *Basidiospores* irregularly ellipsoid to globose, brown, thin-walled, tuberculate, CB−, IKI−, (4–)4.2–5.5(–5.1) × (3.2–)3.8–4.3(–5) µm, Lm = 4.8 µm, Wm = 4 µm, Q = 1.18–1.2 (n = 60/2); tuberculi usually isolated, sometimes in groups of two or more, then bi- to trifurcate in shape, up to 1.2 µm long.

Additional specimens (paratypes) examined: CHINA, Yunnan Province, Maguan County, Mabai Town, Caiyuanzi Village, on the ground, 5 August 2017, J. Wang, Wang 80 (IFP 019404, paratype); Wang 82 (IFP 019405, paratype); on the way from Dalishu Township to Damagu Village, on the ground in Fagaceous forest, 6 August 2017, S. F. Shi, Shi 150 (IFP 019406, paratype); Shi 160 (IFP 019407, paratype).
Figure 6. *Hydnellum inflatum*. (a,b): Basidiocarps; (c,d): SEM of basidiospores; (e–g): Microscopic structures (drawn from IFP 019403); (e): Section of hymenophore trama with basidia; (f): Hyphae from pileus context; (g): Basidiospores. —Scale bars: (a,b) = 1 cm; (c) = 3 μm; (d) = 1 μm; (e,f) = 10 μm; (g) = 5 μm.

Notes: *Hydnellum inflatum* is characterized by the presence of inflated generative hyphae, which makes it similar to *H. cristatum*, *H. granulosum*, *H. mirabile* and *H. piperatum*. This is an important feature that distinguishes from other species. However, *H. cristatum* can be differentiated from *H. inflatum* by the larger pileus (up to 100 mm vs. 75 mm in *H. inflatum*) with tomentose to matted pileal surface, longer spines (up to 5 mm vs. 4 mm in *H. inflatum*), brown context tissues in KOH, bigger basidia (34–46 × 8–9 μm vs. ...
19–33 × 4–6 μm in *H. inflatum*) and basidiospores (5–6 × 4–5 μm vs. 4.2–5 × 3.8–4.3 μm in *H. inflatum*) [27,34]. *H. granulosum* differs in granulose pileal surface, not duplex context, mostly slightly thick-walled hyphae in the context and shorter spines (up to 2 mm vs. up to 4 mm in *H. inflatum*). *H. mirabile* differs in ochraceous yellow and olive brown pileus, yellowish to purplish brown spines and longer spores (5.6–5.8 × 3.8–4.3 μm in *H. inflatum*) [1]. *H. piperatum* differs in umbilicate and greatly pileus (up to 100 mm vs. 75 mm in *H. inflatum*), red haired to sunburn slightly longer spines (up to 5 mm vs. up to 4 mm in *H. inflatum*) and inflated to cylindrical hyphae in the spines [27].

**Hydnellum subg. Rhizomorphum** Y.H. Mu & H.S. Yuan, **subgen. nov.**

*Mycobank MB841198*

**Etymology.** *Rhizomorphum* (Latin), refers to the rhizomorphs-like stipe.

Included species: *Hydnellum gracilipes*, **Hydnellum sp 1**

Type species: *Hydnellum gracilipes* (P. Karst.) P. Karst.

Notes: *Hydnellum gracilipes* and our notable specimen *Hydnellum* sp 1 comprise the subgenus *Rhizomorphum*. Rhizomorph-like stipe are their typical common characteristics. Besides, both species have the monomitic hyphal system with simple-septate generative hyphae [35].

**Hydnellum sp 1**

*Basidiocarps* annual, solitary to gregarious or coalescent. *Pileus* flabelliform to irregularly circular. *Pileal surface* deep red (10C8) to violet-brown (10F8) and felted. *Spines* white (10A1) to brownish red (10D7) and more or less decurrent, up to 1.5 mm long. *Rhizomorphs* stipe-like. *Hyphal system* monomitic, generative hyphae simple-septa. *Basidia* clavate, with four sterigmata. *Basidiospores* irregularly subglobose to globose, tuberculate, (4–)4.1–4.9(–5) × (3.1–)3.2–4(–4.1) μm.

Specimen examined: CHINA, Yunnan Province, Maguan County, on the way from Dalishu Township to Damagu Village, on the ground of angiosperm forest, 6 August 2017, S. F. Shi, Shi 164 (IFP 019436).

**Hydnellum subg. Scabrosum** Y.H. Mu & H.S. Yuan, **subgen. nov.**

*Mycobank MB841199*

**Etymology.** *Scabrosum* (Latin), refers to the pileal surface with scabrosity.

Included species: *Hydnellum amygdaliolens*, *H. coactum*, *H. fagiscabrosum*, *H. fennicum*, *H. grosselepidotum*, *H. illudens*, *H. lepidum*, *H. lidongensis*, *H. nemorosum*, *H. scabrosellum*, *H. scabrosum*, *H. underwoodii*

Type species: *Hydnellum scabrosum* (Fr.) E. Larss., K.H. Larss. & Kõljalg

Notes: There are twelve species, namely *Hydnellum amygdaliolens*, *H. coactum*, *H. fagiscabrosum*, *H. fennicum*, *H. grosselepidotum*, *H. illudens*, *H. lepidum*, *H. lidongensis*, *H. nemorosum*, *H. scabrosellum*, *H. scabrosum* and *H. underwoodii* in this subgenus characterised by planar to depressed and brown pileus, azonate pileal surface with scabrosity, variously-brown spines, not duplex and yellow to orange context, inflated and unclamped generative hyphae and irregularly ellipsoid to globose basidiospore [1,2,26,27,32–34,38,51–54].

**Hydnellum subg. Spongiosum** Y.H. Mu & H.S. Yuan, **subgen. nov.**

*Mycobank MB841200*

**Etymology.** *Spongiosum* (Latin), refers to the spongy pileal surface.

Included species: *Hydnellum ferrugineum*, *H. pineticola*, *H. spongiosipes*, **Hydnellum sp 2**

Type species: *Hydnellum ferrugineum* (Fr.) P. Karst.

Notes: This subgenus includes *Hydnellum ferrugineum*, *H. pineticola*, *H. spongiosipes* and *Hydnellum sp 2*; they all have planoconvex to depressed and brown pileus with spongy pileal surface, purplish brown spines, the monomitic hyphal system with simple-septate generative hyphae and irregularly subglobose basidiospores [1,2,27,34].

**Hydnellum spongiosipes** (Peck) Pouzar, Česká Mykol. 14(2): 130 (1960)

*Hydnum spongiosipes* Peck, Ann. Rep. Reg. N.Y. St. Mus. 50: 111 (1898) (1897)

*Basidiocarps* single to gregarious. *Pileus* flabelliform, planate to subdepressed. *Pileal surface* pale orange (6A3) to dark brown (6F7), velutinous to very spongy, tomentose to
fibrillose. Spines pale orange (6A3) to dark brown (6F7), subdecurrent to decurrent, up to 6 mm long. Stipe central to subeccentric, terete, thick and strong. Hypgal system monomitic; generative hyphae simple-septate. Basidia clavate, with four sterigmata. Basidiospores irregularly subglobose, tuberculate, (5–)5.1–6.1(–6.2) × (4.3–)4.5–5.3(–5.8) µm.

Specimen examined: CHINA, Liaoning Province, Kuandian County, Baishilazi National Nature Reserve, on the ground of Quercus forest, 8 August 2020, H. S. Yuan, Yuan 14517 (IFP 019435).

Notes: The studied sample clustered with Hydnellum spongiosipes (REB-107 and REB-52) in the multi-gene phylogenetic tree with strong support (90% in ML and 1.00 BPP) (Figure 1). The samples REB-107 and REB-52 both show 0.99 similarity to Yuan 14517 in ITS region. Besides this, morphological analyses also confirmed the new record, which is described in detail by Maas Geesteranus (1975) and Baird (2013). This species was recorded to occur widely in the United States and European countries and usually was found under hardwood tree [1,2,27,34].

Hydnellum sp 2
Basidiocarps annual, coalescent. Pileus compound, multiple pilei fused. Pileal surface violet-brown (10E6) and spongy-tomentose. Spines white (10A1) to violet-brown (10E6) and strongly decurrent, up to 2.5 mm long. Stipe short and connate. Hypgal system monomitic, generative hyphae simple-septa. Basidia clavate, with four sterigmata. Basidiospores irregularly subglobose, tuberculate, (3.1–)4–4.3(–4.5) × (3–)3.1–4(–4.1) µm.

Specimen examined: CHINA, Yunnan Province, Nanjian County, Lingbaoshan National Forest Park, on the ground of angiosperm forest, 19 September 2019, H. S. Yuan, Yuan 14387 (IFP 019437).

Hydnellum subg. Subindufibulatum Y.H. Mu & H.S. Yuan, subgen. nov.
MycoBank MB841201
Etymology. Subindufibulatum (Latin), refers to the occasionally clamped hyphae in the context of the pileus.

Included species: Hydnellum caeruleum, H. ferrugipes, H. fibulatum
Type species: Hydnellum caeruleum (Hornem.) P. Karst.

Notes: Hydnellum caeruleum, H. ferrugipes and H. fibulatum make up the subgenus Subindufibulatum and occasional presence of clamped hyphae in the context of the pileus is the dominating trait that distinguishes them from other species. Furthermore, they have dark brown and fibrillose to colliculose pileal surface, orange stipe, context tissues turning olivaceous in KOH and the absence of clamp-connections in the spine trama [2,26,27].

Hydnellum caeruleum (Hornem.) P. Karst., [as ‘coeruleum’], Meddn Soc. Fauna Flora Fenn. 5: 41 (1879)
Hydnum caeruleum Hornem., Fl. Danic. 8(23): 7, tab. 1374 (1808)

Basidiocarps single to gregarious or concrescent. Pileus convex to plane. Pileal surface pastel yellow (4A4) to dark blonde (5D4), tomentose and colliculose. Spines decurrent, up to 6 mm long, orange-white (5A2) to dark brown (6F8). Stipe central and terete. Hypgal system monomitic; most of the generative hyphae with simple-septa, rarely with clamps. Basidia clavate, with four sterigmata. Basidiospores irregularly subglobose, tuberculate, (4.9–)5–6(–6.1) × (4–)4.1–4.9(–5) µm.

Specimen examined: CHINA, Xinjiang Autonomous Region, Huocheng County, Guozigou Forest Park, on the ground in Picea forest, 18 August 2004, Y. L. Wei, Wei 1474a (IFP 019432).

Notes: The phylogenetic analyses showed that the studied sample matched with Hydnellum caeruleum (EBendiksen584-11) with full support (100% in ML and 1.00 BPP) (Figure 1). ITS sequence BLAST also revealed it is 100% identical to H. caeruleum. Besides, our collection shares identical characters with H. caeruleum described by Maas Geesteranus [26] in morphology. This is the first report of this species from China.

Hydnellum fibulatum Y.H. Mu & H.S. Yuan, sp. nov. (Figure 7)
Figure 7. *Hydnellum fibulatum*. (a,b): Basidiocarps; (c,d): SEM of basidiospores; (e–g): Microscopic structures (drawn from IFP 019398); (e): Section of hymenophore trama with basidia; (f): Hyphae from pileus context; (g): Basidiospores. —Scale bars: (a,b) = 2 cm; (c) = 3 µm; (d) = 1 µm; (e,f) = 10 µm; (g) = 5 µm.

MycoBank MB839037

*Etymology.* *Fibulatum* (Latin), refers to the generative hyphae with occasional clamp-connections.
Type: CHINA, Liaoning Province, Benxi County, Guanmenshan National Forest Park, on the ground in Quercus forest, 29 August 2020, H. S. Yuan, Yuan 14656 (holotype IFP 019398).

**Basidiocarps** annual, solitary to gregarious, soft and leathery when fresh, becoming woody and light in weight upon drying; taste mild, odor none when dry. **Pileus** apllanate, circular when young, later flabelliform with age, up to 45 mm diam and 3–7 mm thick at center. **Pileal surface** light brown (7D7) to dark brown (8F4), obscurely zonate, pubescent when fresh, becoming fibrillose, rugose when dry; margin white (6A1) when fresh, brown (6E6) when dry, incurved, sometimes lobed. **Spine surface** pinkish white (7A2) to brown (7E7) when fresh, orange-white (5A2) to brown (6E6) when dry; spines up to 1.5 mm long, base up to 0.2 mm diam, conical, 3–4 per mm, more or less decurrent on stipe, without spines at pileus margin, brittle when dry. **Context** not duplex, up to 5 mm thick, light brown (6D4) to dark brown (6F4), woody. **Stipe** central to lateral, up to 3.5 cm long and 1 cm diam, single, leathery when fresh, woody upon drying, light orange (5A5) to brown (6E7), pubescent, solid inner, cylindrical or attenuate downwards with bulbous base when old. **Hyphal structure:** hyphal system monomitic; generative hyphae with mostly simple-septa, occasionally clamped, CB+ in slightly thick-walled hyphae, IKI–; tissues olivaceous in KOH. **Context:** generative hyphae hyaline, slightly thick-walled, occasionally branched, simple-septate, occasionally clamped, straight, regularly arranged, sometimes flexuous and collapsed, mostly 3–5 µm diam. **Spines:** generative hyphae hyaline, thin- to slightly thick-walled, moderately branched, more or less parallel along spines, frequently simple-septate, straight, 2–4 µm diam. **Cystidia** and cystidioles absent. **Basidia** clavate, thin-walled, with four sterigmata (2–5 µm long), simple-septate at base, 15–47 × 5–9 µm; basidioles similar to basidia. **Basidiospores** irregularly ellipsoid to globose, brown, thin-walled, tuberculate, CB–, IKI–, (4.2–)4.4–5.8(–6) × (4–)4.1–4.9(–5.1) µm, Lm = 5.2 µm, Wm = 4.3 µm, Q = 1.12–1.21 (n = 60/2); tuberculi usually isolated, sometimes in groups of two or more, then bi- to trifurcate in shape, up to 1 µm long.

Additional specimen (paratype) examined: CHINA, Liaoning Province, Benxi County, Guanmenshan National Forest Park, on the ground in Quercus forest, 29 August 2020, H. S. Yuan, Yuan 14646 (IFP 019399, paratype).

Notes: Hydnellum caeruleum and *H. ferrugipes* have an adjacent phylogenetic relationship with *H. fibulatum* according to the phylogenetic tree (Figure 1). *H. caeruleum* and *H. fibulatum* have similar morphological characteristics, such as a flat and velutinous pileus when immature, white pileal margin when fresh, central, terete and tomentose stipe, olivaceous context tissue in KOH, presence of occasional clamp-connections in the context and simple-septate hyphae in the spines. However, *H. caeruleum* can be distinguished by having a larger pileus (up to 80 mm vs. 45 mm in *H. fibulatum*), rough or colliculose pileal surface when mature, duplex and zonate context [2,26]. *H. ferrugipes* resembles *H. fibulatum* in having a white pileal margin when fresh, tomentose and orange to brown stipe, orange-white to brown spines when dry, regularly arranged and occasionally clamped hyphae in the context, unclamped hyphae in the spines and basidia sterigmata with similar size. However, *H. ferrugipes* differs from *H. fibulatum* in the infundibuliform pileus with pitted to subnodulose or subcolliculose pileal surface, blue-gray or grayish orange context, considerably longer spines (up to 6 mm vs. 1.5 mm in *H. fibulatum*) and wider basidiospores (5–6 µm vs. 4.1–4.9 µm in *H. fibulatum*) [27,34].

**Hydnellum subg. Violaceum** Y.H. Mu & H.S. Yuan, subgen. nov.

*Hydnellum fuligineoviolaceum*, *H. fuscoindicum*, *H. glaucopus*, *H. joeides*, *H. roseoviolaceum* Type species: *Hydnellum fuligineoviolaceum* (Kalchbr.) E. Larss., K.H. Larss. & Kõljalg

Notes: Five species, *Hydnellum fuligineoviolaceum*, *H. fuscoindicum*, *H. glaucopus*, *H. joeides* and *H. roseoviolaceum*, comprise the subgenus *Violaceum*. They share the following features: violaceous basidiocarps, pileal surface with appressed scales, purplish con-
text, the presence of inflated generative hyphae and the simple-septate haphae in all tissue [1,2,6,27,33,53].

Hydnellum subg. Zonatum Y.H. Mu & H.S. Yuan, subgen. nov.
MycoBank MB841203

Etymology. Zonatum (Latin), refers to the concentrically zonate pileal surface.

Included species: Hydnellum atrorubrum, H. bomiense, H. concrescens, H. dianthifolium, H. parvum, H. rubidofuscum, H. scrobiculatum, H. squamulosum, H. sulcatum, H. yunnanense, Hydnellum sp 3, Hydnellum sp 4, Hydnellum sp 5

Type species: Hydnellum scrobiculatum (Fr.) P. Karst.

Notes: The subgenus Zonatum contains fourteen taxa, Hydnellum atrorubrum, H. bomiense, H. concrescens, H. dianthifolium, H. parvum, H. rubidofuscum, H. scrobiculatum, H. squamulosum, H. subsuccosum, H. sulcatum, H. yunnanense, Hydnellum sp 3, Hydnellum sp 4 and Hydnellum sp 5. The concentrically zonate pileal surface is their most prominently mutual peculiarity. Additionally, the absence of clamp-connections in the context of the pileus and the spine trama is another important common feature [1,2,6,27,34,36].

Hydnellum atrorubrum Y.H. Mu & H.S. Yuan, sp. nov. (Figure 8)
MycoBank MB839032

Etymology. Atrorubrum (Latin), refers to the dark ruby red pileal surface.

Type: CHINA, Yunnan Province, Yulong County, on the ground in Fagaceous forest, 23 July 2018, Y. L. Wei, Wei 8261 (holotype IFP 019377).

Basidiocarps annual, solitary to gregarious or several pilei fused to form a compound pileus, soft and leathery when fresh, becoming woody and light in weight upon drying; taste slightly bitter, odor slightly fragrant when dry. Pileus applanate and flabelliform to irregularly circular when young, later depressed or subinfundibuliform to rounded with age, up to 48 mm diam and 3–8 mm thick at center. Pileal surface light brown (7D7) to dark ruby (12F8), usually concentrically zoned, flocculose when fresh, becoming fibrillose to glabrescent when dry; margin white (7A1) when fresh, brown (7E5) when dry, even to slightly irregular, occasionally wavy or lobed. Spine surface white (6A1) to dark brown (6F6) when fresh, grayish orange (5B4) to brown (6E8) when dry; spines up to 3.5 mm long, base up to 0.4 mm diam, conical, 3–5 per mm, decurrent to strongly decurrent on stipe, without spines at pileus margin, brittle when dry. Context not duplex, up to 6 mm thick, brown (6E6), corky. Stipe central, up to 3.5 cm long and 1.5 cm diam, sometimes conenate, leathery when fresh, corky upon drying, pinkish (8A2) to reddish brown (8E6), velutinous, inside solid, cylindrical or attenuate downwards with bulbous base when old. Hyphal structure: hyphal system monomitic; generative hyphae with simple-septa, CB+ in slightly thick-walled hyphae, IKI–; tissues olivaceous in KOH. Context: generative hyphae hyaline, thin- to slightly thick-walled, occasionally branched, simple-septate, straight, regularly arranged, sometimes flexuous and collapsed, mostly 4–6 µm diam. Spines: generative hyphae hyaline, thin- to slightly thick-walled, moderately branched, more or less parallel along spines, frequently simple-septate, straight, 2–4 µm diam. Cystidia and cystidioles absent. Basidia clavate, thin-walled, with four sterigmata (4–6 µm long), simple-septate at base, 20–48 × 5–8 µm; basidiodes similar to basidia. Basidiospores irregular ellipsoid, brown, thin-walled, tuberculate, CB–, IKI–, (4.1–)4.5–6(–6.1) × (3.2–)3.9–5.1(–6) µm, Lm = 5 µm, Wm = 4.4 µm, Q = 1.14–1.21 (n = 60/2); tuberculi usually isolated, sometimes in groups of two or more, then bi- to trifurcate in shape, up to 1.1 µm long.

Additional specimens (paratypes) examined: CHINA, Yunnan Province, Yulong County, on the ground in Fagaceous forest, Y. L. Wei, 23 July 2018, Wei 8290 (IFP 019378, paratype); Wei 8312 (IFP 019379, paratype); Wei 8315 (IFP 019380, paratype); Wei 8319 (IFP 019381, paratype).
Figure 8. *Hydnellum atrorubrum*. (a): Basidiocarps; (b,c): SEM of basidiospores; (d–f): Microscopic structures (drawn from IFP 019377); (d): Section of hymenophore trama with basidia; (e): Hyphae from pileus context; (f): Basidiospores. —Scale bars: (a) = 2.5 cm; (b) = 3 μm; (c) = 1 μm; (d,e) = 10 μm; (f) = 5 μm.

Notes: Phylogenetically, *Hydnellum atrorubrum* has a close relationship with *H. subsuccosum*. Morphologically, *H. subsuccosum* is similar to *H. atrorubrum* in having gregarious
to confluent basidiocarps with zonate pileal surface and lobed pileal margin, brown context, cylindrical or attenuate downwards stipe, decurrent and similar length spines, the monomitic hyphal system with uninflated and simple-septate generative hyphae, basidia of similar shape and width, as well as basidiospores of similar length. However, *H. subsuccosum* can be differentiated by scabrous to nodulose and orange-white to camel pileal surface, black spines and presence of subglobose basidiospores [27]. *H. auratile* is comparable to *H. atrorubrum* in having similar size, depressed to infundibuliform or flabelliform and concentrically zoned pileus with undulate margin, tomentose and reddish-brown stipe, non-duplex context, thin- to slightly thick-walled and unclamped generative hyphae. However, *H. auratile* differs from *H. atrorubrum* by orange or orange-brown to dark red-brown pileus with entire or deeply split margin and tawny to purplish brown spines [26].

**Hydnellum bomiense** Y.H. Mu & H.S. Yuan, *sp. nov.* (Figure 9)

MycoBank MB839035

**Etymology.** *Bomiense*, refers to the Bomi County, where the specimens were collected.

Type: CHINA, Xizang Autonomous Region, Bomi County, on the ground in Fagaceous forest, 19 July 2019, H. S. Yuan, Yuan 13767 (holotype IFP 019382).

**Basidiocarps** annual, solitary to gregarious, soft and leathery when fresh, becoming woody and light in weight upon drying; taste acrid, odor slightly fragrant when dry. **Pileus** infundibuliform when young, later applanate and irregularly circular with age, up to 26 mm diam and 2–4 mm thick at center. **Pileal surface** grayish yellow (4B4), brown (7E7) to dark brown (7F8), obscurely concentrically zonate, tomentose, scrupose when fresh, becoming fibrillose or glabrous when dry; margin white (5A1) when fresh, grayish orange (5B4) when dry, involute and wavy, sometimes lobed or rimose with age. **Spine surface** white (6A1) to brown (6E7) when fresh, light brown (6D6) to dark brown (7F8) when dry; spines up to 1.1 mm long, base up to 0.2 mm diam, conical, 4–6 per mm, more or less decurrent on stipe, without spines at pileus margin, brittle when dry. **Context** not duplex, up to 4 mm thick, brown (6E5), woody. **Stipe** central to lateral, up to 2 cm long and 0.5 cm diam, woody upon drying, grayish orange (5B5) to dark brown (7F7), rugose, solid inner, terete or attenuate downwards with bulbous base when old. **Hyphal structure:** hyphal system monomitic; generative hyphae with simple-septa, CB+ in slightly thick-walled hyphae, IKI–; tissues olivaceous in KOH. **Context:** generative hyphal hyaline, thin- to slightly thick-walled, frequently branched, simple-septate, straight, regularly arranged, sometimes flexuous and collapsed, mostly 4–6 μm diam. **Spines:** generative hyphal hyaline, thin-walled, occasionally branched, more or less parallel along spines, frequently simple-septate, straight, 2–4 μm diam. **Cystidia** and cystidioles absent. **Basidia** clavate, thin-walled, with four sterigmata (1.5–3 μm long), simple-septate at base, 15–42 × 4–7 μm; basidioles similar to basidia. **Basidiospores** irregularly ellipsoid to subglobose, brown, thin-walled, tuberculate, CB–, IKI–, (4–)4.1–5.1(–5.2) × (3–)3.3–4.5(–4.8) μm, Lm = 4.7 μm, Wm = 4 μm, Q = 1.18–1.21 (n = 60/2); tuberculi usually isolated, sometimes in groups of two or more, then bi- to trifurcate in shape, up to 1 μm long.

Additional specimen (paratype) examined: CHINA, Xizang Autonomous Region, Bomi County, on the ground with moss in Fagaceous forest, 19 July 2019, H. S. Yuan, Yuan 13759 (IFP 019383, paratype).
Figure 9. *Hydnellum bomiense*. (a,b): Basidiocarps; (c,d): SEM of basidiospores; (e–g): Microscopic structures (drawn from IFP 019382); (e): Section of hymenophore trama with basidia; (f): Hyphae from pileus context; (g): Basidiospores. —Scale bars: (a,b) = 1 cm; (c) = 3 μm; (d) = 1 μm; (e,f) = 10 μm; (g) = 5 μm.

Notes: This species clustered with two samples from Estonia and Costa Rica, and formed an independent clade (Figure S1). *Hydnellum bomiense* and *H. dianthifolium* are closely related based on nucleotide sequence analyses and possess common morphological features: separate to coalescing or grouped basidiocarps with decurrent spines, cylindrical stipe, absence of clamp-connections and brown, tuberculate and irregularly ellipsoid to
subglobose basidiospores of similar size with isolated to bifurcate tuberculi. However, *H. dianthifolium* differs from *H. bomiense* by having slender, turbinate and coralloid basidiocarps that split radially to form erect, coralloid or flower-shaped lobed pilei, not perceptibly zoned context and thick-walled and encrusted context hyphae [36]. Meanwhile, *H. concrescens* and *H. scrobiculatum* are also in a big clade with *H. bomiense* in Figure 1, and concentrically zonate pileal surface is their common characteristic. However, *H. concrescens* differs by quite larger pileus (up to 120 mm vs. up to 26 mm in *H. bomiense*), duplex context and longer basidia sterigmata (3–4 µm vs. 1.5–3 µm in *H. bomiense*) [27,34]. *H. scrobiculatum* differs in subcolliculose to scrobiculate pileal surface and longer spines (up to 3 mm vs. 1.1 mm in *H. bomiense*) [27,34].

**Hydnellum rubidofuscum** Y.H. Mu & H.S. Yuan, sp. nov. (Figure 10)

MycoBank MB839041

*Etymology.* *Rubidofuscum* (Latin), refers to the reddish brown pileal surface.

*Type:* CHINA, Liaoning Province, Xinbin County, Gangshan Nature Reserve, on the ground in *Quercus* forest, 12 August 2020, H. S. Yuan, Yuan 14561 (holotype IFP 019408).

**Basidiocarps** annual, solitary to gregarious or multiple pilei overlapping and fused to form a compound cluster, soft and leathery when fresh, becoming woody and light in weight upon drying; taste mild, odor slightly fragrant when dry. *Pileus* applanate to infundibuliform when young, later depressed to flabelliform or irregularly circular with age, up to 70 mm diam and 4–10 mm thick at center. *Pileal surface* reddish brown (8E8), obscurely concentrically zonate, glabrous to scrupose when fresh, becoming fibrillose to virgate when dry; margin white (6A1) to orange-white (6A2) when fresh, brownish orange (6C4) when dry, even, sometimes lobed with age. *Spine surface* grayish brown (8D3) to reddish brown (8E7) when fresh, brown (6E6) to dark brown (6F7) when dry; spines up to 3 mm long, base up to 0.2 mm diam, conical, 4–6 per mm, strongly decurrent on stipe, without spines at pileus margin, brittle when dry. *Context* not duplex, up to 10 mm thick, brown (6E6), woody. *Stipe* central to lateral, up to 3.5 cm long and 2 cm diam, sometimes connate, leathery when fresh, woody upon drying, light brown (7D6) to brown (7E6), pubescent, solid inner, cylindrical to flat or attenuate downwards with bulbous base when old. *Hyphal structure:* hyphal system monomitic; generative hyphae with simple-septa, CB+ in slightly thick-walled hyphae, IKI−; tissues olivaceous in KOH. *Context:* generative hyphae hyaline, thin- to slightly thick-walled, occasionally branched, simple-septate, straight, regularly arranged, sometimes flexuous and collapsed, mostly 3–6 µm diam. *Spines:* generative hyphae hyaline, thin-walled, occasionally branched, more or less parallel along spines, frequently simple-septate, straight, 2–3 µm diam. *Cystidia* and cystidioles absent. *Basidia* clavate, thin-walled, with four sterigmata (1–4 µm long), simple-septate at base, 14–37 × 4–6 µm; basidiocarps similar to basidia. *Basidiospores* irregularly ellipsoid to subglobose, brown, thin-walled, tuberculate, CB−, IKI−, (4–)4.1–5(–5.1) × (3.8–)3.9–4.6(–4.8) µm, Lm = 4.6 µm, Wm = 4.1 µm, Q = 1.11–1.12 (n = 60/2); tuberculi usually isolated, sometimes in groups of two or more, then bi- to trifurcate in shape, up to 1 µm long.

Additional specimens (paratypes) examined: CHINA, Liaoning Province, Xinbin County, Gangshan Nature Reserve, on the ground in *Quercus* forest, 12 August 2020, H. S. Yuan, Yuan 14559 (IFP 019409, paratype); Yuan 14560 (IFP 019410, paratype); Yuan 14563 (IFP 019411, paratype); 26 August 2020, H. S. Yuan, Yuan 14586 (IFP 019412, paratype); Yuan 14587 (IFP 019413, paratype); 12 September 2020, H. S. Yuan, Yuan 14792 (IFP 019414, paratype); Yuan 14794 (IFP 019415, paratype); Yuan 14800 (IFP 019416, paratype); Benxi County, Guanmenshan National Forest Park, on the ground in *Quercus* forest, 29 August 2020, H. S. Yuan, Yuan 14654 (IFP 019417, paratype).
Figure 10. Hydnellum rubidofuscum. (a): Basidiocarps; (b,c): SEM of basidiospores; (d–f): Microscopic structures (drawn from IFP 019408); (d): Section of hymenophore trama with basidia; (e): Hyphae from pileus context; (f): Basidiospores.

—Scale bars: (a) = 1 cm; (b) = 3 μm; (c) = 1 μm; (d,e) = 10 μm; (f) = 5 μm.

Notes: Phylogenetically, Hydnellum rubidofuscum is closely related to H. bomiense and H. dianthifolium (Figure 1). Morphologically, infundibuliform pileus when young,
concentrically zonate pileal surface and irregularly ellipsoid to subglobose basidiospores are their common features. However, *H. bomiense* can be distinguished by smaller pileus (up to 26 mm vs. up to 70 mm in *H. rubidofuscum*), yellow to dark brown pileal surface and shorter spines (up to 1.1 mm vs. up to 3 mm in *H. rubidofuscum*). *H. dianthifolium* differs by subpubescent pileal surface, reddish-brown to vinaceous-brown context, thick-walled and rarely branched hyphae in the context and context tissue turning blue-green in KOH [36]. The reddish brown pileal surface is very similar to that of *H. scrobiculatum*. Furthermore, *H. scrobiculatum* also has a single to gregarious or concentric basidiocarp with applanate or infundibuliform pileus, obscurely concentrically zonate pileal surface, simple or conuate, to eccentric and velutinous stipe, reddish brown and decurrent spines and the monomitic hyphal system. However, the major differences are that *H. scrobiculatum* has a fungoid or no odor, a scrobiculate and rugulose pileal surface, duplex and zonate context and longer basidiospores (5.4–6.4 μm vs. 4.1–5 μm in *H. rubidofuscum*) [26,27,34].

**Hydnellum squamulosum** Y.H. Mu & H.S. Yuan, **sp. nov.** (Figure 11)

MycoBank MB839042

*Etymology.* *Squamulosum* (Latin) refers to the minutely scaly pileal surface.

*Holotype.* CHINA, Xizang Autonomous Region, Bomi County, on the ground in *Picea* mixed forest, 17 July 2019, *H. S. Yuan*, Yuan 13615 (holotype IFP 019418).

*Basidiocarps* annual, solitary to gregarious or coalescent to form complex pileus, soft and leathery when fresh, becoming corky and light in weight upon drying; taste none, odor none when dry. *Pileus* circular when young, circular or semicircular with age, applanate, up to 35 mm diam and 4–8 mm thick at center. *Pileal surface* pastel red (7A4) to dark Magenta (13F7), zonate, floccose to woolly, squamulose when fresh, becoming fibrillose and scrobiculate when dry; margin white (7A1) when fresh, grayish orange (5B3) when dry, involute and wavy, sometimes lobed with age. *Spine surface* pale red (7A3) to reddish brown (8E8) when fresh, grayish orange (5B4) to dark brown (8F7) when dry; spines up to 2 mm long, base up to 0.2 mm diam, conical, 3–6 per mm, decurrent on stipe, without spines at pileus margin, brittle when dry. *Context* not duplex, up to 9 mm thick, reddish brown (8E6), soft corky. *Stipe* central to lateral, up to 4 cm long and 1 cm diam, sometimes conuate, leathery or freshy when fresh, soft corky upon drying, pale red (11A3), tomentose, solid inner, context with a dark zone present at centre, terete to flat or attenuate downwards with bulbous base when old. *Hyphal structure:”* hyphal system monomitic; generative hyphae with simple-septa, occasionally encrusted, CB+ in slightly thick-walled hyphae, IKI−; tissues olivaceous in KOH. *Context:* generative hyphae hyaline, thin- to slightly thick-walled, moderately branched, simple-septate, straight, regularly arranged, sometimes flexuous and collapsed, mostly 4–5 μm diam. *Spines:* generative hyphae hyaline, thin-walled, moderately branched, more or less parallel along spines, frequently simple-septate, straight, 2–4 μm diam. *Cystidia* and cystidioles absent. *Basidia* clavate, thin-walled, with four sterigmata (2–3 μm long), simple-septate at base, 8–38 × 4–6 μm; basidioles similar to basidia. *Basidiospores* irregularly ellipsoid to globose, brown, thin-walled, tuberculate, CB-, IKI−, (4–)4.1–5(−5.1) × (3.2–)3.3–4.1(−4.2) μm, Lm = 4.4 μm, Wm = 3.8 μm, Q = 1.14–1.16 (n = 60/2); tuberculi usually isolated, sometimes in groups of two or more, then bi- to trifurcate in shape, up to 1 μm long.

Additional specimens (paratypes) examined: CHINA, Xizang Autonomous Region, Bomi County, on the ground in *Picea* mixed forest, 17 July 2019, *H. S. Yuan*, Yuan 13617 (IFP 019419, paratype); Yuan 13625 (IFP 019420, paratype); Yuan 13626 (IFP 019421, paratype); Yuan 13627 (IFP 019422, paratype); on the ground with moss in *Picea* mixed forest, 19 July 2019, *H. S. Yuan*, Yuan 13743 (IFP 019423, paratype).
Figure 11. Hydnellum squamulosum. (a): Basidiocarps; (b,c): SEM of basidiospores; (d–f): Microscopic structures (drawn from IFP 019418); (d): Section of hymenophore trama with basidia; (e): Hyphae from pileus context; (f): Basidiospores. —Scale bars: (a) = 1 cm; (b) = 3 µm; (c) = 1 µm; (d,e) = 10 µm; (f) = 5 µm.

Notes: Hydnellum squamulosum and H. concrescens are closely related in the phylogenetic tree and share similar morphological and anatomical characteristics: a solitary to
gregarious or coalescent basidiocarp with fibrillose, squamulose and zonate pileal surface, irregularly lobed margin, decurrent and reddish-brown spines, not duplex context in the pileus, zonate context in the stipe, context tissue becoming olivaceous in KOH, and tuberculate basidiospores. However, *H. concrescens* can be differentiated by depressed or in-fundibuliform basidiocarps, reddish white to dark brown pileal margin, larger pileus (up to 120 mm vs. 35 mm in *H. squamulosum*), longer basidia sterigmata (up to 5 µm vs. up to 3 µm in *H. squamulosum*) and larger basidiospores (5–6 × 4–5 µm vs. 4.1–5 × 3.3–4.1 µm in *squamulosum*) [2,27,34]. *H. fraudulentum* is similar to *H. squamulosum* in having a squamulose-fibrillose pileal surface, cylindrical or connate stipe, context tissue olivaceous in KOH, thin-to slightly thick-walled and unclamped hyphae in the context, basidia of similar shape, and brown and tuberculate basidiospores. However, it differs from *H. squamulosum* in having depressed, azonate and yellow-brown to dark brown pilei, purplish brown and slightly longer spines (up to 2.5 mm vs. 2 mm in *H. squamulosum*), wider basidia (6–7 µm vs. 4–6 µm in *H. squamulosum*) with longer sterigmata (3.6–4.5 µm vs. 2–3 µm in *H. squamulosum*) and bigger basidiospores (6.3–7 × 4.5–4.7 µm vs. 4.1–5 × 3.3–4.1 µm in *H. squamulosum*) [26].

*Hydnellum sulcatum* Y.H. Mu & H.S. Yuan, sp. nov. (Figure 12) MycoBank MB839043;

*Etymology*. Sulcatum (Latin), refers to the often grooved pileal surface.

*Type*. CHINA, Liaoning Province, Benxi County, Guanmenshan National Forest Park, on the ground of *Quercus* forest, 29 August 2020, H. S. Yuan, Yuan 14649 (holotype IFP 019424).

*Basidiocarps* annual, solitary to gregarious or multiple pilei overlapping and fused to form a compound cluster, soft and leathery when fresh, becoming woody and light in weight upon drying; taste mild, odor slightly fragrant when dry. *Pileus* subinfundibuliform when young, later applanate to flabelliform or circular with age, up to 65 mm diam and 3–6 mm thick at center. *Pileal surface* dark brown (9F4), obscurely concentrically zonate, often grooved, scabrous to fibrous when fresh, becoming fibrillose, rugose when dry; margin white (6A1) when fresh, light brown (6D5) when dry, even, sometimes lobed. *Spine surface* brown (7E7) when fresh, brown (6E5) to dark brown (7F5) when dry; spines up to 1.5 mm long, base up to 0.1 mm diam, conical, 5–7 per mm, more or less decurrent on stipe, without spines at pileus margin, brittle when dry. *Context* not duplex, up to 6 mm thick, brown (7E6), woody. *Stipe* lateral, up to 2 cm long and 1.5 cm diam, sometimes connate, leathery when fresh, woody upon drying, brown (7E5), pubescent, inside solid, cylindrical to flat or attenuate downwards with bulbous base when old. *Hyphal structure*: hyphal system monomitic; generative hyphae with simple-septa, CB+ in slightly thick-walled hyphae, IKI–; tissues olivaceous in KOH. *Context*: generative hyphae hyaline, thin-walled, moderately branched, simple-septate, straight, regularly arranged, sometimes flexuous and collapsed, mostly 4–6 µm diam. *Spines*: generative hyphae hyaline, thin to slightly thick-walled, moderately branched, more or less parallel along spines, often simple-septate, straight, 2–3 µm diam. *Cystidia* and cystidioles absent. *Basidia* clavate, thin-walled, with four sterigmata (2–3 µm long), simple-septate at base, 20–30 × 4–8 µm; basidioles similar to basidia. *Basidiospores* irregular ellipsoid to subglobose, brown, thin-walled, tuberculate, CB–, IKI–, (4–)4.1–5.8(–5.9) × (3.9–)4–4.6(–4.8) µm, Lm = 4.8 µm, Wm = 4.3 µm, Q = 1.14–1.19 (n = 60/2); tuberculi usually isolated, sometimes in groups of two or more, then bif- to trifurcate in shape, up to 0.9 µm long.

Additional specimens (paratypes) examined: CHINA, Liaoning Province, Kuandian County, Baishilazi National Nature Reserve, on the ground of *Quercus* forest, 8 August 2020, H. S. Yuan, Yuan 14521 (IFP 019425, paratype); Benxi County, Guanmenshan National Forest Park, on the ground of *Quercus* forest, 29 August 2020, H. S. Yuan, Yuan 14638 (IFP 019426, paratype); Yuan 14658 (IFP 019427, paratype); Yuan 14660 (IFP 019428, paratype).
Figure 12. *Hydnellum sulcatum*. (a): Basidiocarps; (b,c): SEM of basidiospores; (d–f): Microscopic structures (drawn from IFP 019424); (d): Section of hymenophore trama with basidia; (e): Hyphae from pileus context; (f): Basidiospores. —Scale bars: (a) = 2 cm; (b) = 3 μm; (c) = 1 μm; (d,e) = 10 μm; (f) = 5 μm.

Notes: *Hydnellum parvum* has a close phylogenetic relationship with *H. sulcatum*. The former species resembles the latter by compound fused pilei and rugulose pileal surface.
However, the latter has a thinner stipe (0.7 × 0.2 cm vs. 2 × 1.5 cm in *H. sulcatum*), slightly longer spines (up to 2 mm vs. 1.5 mm in *H. sulcatum*) and shorter basidiospores (3–4 µm vs. 4.1–5.8 µm in *H. sulcatum*) [27]. *H. subsuccosum* resembles *H. sulcatum* by concentrically zonate pileus with similar size, context hyphae of similar width, the absence of clamp-connections and brown and subglobose basidiospores. However, *H. subsuccosum* differs by orange white to camel and nodulose or pitted pileal surface, longer spines (up to 3 mm vs. 1.5 mm in *H. sulcatum*) and basidioles similar to basidia (4–6 µm vs. 3–4 µm in *H. sulcatum*) and slightly longer tuberculi (up to 1.1 µm vs. 0.9 µm in *H. sulcatum*).

*Hydnellum yunnanense* Y.H. Mu, X.H. Wang & H.S. Yuan, sp. nov. (Figure 13) MycoBank MB839044

*Etymology*. Yunnanense, refers to the Yunnan Province, where the specimens were collected.

*Type*: CHINA, Yunnan Province, Nanjian County, Lingbaoshan National Forest Park, on the ground, 19 September 2019, H. S. Yuan, Yuan 14386 (holotype IFP 019429).

*Basidiocarps* annual, solitary to gregarious, soft and leathery when fresh, becoming woody and light in weight upon drying; taste mild, odor slightly fragrant when dry. *Pileus* subinfundibuliform when young, later flabelliform with age, up to 21 mm diam and 3–5 mm thick at center. *Pileal surface* grayish red (10D6) to dark brown (9F8), obscurely concentrically zonate, velutinate to tomentose when fresh, becoming rugulose to glabrescent when dry; margin white (6A1) when fresh, light brown (6D4) when dry, even, sometimes eroded with age. *Spine surface* white (10A1) to grayish red (10D6) when fresh, pale orange (5A3) to brown (6E7) when dry; spines up to 1.5 mm long, base up to 0.1 mm diam, conical, 5–8 per mm, more or less decurrent on stipe, without spines at pileus margin, brittle when dry. *Context* not duplex, up to 5 mm thick, reddish brown (8E4), woody. *Stipe* central to lateral, up to 4 cm long and 0.7 cm diam, sometimes connate, leathery when fresh, woody upon drying, brown (7E6), tomentose, solid inner, context with a dark line present at centre, cylindrical to attenuate downwards or broadening below with bulbous base when old. *Hyphal structure*: hyphal system monomitic; generative hyphae with simple-septa, CB+ in slightly thick-walled hyphae, IKI–; tissues olivaceous in KOH. *Context*: generative hyphae hyaline, thin- to slightly thick-walled, moderately branched, simple-septate, straight, regularly arranged, sometimes flexuous and collapsed, mostly 3–5 µm diam. *Spines*: generative hyphae hyaline, thin- to slightly thick-walled, frequently branched, more or less parallel along spines, often simple-septate, straight, 2–5 µm diam. *Cystidia* and cystidioles absent. *Basidia* clavate, thin-walled, with four sterigmata (2–4 µm long), simple-septate at base, 13–28 × 4–7 µm; basidioles similar to basidia. *Basidiospores* irregularly ellipsoid to subglobose, brown, thin-walled, tuberculate, CB–, IKI–, (4.1–)4.2–5.1(–5.3) × (3.4–)3.5–4.5(–5) µm, Lm = 4.7 µm, Wm = 4 µm, Q = 1.17–1.18 (n = 60/2); tuberculi usually isolated, sometimes in groups of two or more, then bi- to trifurcate in shape, up to 1.2 µm long.

Additional specimens (paratypes) examined: CHINA, Yunnan Province, Nanjian County, Lingbaoshan National Forest Park, on the ground, 19 September 2019, H. S. Yuan, Yuan 14396 (IFP 019430, paratype); Maguan County, Dalishu Township, Adushangba Village, on the ground, 7 August 2017, S. F. Shi, Shi 212 (IFP 019431, paratype).
Figure 13. *Hydnellum yunnanense*. (a,b): Basidiocarps; (c,d): SEM of basidiospores; (e–g): Microscopic structures (drawn from IFP 019429); (e): Section of hymenophore trama with basidia; (f): Hyphae from pileus context; (g): Basidiospores. —Scale bars: (a,b) = 1 cm; (c) = 3 μm; (d) = 1 μm; (e,f) = 10 μm; g = 5 μm.

Notes: The phylogenetic analyses support that *Hydnellum yunnanense* is sister to *H. sulcatum* (Figure 1). Morphologically, *H. sulcatum* resembles *H. yunnanense* in having an annual, solitary to gregarious basidiocarp with subinfundibuliform to flabelliform pileus with equal-length spines, a brown, pubescent, cylindrical stipe, olivaceous context tissue in KOH and basidiospores of similar shape. However, it differs from *H. yunnanense*...
in having a broader pileus (up to 65 mm vs. 21 mm in *H. yunnanense*) with scabrous to squamulose pileal surface and light brown pileal margin and shorter tuberculi (up to 0.9 µm vs. 1.2 µm in *H. yunnanense*). *H. rubidofuscum* resembles *H. yunnanense* by infundibuliform to flabelliform and concentrically zonate pileus, not duplex and woody context, thin- to slightly thick-walled and simple-septate hyphae in the context, basidia of similar width and basidiospores of similar shape and size. However, *H. rubidofuscum* differs by larger pileus (up to 70 mm vs. up to 21 mm in *H. yunnanense*) with reddish brown and scrupose, fibrillose to virgate pileal surface, grayish brown to reddish brown and longer spines (up to 3 mm vs. up to 1.5 mm in *H. yunnanense*) and thin-walled generative hyphae in the spines.

**Hydnellum sp 3**

*Basidiocarps* annual, solitary. *Pileus* applanate, flabelliform. *Pileal surface* brown (7E7) to dark brown (7F7), concentrically zonate and pubescent. *Spines* reddish brown (9E6) and more or less decurrent, up to 1 mm long. *Stipe* lateral, cylindrical and slender. *Hyphal system* monomitic, generative hyphae simple-septa. *Basidia* clavate, with four sterigmata. *Basidiospores* irregularly subglobose, tuberculate, (4.8–)4.9–5.2(–5.3) × (4–)4.1–4.8(–5) µm.

Specimen examined: CHINA, Yunnan Province, Nanjian County, Lingbaoshan National Forest Park, on the ground of angiosperm forest, 19 September 2019, H. S. Yuan, Yuan 14388 (IFP 019438).

**Hydnellum sp 4**

*Basidiocarps* annual, solitary to gregarious. *Pileus* irregularly flabelliform. *Pileal surface* grayish yellow (4B3) to yellowish brown (5E8), obscurely concentrically zonate and glabrescent. *Spines* yellowish brown (5D5) and more or less decurrent, up to 2 mm long. *Stipe* lateral and cylindrical. *Hyphal system* monomitic, generative hyphae simple-septa. *Basidia* clavate, with four sterigmata. *Basidiospores* irregularly subglobose, tuberculate, (4.1–)4.2–5.3(–6) × (4–)4.1–4.3(–4.8) µm.

Specimen examined: CHINA, Yunnan Province, Maguan County, Dalishu Township, on the ground in Fagaceous forest, 14 October 2017, J. Wang, Wang 295 (IFP 019439).

**Hydnellum sp 5**

*Basidiocarps* annual, solitary. *Pileus* irregularly circular. *Pileal surface* zonate, velutinous and strigose with lobed margin. *Spines* decurrent, up to 1 mm long. *Stipe* lateral, cylindrical and broadened below with bulbous base when old. *Hyphal system* monomitic, generative hyphae simple-septa. *Basidia* clavate, with four sterigmata. *Basidiospores* irregularly ellipsoid to subglobose, tuberculate, (4–)4.1–5.5(–5.6) × (3–)3.1–4.7(–5.2) µm.

Specimen examined: CHINA, Liaoning Province, Xinbin County, Gangshan Nature Reserve, in the angiosperm forest dominated by *Quercus liaotungensis*, 26 August 2020, H. S. Yuan, Yuan 14594 (IFP 019440).

**Other Hydnellum species**

*Hydnellum complicatum*, *H. cumulatum*, *H. diabolus*, *H. geogenium*, *H. lundellii*, *H. martioflavus*, *H. peckii*, *H. regium*, *H. versipelle*

**Hydnellum peckii** Banker, in Peck, Bull. N.Y. St. Mus. 157: 28 (1912) (1911)

*Basidiocarps* single to concrescent. *Pileus* turbinate or elliptical, planar or subdepressed. *Pileal surface* white (6A1) to light orange (6A4), colliculose, rarely scrobiculate and glabrous. *Spines* brownish orange (7C4), decurrent, up to 3 mm long. *Stipe* central and terete. *Hyphal system* monomitic; generative hyphae mostly with clamp-connections, minority of simple-septa. *Basidia* clavate, with simple-septate at base and four sterigmata. *Basidiospores* irregularly subglobose, tuberculate, (4.1–)4.2–5.1(–5.3) × (3.8–)3.9–4.4(–4.6) µm.

Specimens examined. CHINA, Xizang Autonomous Region, Bomi County, on the ground in *Pinus* mixed forest, 19 July 2019, H. S. Yuan, Yuan 13708 (IFP 019343); Yuan 13720 (IFP 019434).

Notes: The studied samples were found in high altitude *Pinus* mixed forest. These two specimens clustered with two other samples (SSvantesson328 and ELarsson174-14) of *Hydnellum peckii* from Europe with full support (100% in ML and 1.00 BPP) (Figure 1). The ITS+LSU sequence identity between the specimens from China and Europe was 0.99 in
Bioedit pairwise alignment. In morphology, the characters of our specimens overlap with those of *H. peckii* [1,27]. Therefore, we introduce *H. peckii* as a new record to China.

**Key to species of *Hydnellum* from China**

1. Basidiocarps fleshy
   1.→ Basidiocarps woody
2. Pileal surface not scaled
   2.→ Pileal surface scaled
3. Pileal surface with ascend squama
   3.→ Pileal surface with appressed squama
4. Context tissue olivaceous in KOH
   4.→ Context tissue blue-green in KOH
5. Hyphae with clamp-connections in the context
   5.→ Hyphae without clamp-connections in the context and spines
6. Basidiocarps with dark violet spines underneath pileus
   6.→ Basidiocarps with different colored spines underneath pileus
7. Pileal surface fibrilllose, rugose when dry, spines up to 1.5 mm long
   7.→ Pileal surface pitted, colliculose when dry, spines up to 6 mm long
8. Inflated hyphae present from the context
   8.→ Inflated hyphae absent in the context
9. Generative hyphae mostly inflated in the context, pileal surface scrobiculate when dry
   9.→ Generative hyphae occasionally inflated in the context, pileal surface granulose when dry
10. Stipe thin, rhizomorphs-like
   10.→ Stipe cylindrical to flattened
11. Pileal surface colored brownish orange to brownish red
   11.→ Pileal surface differently colored
12. Pileal margin involute and wavy, sometimes lobed or rimose
   12.→ Pileal margin even or effused, sometimes lobed or eroded
13. Pileal surface glabrescent
   13.→ Pileal surface not glabrescent
14. Pileal surface azonate and spongy
   14.→ Pileal surface obsurely concentrically zonate to zonate and not spongy
15. Pileal surface floccose to squamulose when fresh, context corky
   15.→ Pileal surface tomentose and scrupose when fresh, context woody
16. Basidiocarps single to gregarious and stipe single and long
   16.→ Basidiocarps coalescent and stipe connate and short
17. Stipe context with a dark line at centre
   17.→ Stipe context without a dark line at centre
18. Pileus and spines grayish red
   18.→ Pileus brown and spines reddish brown
19. Spines up to 3 or 3.5 mm long
   19.→ Spines up to 1 or 1.5 mm long
20. Pileus light brown to dark ruby
   20.→ Pileus reddish brown
21. Basidiocarps gregarious or multiple pilei overlapping and pileal surface often grooved, scabrous to fibrous
   21.→ Basidiocarps solitary and pileal surface velutinous and strigose

5. Discussion

Baird et al. [27] constructed a phylogenetic tree of Bankeraceae using ITS sequences of specimens from the temperate southeastern United States, and suggested that neither *Hydnellum* nor *Sarcodon* were monophyletic. In the current study, phylogenetic analyses using four loci (nLSU + ITS + SSU + RPB2) of *Hydnellum* and *Sarcodon* were carried out using sequences from Europe, Asia and America. Our results also verify that *Sarcodon* is paraphyletic; with regard to *Hydnellum*, some species of *Sarcodon* nesting among *Hydnellum* species. Larsson et al. [31] provided phylogenetic analyses on *Hydnellum* and *Sarcodon* based on ITS and LSU sequences, confirming that *Sarcodon* makes *Hydnellum* paraphyletic and the genus limits were revised, 12 species of *Sarcodon* moved to *Hydnellum*. Morphologically,
Violaceum corresponds to the violaceous basidiocarps and includes H. subsuccosum; the subgenus H. underwoodii includes H. illudens and (includes H. atrospinosum (II) Pileus composed mostly of simple-septate hyphae with occasional clamp-connections. The posterior positions for most species in Hydnellum S. aspratus has a concentrically zonate pileal surface and includes H. atrorubrum and H. ferrugineum and includes H. amygdaliolens and H. gracilipes and six other species; the subgenus Caesispinosum has the appearance of inflated hypha in the context of the pileus and includes H. cristaatsum, H. granulosum, H. inflatum, H. mirabile and H. piperatum; the subgenus Rhizomorphum has rhizomorphs-like stipe and includes H. gracilipes and Hydnellum sp 1; the subgenus Scabrosus has pileal surface with scabrosity and includes H. amygdaлиolens, H. coactum, H. fagiscabrosum, H. fennicium, H. grosselepidotum, H. illudens, H. lepidum, H. lidongensis, H. nemorosum, H. scabrosellum, H. scabrosus and H. underwoodii; the subgenus Spongiosum corresponds to a spongy pileal surface and includes H. ferrugineum, H. pinetica, H. spongiosipes and Hydnellum sp 2; the subgenus Violaceum corresponds to the violaceous basidiocarps and includes H. fulgineoviolaceum, H. fuscoindicalum, H. glaucopus, H. joedise and H. roseoviolaceum; the subgenus Zonatum has a concentrically zonate pileal surface and includes H. atrorubrum, H. bomiense, H. concrescens, H. dianthifolium, H. parsum, H. rubidofuscum, H. scrobiculatum, H. squamulosum, H. subfuscosus, H. sulcatum, H. yunnanense, Hydnellum sp 3, Hydnellum sp 4 and Hydnellum sp 5. Group V corresponds to the subgenus Subindufibulatum, having occasionally clamped hyphae in the context of the pileus, and includes H. caeruleum, H. ferrugipes and H. fibulatum. Group V corresponds to all hyphae clamped in the pileus and the spines, incorporating two subgenera of Hydnellum and six Sarcodon species; the subgenus Hydnellum has dark spines and includes H. atrospinosum and H. suaveolens; the subgenus Caesispinosum has blue spines and includes H. cyanopodium and H. scleropodium; H. geogenium is morphologically related to other species in Group V, but is distantly related in the phylogenetic tree; Sarcodon clade S. aspratus, S. imbricatus, S. leucopus, S. quercinofibulatus, S. scabripes and S. squamosus have the characteristics of long spores compared with the Hydnellum species. Therefore, the classification system using hyphal structure type and phylogenetic subgenera can fix the positions for most species in Hydnellum and Sarcodon, except for some species in Groups III, IV and those without phylogenetic support.

The specimens involved in this study were collected from the northeast, northwest and southwest regions of China, where industrial pollution is relatively low and vegetation is relatively abundant. The forests are primarily dominated by Pinaceae and Fagaceae trees such as Pinus spp., Picea spp., Quercus spp., Lithocarpus spp. and a small portion of other tree families. Thus, we speculated that these species may form an ectomycorrhizal association with Pinaceae and Fagaceae host trees. The species diversity and basidiocarps richness of stipitate hydnoid fungi represented by Hydnellum and Sarcodon species have
shown a declining trend across Europe and some regions of North America during the 1970s to 2000s [6,55–57]; the phenomenon is most probably caused by forest management, air pollutants, forest soil acidification, nitrogen deposition and forest succession, among other causes [19,58–61]. Many stipitate hydnoid fungi have been included in national Red Lists in Europe [27,62–64]. With the rapid industrialization in China over the past four decades, a significant decline of basidiocarps has also been observed during the course of our field investigation. The identification and description of stipitate hydnoid fungi in this paper will contribute to the understanding of species diversity and provide baseline data for the evaluation and protection of these fungi in China.

Table 3. Hyphal-septa type observations in the context of the pileus and the spine trama in the species of Hydnellum and Sarcodon.

| Group | Subgenus | Species | Pileus | Spines | References |
|-------|----------|---------|--------|--------|------------|
| Croceum | Hydnellum aurantiacum | simple-septa | simple-septa | Maas Geesteranus 1975 [1] |
| | H. auratile | simple-septa | simple-septa | Maas Geesteranus 1971 [26] |
| | H. brunneorubrum | simple-septa | simple-septa | In this study |
| | H. chrysium | simple-septa | simple-septa | Baird 1986 [51] |
| | H. earlianum | simple-septa | simple-septa | Baird et al. 2013 [27] |
| | H. cristatum | simple-septa | simple-septa | Baird et al. 2013 [27] |
| | H. granulosum | simple-septa | simple-septa | In this study |
| | H. inflatum | simple-septa | simple-septa | In this study |
| | H. piperatum | simple-septa | simple-septa | Baird et al. 2013 [27] |
| | H. mirabile | simple-septa | simple-septa | Maas Geesteranus 1975 [1] |
| | H. gracilipes | simple-septa | simple-septa | Koljal & Renvall 2000 [35] |
| | H. amygdaliolens | simple-septa | simple-septa | Rubio Casas et al. 2011 [32] |
| Scabrosum | H. coactum | simple-septa | simple-septa | Mu et al. 2020 [38] |
| | H. fagiscabrosum | simple-septa | simple-septa | Nitare et al. 2021 [53] |
| | H. fennicum | simple-septa | simple-septa | Hahn et al. 2018 [54] |
| | H. grosselepidotum | simple-septa | simple-septa | Mu et al. 2020 [38] |
| | H. illudens | simple-septa | simple-septa | Nitare et al. 2021 [53] |
| | H. lepidum | simple-septa | simple-septa | Maas Geesteranus 1975 [1] |
| | H. lidongensis | simple-septa | simple-septa | Mu et al. 2020 [38] |
| | H. nemorosum | simple-septa | simple-septa | Nitare et al. 2021 [53] |
| | H. scabrosellum | simple-septa | simple-septa | Nitare et al. 2021 [53] |
| | H. scabrosum | simple-septa | simple-septa | Baird et al. 2013 [27] |
| | H. underwoodii | simple-septa | simple-septa | Baird et al. 2013 [27] |
| | H. ferrugineum | simple-septa | simple-septa | Baird et al. 2013 [27] |
| | H. pineticola | simple-septa | simple-septa | Baird et al. 2013 [27] |
| Spongiosum | H. spongiosipes | simple-septa | simple-septa | Baird et al. 2013 [27] |
| | Hydnellum sp 2 | simple-septa | simple-septa | In this study |
| Violaceum | H. fuligineoviolaceum | simple-septa | simple-septa | Maas Geesteranus 1971 [26] |
| | H. hiscoindicum | simple-septa | simple-septa | Maas Geesteranus 1967 [65] |
| | H. glaucopus | simple-septa | simple-septa | Maas Geesteranus 1975 [1] |
| | H. joëdes | simple-septa | simple-septa | Baird et al. 2013 [27] |
| | H. roseoviolaceum | simple-septa | simple-septa | Nitare et al. 2021 [53] |
Table 3. Cont.

| Group     | Subgenus     | Species            | Pileus          | Spines          | References                      |
|-----------|--------------|--------------------|-----------------|-----------------|---------------------------------|
| I         | Zonatum      | H. atrorubrum      | simple-septa    | simple-septa    | In this study                   |
|           |              | H. bomiense        | simple-septa    | simple-septa    | In this study                   |
|           |              | H. concrencens     | simple-septa    | simple-septa    | Baird et al. 2013 [27]          |
|           |              | H. dianthifolium   | simple-septa    | simple-septa    | Loizides et al. 2016 [36]       |
|           |              | H. parcum          | simple-septa    | simple-septa    | Baird et al. 2013 [27]          |
|           |              | H. rubidofuscum     | simple-septa    | simple-septa    | In this study                   |
|           |              | H. scrobiculatum   | simple-septa    | simple-septa    | Baird et al. 2013 [27]          |
|           |              | H. squamulosum     | simple-septa    | simple-septa    | In this study                   |
|           |              | H. subsuccosum     | simple-septa    | simple-septa    | Baird et al. 2013 [27]          |
|           |              | H. sulcatum        | simple-septa    | simple-septa    | In this study                   |
|           |              | H. yunnanense      | simple-septa    | simple-septa    | In this study                   |
|           |              | Hydnellum sp 3     | simple-septa    | simple-septa    | In this study                   |
|           |              | Hydnellum sp 4     | simple-septa    | simple-septa    | In this study                   |
|           |              | Hydnellum sp 5     | simple-septa    | simple-septa    | In this study                   |
|           |              | Others             |                 |                 |                                 |
|           |              | H. complicatum     | simple-septa    | simple-septa    | Baird et al. 2013 [27]          |
|           |              | H. cumulatum       | simple-septa    | simple-septa    | Baird et al. 2013 [27]          |
|           |              | H. lundellii       | simple-septa    | simple-septa    | Maas Geesteranus 1975 [1]       |
|           |              | H. martiofascum    | simple-septa    | simple-septa    | Baird et al. 2013 [27]          |
|           |              | H. caeruleum       | simple-septa,   | simple-septa    | Baird & Khan 1986 [2];          |
|           |              |                    | occasionally    |                 | In this study                   |
|           |              |                    | with clamp-    |                 |                                 |
|           |              |                    | connections   |                 |                                 |
| II        | Subindufibulatum | H. ferrugipes     | simple-septa,   | simple-septa    | Baird et al. 2013 [27]          |
|           |              |                    | occasionally   |                 |                                 |
|           |              |                    | with clamp-    |                 |                                 |
|           |              |                    | connections   |                 |                                 |
|           |              |                    | simple-septa,  |                 |                                 |
|           |              |                    | occasionally   |                 |                                 |
|           |              |                    | with clamp-    |                 |                                 |
|           |              |                    | connections   |                 |                                 |
|           |              | H. fibulatum       | mostly with    | mostly with     | Baird et al. 2013 [27];         |
|           |              |                    | clamp-        | clamp-          | In this study                   |
|           |              |                    | connections,   | connections,    |                                 |
|           |              |                    | minority of   | minority of     |                                 |
|           |              |                    | simple-septa  | simple-septa    |                                 |
|           |              | Others             |                 |                 |                                 |
|           |              | H. peckii          | mostly with    | mostly with     | Baird et al. 2013 [27];         |
|           |              |                    | clamp-        | clamp-          | In this study                   |
|           |              |                    | connections,   | connections,    |                                 |
|           |              |                    | minority of   | minority of     |                                 |
|           |              |                    | simple-septa  | simple-septa    |                                 |
| III       | Others       | H. versipelle      | mostly with    | mostly with     | Baird et al. 2013 [27]          |
|           |              |                    | clamp-        | clamp-          |                                 |
|           |              |                    | connections,   | connections,    |                                 |
|           |              |                    | minority of   | minority of     |                                 |
|           |              |                    | simple-septa  | simple-septa    |                                 |
| IV        | Others       | H. diabolus        | clamp-connections | simple-septa | Baird et al. 2013 [27]          |
|           |              | Hydnellum          | clamp-connections | clamp-connections | In this study                   |
|           |              | H. atrospinosum    | clamp-connections | clamp-connections | Baird et al. 2013 [27]          |
|           |              | H. suaveolens      | clamp-connections | clamp-connections |                                 |
| V         | Caespispinosum | H. cyanopodium    | clamp-connections | clamp-connections | Baird 1986 [51]                 |
|           |              | H. scleropodium   | clamp-connections | clamp-connections | Harrison 1964 [33]              |
Table 3. Cont.

| Group | Subgenus | Species          | Pileus          | Spines          | References                          |
|-------|----------|------------------|-----------------|-----------------|-------------------------------------|
|       | Others   | *H. geogenium*   | clamp-connections | clamp-connections | Baird et al. 2013 [27]             |
|       |          | *Sarcodon aspratus* | clamp-connections | clamp-connections | Maas Geesteranus 1971 [26]         |
|       |          | *S. imbricatus*   | clamp-connections | clamp-connections | Baird et al. 2013 [27]             |
|       |          | *S. leucopus*     | clamp-connections | clamp-connections | Mleczko et al. 2011 [66]           |
|       |          | *S. quercinofibulatus* | clamp-connections | clamp-connections | Pérez-De-Gregorio et al. 2011 [67] |
|       |          | *S. scabripes*    | clamp-connections | clamp-connections | Baird et al. 2013 [27]             |
|       |          | *S. squamosus*    | clamp-connections | clamp-connections | Baird 1986 [34]                    |
| V     | *Sarcodon*|                  |                 |                 |                                     |
|       | Others   | *H. regium*      | hyphae with few simple-septa and with a few clamp-connections |                 | Harrison 1964 [33]                |

**Supplementary Materials:** The following are available online at https://www.mdpi.com/article/10.3390/jof7100818/s1, Figure S1: Maximum likelihood tree illustrating the phylogeny of *Hydnellum* and *Sarcodon* based on ITS sequence dataset.

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