Morphology and molecular phylogeny reveal five new species of *Hydnellum* (Bankeraceae, Thelephorales) from China

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The genus *Hydnellum* is a kind of ectomycorrhizal fungi that can play a role in the material cycle by connecting the plant roots to the soil, and some species of *Hydnellum* are medicinal fungi with vital research value. The species diversity of *Hydnellum* is unclear in China. In this study, five new species of *Hydnellum* are described from China based on morphological characters and phylogenetic analyses inferred from two datasets of ITS + LSU and ITS + LSU + SSU + RPB2 sequences. *H. chocolatum* is characterized by its chocolate basidiomata with the fibrillose, spongy to tomentose pileal surface, and subglobose to globose basidiospores measuring (4.5–)5–6 × 4–5(–5.8) µm. *H. concentricum* is characterized by its zonate pileal surface, thin context, short stipe, presence of both simple septa and clamp connections in generative hyphae of spines, and subglobose to globose basidiospores measuring (4.5–)5–6 × 4–5(–5.8) µm. *H. crassipileatum* is characterized by its thick pileus with the reddish brown to grayish brown pileal surface, and subglobose to ellipsoidal basidiospores measuring (3.5–)4–5(–5.2) × (3.2–)3.5–5 µm. *H. melanocarpum* is characterized by its vinaceous brown to black pileus with spongy pileal surface, presence of both simple septa and clamp connections in generative hyphae of spines, and subglobose to ellipsoidal basidiospores measuring (3.5–)4–5(–5.2) × (3.2–)3.5–5 µm. *H. radiatum* is characterized by its radially aligned stripes on pileal surface, grayish brown context, short stipe, and subglobose to ellipsoidal basidiospores measuring (3.5–)4–5(–5.5) × 3–4.5 µm. Full descriptions, illustrations, and phylogenetic trees to show the placement of the new species are provided.

**KEYWORDS**
Bankeraceae, ectomycorrhizal fungi, multi-gene phylogeny, stipitate hydnoids, taxonomy
Introduction

Stipitate hydnoid fungi of the family Bankeraceae are ectomycorrhizal symbionts of trees in a broad spectrum of forests (Holec and Kučera, 2018), which can provide nutrients and water to roots by exchanging photosynthates from trees and improve the absorption capacity of trees to soil nutrients such as phosphorous (Erland and Taylor, 1999; Parfitt et al., 2007). In some forests, fewer ectomycorrhizal fungi have produced basidiomata (Arnolds, 1991, 2010) and become the emphasis of conservation in Europe (Parfitt et al., 2007). And some species are medicinal fungi, such as *H. concrescens* (Pers.) Banker which has an inhibitory action on syncytium formation, trafficking of glycoprotein and hemagglutinin-neuraminidase (HN) to the cell surface (Lee et al., 2012).

*Hydnellum* P. Karst., typed by *H. suaveolens* (Scop.) P. Karst., is a member of stipitate hydnoids. The genus *Hydnellum* together with *Phellodon* P. Karst. and *Sarcodon* Quél. ex P. Karst was affiliated to Bankeraceae Donk of Thelephorales Corner ex Oberw. The genus *Hydnellum* was established by Karsten (1879). At first, many species of the Bankeraceae including *Hydnellum* were originally classified into the Hydnaceae because of their dentate hymenium (Banker, 1906). Donk established the family Bankeraceae, which consisted of only two genera *Bankera* and *Phellodon* (Donk, 1961). Jülich (1981) revised the classification system of Basidiomycetes and classified *Hydnellum* into the Bankeraceae. The genus *Hydnellum* is characterized by annual basidiomata with a zonate or an azonate pileal surface, spinous and white to orange, gray blue, light brown, or dark brown spines, and centrally or eccentrically stipitate; a monomitic system of Basidiomycetes and classified (Donk, 1961). Jülich (1981) revised the classification system of Basidiomycetes and classified *Hydnellum* into the Bankeraceae. The genus *Hydnellum* is characterized by annual basidiomata with a zonate or an azonate pileal surface, spinous and white to orange, gray blue, light brown, or dark brown spines, and centrally or eccentrically stipitate; a monomitic hyphal system with simple septa or clamped generative hyphae, and subglobose to globose and tuberculate basidiospores (Baird and Khan, 1986; Baird et al., 2013). *Hydnellum* is often confused with *Phellodon* and *Sarcodon* because of the similar basidiomata with a hymenium made up of spines (Baird et al., 2013). While the basidiospores in the *Phellodon* species are hyaline, the basidiospores in *Hydnellum* and *Sarcodon* are yellow to brown-tinted (Maas Geesteranus, 1975). Besides, *Sarcodon* differs from *Hydnellum* mainly by its brittle fleshy substance (Banker, 1906) and larger basidiospores (7.4-9 μm; Larsson et al., 2019).

Morphological features, including macroscopic morphological and microscopic morphological characteristics, were commonly used to identify *Hydnellum* species in the past (Banker, 1906; Maas Geesteranus, 1962, 1971; Harrison, 1964; Hrouda, 1999). Banker (1906) conducted a study of hydnaceous fungi of the Czech Republic and Slovakia, and 11 species of *Hydnellum* were newly described. Harrison (1964) conducted a systematic study of the stipitate hydnoids of the Bankeraceae from North America and described 10 species of *Hydnellum*. However, traditional morphology-based generic restrictions are ambiguous (Larsson et al., 2019). Mycologists have used morphological characters and phylogenetic analyses to study the taxonomy of *Hydnellum* in recent years (Ainsworth et al., 2010; Baird et al., 2013; Larsson et al., 2019; Mu et al., 2021). Baird et al. (2013) reevaluated the species of stipitate hydnoids from the southern United States, and 41 distinct taxa were determined including 19 species of *Hydnellum*. Larsson et al. (2019) reassessed the generic limits for *Hydnellum* and *Sarcodon*, and transferred 12 species from *Sarcodon* to *Hydnellum* based on ITS and nLSU sequences, which make the division of the genera clearer. Currently, about 70 species have been described and transferred to the genus according to the records in Index Fungorum (Accessed 7 May 2022).

Species in Bankeraceae are associated with coniferous trees in forest ecosystems and are widely distributed in the northern hemisphere. Stipitate hydnoids were often found in forests on mesic to dry, sandy to loamy soils with, at the most, a thin humus and litter layer (Arnolds, 2010). According to a survey conducted in the Netherlands about 22 species of hydnoid fungi, 12 are associated with deciduous trees older than 40 years, mainly *Quercus robur, Quercus rubra*, and *Fagus sylvatica*, and 10 are associated with coniferous trees, almost exclusively with Scots pine (*Pinus sylvestris*) (Arnolds, 2003). However, herb-rich spruce (*Picea abies*) forests on more or less calcareous soils rich in minerals constitute a third important habitat for hydnoid fungi (Arnolds, 2010). These three types of hosts corresponded well in our investigation (Table 2).

Macrofungi have important ecological and economical values. The species diversity, taxonomy, and phylogeny of macrofungi have been extensively investigated in recent years, and many new species have been discovered (Han et al., 2016; Cui et al., 2019; Mu et al., 2019, 2021; Shen et al., 2019; Sun et al., 2020; Cao et al., 2021; Deng et al., 2021, 2022; Liu et al., 2021a,b, 2022a,b; Song et al., 2021, 2022; Zhang et al., 2021; Ji et al., 2022; Wang et al., 2022). During our investigations on macrofungi from China, 90 specimens of *Hydnellum* were collected with different morphological characteristics. The morphological observation and phylogenetic analyses based on ITS + nLSU and ITS + LSU + nSSU + RPB2 combined matrices were conducted to confirm the affinity of the undescribed species corresponding to *Hydnellum*. Five new species were described in detail and illustrated.

Materials and methods

Morphological study

The specimens used in this study were deposited at the herbarium of the Institute of Microbiology, Beijing Forestry
| Species                        | Specimen no. | Locality | GenBank accession no. | ITS  | nrLSU | nSSU | RPB1 | RPB2 |
|-------------------------------|--------------|----------|-----------------------|------|-------|------|------|------|
| Amaurodon aquicoeruleus       | UK 452       | Australia| AM490944 AM490944     | -    | -     | -    | -    | -    |
| A. viridis                    | KHLarsson14947b | Norway  | MK602707 MK602707    | -    | -     | -    | -    | -    |
| Hydnellum ampygaloisens       | GB-0202072   | France   | MW144290 MW144290   | -    | -     | -    | -    | -    |
| H. ampygaloisens              | SC-2011      | -        | IN376763 -            | -    | -     | -    | -    | -    |
| H. atrorubrum                 | Wei 8315     | China    | MWS79937 -            | -    | -     | -    | -    | -    |
| H. atrorubrum                 | Wei 8261     | China    | MWS79936 MWS79884 MWS79910 | -    | -     | -    | -    | -    |
| H. atrorubrum                 | Yuan 6514    | China    | MWS79940 MWS79886 MWS79913 | -    | -     | -    | -    | -    |
| H. atropinum                  | Yuan 6520    | China    | MWS79912 MWS79912    | -    | -     | -    | -    | -    |
| H. aurantiacum                | RGCarlsson08-105 | Sweden | MK602711 MK602711    | -    | -     | -    | -    | -    |
| H. aurantiacum                | ElBendiksen177-07 | Norway | MK602712 MK602712    | -    | -     | -    | -    | -    |
| H. auratile                   | OF294095     | Norway   | MK602714 MK602714    | -    | -     | -    | -    | -    |
| H. auratile                   | OF242763     | Norway   | MK602715 MK602715    | -    | -     | -    | -    | -    |
| H. hombiensis                 | Yuan 13759   | China    | MWS79941 MWS79887 MWS79914 | -    | OK254206 |
| H. hombiensis                 | Yuan 13767   | China    | MWS79942 MWS79915    | -    | -     | -    | -    | -    |
| H. brunneorubrum              | Yuan 12997   | China    | MWS79944 MWS79889 MWS79917 | -    | OK254217 |
| H. brunneorubrum              | Yuan 14339   | China    | MWS79943 MWS79888 MWS79916 | -    | OK254216 |
| H. brunneorubrum              | Yuan 14668   | China    | MWS79945 MWS79889 MWS79918 | -    | OK254218 |
| H. caeruleum                  | OF291140     | Norway   | MK602717 MK602717    | -    | -     | -    | -    | -    |
| H. caeruleum                  | ElBendiksen575-11 | Norway | MK602718 MK602718    | -    | -     | -    | -    | -    |
| H. chloclatum                 | Cui 18545    | China    | ON603657 -            | -    | -     | -    | -    | -    |
| H. chloclatum                 | Cui 18543    | China    | ON603656 ON603638 ON603646 ON605658 | -    | -     | -    | -    | -    |
| H. chrysinum                  | SC071        | -        | KJS34291 -            | -    | -     | -    | -    | -    |
| H. coactum                    | Wei 8094     | China    | MN846278 MN846287    | -    | -     | -    | -    | -    |
| H. coactum                    | Shi 181      | China    | MN846279 MN846288    | -    | -     | -    | -    | -    |
| H. complicatum                | REB-71       | United States | KC571711 | -    | -     | -    | -    | -    |
| H. complicatum                | REB-329      | United States | KC571712 | -    | -     | -    | -    | -    |
| H. concentricum              | Cui 17017    | China    | ON603658 ON603639 ON603647 ON605659 ON605666 | -    | -     | -    | -    | -    |
| H. concentricum              | Cui 17098    | China    | - ON603640 ON603648 ON605660 | -    | -     | -    | -    | -    |
| H. concrescens                | REB-385      | United States | JN135182 | -    | -     | -    | -    | -    |
| H. concrescens                | REB-65       | United States | KC571713 | -    | -     | -    | -    | -    |
| H. concrescens                | REB-384      | United States | KC571714 | -    | -     | -    | -    | -    |
| H. crassipilatum              | Cui 17021    | China    | ON603660 ON603641 ON603649 ON605661 ON605668 | -    | -     | -    | -    | -    |
| H. crassipilatum              | Cui 17019    | China    | ON603659 ON603642 ON603650 ON605662 | -    | -     | -    | -    | -    |
| H. cristatum                  | 4446         | Canada   | KM406974 -            | -    | -     | -    | -    | -    |
| H. cristatum                  | REB-169      | United States | JN135174 | -    | -     | -    | -    | -    |
| H. cumulatum                  | SEW 69       | United States | AYS69026 | -    | -     | -    | -    | -    |
| H. cumulatum                  | REB-342      | United States | JN135172 | -    | -     | -    | -    | -    |
| H. cyanopodium                | SEW 85       | United States | AYS69027 | -    | -     | -    | -    | -    |
| H. diabolus                   | KAH13873     | Canada   | AF51863 -            | -    | -     | -    | -    | -    |
| H. diasthifolium              | ML902162HY   | -        | KK619420 -            | -    | -     | -    | -    | -    |
| H. diasthifolium              | ML61211HY    | -        | KK619419 -            | -    | -     | -    | -    | -    |
| H. earlilimon                 | REB-375      | United States | JN135179 | -    | -     | -    | -    | -    |
| H. earlilimon                 | REB-75       | United States | KC571724 | -    | -     | -    | -    | -    |
| H. fagiscabrosum              | GB-0195621   | Sweden   | MW144293 MW144293    | -    | -     | -    | -    | -    |
| H. fagiscabrosum              | GB-0195805   | Sweden   | MW144294 MW144294    | -    | -     | -    | -    | -    |
| H. fagiscabrosum              | GB-0195625   | Sweden   | MW144292 MW144292    | -    | -     | -    | -    | -    |
| H. fenicicum                  | OF242833     | Norway   | MK602738 MK602738    | -    | -     | -    | -    | -    |

(Continued)
| Species                     | Specimen no. | Locality       | GenBank accession no. |
|-----------------------------|--------------|----------------|-----------------------|
| *H. fennicum*               | SWesterberg110909 Sweden | MK602739 MK602739 | - - -                  |
| *H. ferrugineum*            | ELarsson 356-16 Sweden | MK602721 MK602721 | - - -                  |
| *H. ferrugineum*            | ELarson 197-14 Sweden | MK602722 MK602722 | - - -                  |
| *H. ferrugipes*             | REB-176 United States | KCS71727 - - - | - - -                  |
| *H. ferrugipes*             | REB-68 United States | JN135176 - - - | - - -                  |
| *H. fibulatum*              | Yuan 14646 China | MW579957 - | MW579926 -               |
| *H. fibulatum*              | Yuan 14656 China | MW579927 - | MW579958 -               |
| *H. fulgineoviolaceum*      | LA120818 Sweden | MK602740 MK602740 | - - -                  |
| *H. fulgineoviolaceum*      | BNylen130918 Sweden | MK602741 MK602741 | - - -                  |
| *H. fuscoindicum*           | OSC 113641 United States | EU669230 EU669280 | - - -                  |
| *H. fuscoindicum*           | OSC 107844 United States | EU669229 EU669279 | - - -                  |
| *H. geogenium*              | EBendiksen526-11 Norway | MK602725 MK602725 | - - -                  |
| *H. geogenium*              | OF296213 Norway | MK602724 MK602724 | - - -                  |
| *H. geogenium*              | OF66379 Norway | MK602723 MK602723 | - - -                  |
| *H. glaucopus*              | RGCarlsson13-060 Sweden | MK602743 MK602743 | - - -                  |
| *H. glaucopus*              | JNitaro06091 Sweden | MK602744 MK602744 | - - -                  |
| *H. gracilipes*             | ELarsson 219-11 Sweden | MK602727 MK602727 | - - -                  |
| *H. gracilipes*             | GB-1113779 Sweden | MK602726 MK602726 | - - -                  |
| *H. granulosum*             | Yuan 12213a China | MW579948 MW579893 MW579921 | OK254213 |
| *H. granulosum*             | Yuan 12213b China | MW579947 MW579892 MW579920 | OK254212 |
| *H. grosslepidotum*         | Wei 8120 China | MN846274 MN846283 | - - -                  |
| *H. grosslepidotum*         | Wei 8015 China | MN846276 MN846285 | - - -                  |
| *H. iulidens*               | OF-76340 Norway | MW144334 MW144334 | - - -                  |
| *H. iulidens*               | OF-242769 Norway | MW144335 MW144335 | - - -                  |
| *H. iulidens*               | OF-68659 Norway | MW144333 MW144333 | - - -                  |
| *H. inflatum*               | Wang 80 China | MW579949 MW579949 MW579922 | OK254210 |
| *H. inflatum*               | Shi 506 China | OK254210 MW579895 | OK254210 OK254211 |
| *H. joecides*               | RGCarlsson11-090 Sweden | MK602749 MK602749 | - - -                  |
| *H. joecides*               | KHjortstam17589 Sweden | MK602750 MK602750 | - - -                  |
| *H. joecides*               | JNitaro10829 Sweden | MK602751 MK602751 | - - -                  |
| *H. lepidum*                | EGrundell10916 Sweden | MK602753 MK602753 | - - -                  |
| *H. lindogena*              | JNitaro10829 Sweden | MK602754 MK602754 | - - -                  |
| *H. lindogena*              | Wei 8329 China | MN846281 MN846280 | - - -                  |
| *H. lindogena*              | Wei 8365 China | MN846280 MN846289 | - - -                  |
| *H. lundellii*              | Strivdval10049 Sweden | MK602758 MK602758 | - - -                  |
| *H. lundellii*              | OF242639 Norway | MK602759 MK602759 | - - -                  |
| *H. lundellii*              | OF295814 Norway | MK602760 MK602760 | - - -                  |
| *H. martioflavus*           | OF242872 Norway | MK602761 MK602761 | - - -                  |
| *H. martioflavus*           | OF242435 Norway | MK602762 MK602762 | - - -                  |
| *H. martioflavus*           | ADeln110884 Sweden | MK602763 MK602763 | - - -                  |
| *H. melanocarpum*           | Cui 18566 China | ON603661 - | ON603651 -                  |
| *H. melanocarpum*           | Cui 18557 China | ON603662 ON603643 ON603652 | - - |
| *H. melanocarpum*           | Cui 18559 China | ON603663 ON603644 ON603653 | ON603667 |
| *H. mirabile*               | SLund140912 Sweden | MK602730 MK602730 | - - -                  |
| *H. mirabile*               | RGCarlsson11-119 Sweden | MK602728 MK602728 | - - -                  |
| *H. mirabile*               | ELarson17014 Sweden | MK602729 MK602729 | - - -                  |
| *H. nemorusum*              | GB-0195631 Sweden | MW144373 MW144373 | - - -                  |

(Continued)
| Species          | Specimen no. | Locality  | GenBank accession no. | ITS  | nrLSU | nSSU | RPB1 | RPB2 |
|------------------|--------------|-----------|-----------------------|------|-------|------|------|------|
| H. nemorosum     | O-F-242352   | Norway    | MW144372              | MW144372 | -   | -   | -   | -   |
| H. parvum        | REB-131      | United States | IN135187            | -   | -   | -   | -   | -   |
| H. parvum        | REB-392      | United States | KC571717            | -   | -   | -   | -   | -   |
| H. peckii        | SSvantesson328 | Norway    | MK602731              | MK602731 | -   | -   | -   | -   |
| H. peckii        | ELarsson174-14 | Sweden    | MK602732              | MK602732 | -   | -   | -   | -   |
| H. peckii        | EBendiksen 567-11 | Norway     | MK602733              | MK602733 | -   | -   | -   | -   |
| H. pinetica      | REB-49       | United States | KC571733            | -   | -   | -   | -   | -   |
| H. pinetica      | REB-43       | United States | IN135175            | -   | -   | -   | -   | -   |
| H. piperatum     | REB-332      | United States | IN135173            | -   | -   | -   | -   | -   |
| H. piperatum     | REB-304      | United States | KC571723            | -   | -   | -   | -   | -   |
| H. radiatum      | Cui 17130    | China     | ON603664              | ON603645 | ON603654 | ON605663 | ON605669 | - |
| H. radiatum      | Cui 16254    | China     | ON603665              | -   | ON603655 | ON605664 | -   | -   |
| H. regium        | SEW 93       | United States | AY569031            | -   | -   | -   | -   | -   |
| H. roseoaloeaecc | GB-0195687   | Sweden    | MW144375              | MW144375 | -   | -   | -   | -   |
| H. roseoaloeaecc | GB-0195936   | Sweden    | MW144374              | MW144374 | -   | -   | -   | -   |
| H. rubidofuscum  | Yuan 14587   | China     | MW579852              | MW579897 | MW579925 | -   | OK254208 | - |
| H. rubidofuscum  | Yuan 14561   | China     | MW579851              | MW579896 | MW579924 | -   | OK254207 | - |
| H. rubidofuscum  | Yuan 14654   | China     | MW579893              | MW579898 | -   | -   | OK254209 | - |
| H. scabriulatum  | GB-0195806   | Sweden    | MW144377              | MW144377 | -   | -   | -   | -   |
| H. scabriulatum  | GB-0195791   | Sweden    | MW144378              | MW144378 | -   | -   | -   | -   |
| H. scabriulatum  | GB-0195689   | Sweden    | MW144379              | MW144379 | -   | -   | -   | -   |
| H. scabrosum     | OF295824     | Norway    | MK602764              | MK602764 | -   | -   | -   | -   |
| H. scabrosum     | OF360777     | Norway    | MK602765              | MK602765 | -   | -   | -   | -   |
| H. scabrosum     | OF292320     | Norway    | MK602766              | MK602766 | -   | -   | -   | -   |
| H. scrobiculatum | REB-3        | United States | IN135186            | -   | -   | -   | -   | -   |
| H. scrobiculatum | REB-352      | United States | KC571740            | -   | -   | -   | -   | -   |
| H. spongiosipes  | REB-78       | United States | IN135181            | -   | -   | -   | -   | -   |
| H. spongiosipes  | SEW 86       | United States | AY569021            | -   | -   | -   | -   | -   |
| H. spongiosipes  | REB-107      | United States | KC571743            | -   | -   | -   | -   | -   |
| H. spongiosipes  | REB-52       | United States | IN135184            | -   | -   | -   | -   | -   |
| H. squamulosum   | Yuan 13625   | China     | MW579896              | MW579899 | -   | -   | OK254204 | - |
| H. squamulosum   | Yuan 13743   | China     | MW579895              | MW579895 | -   | -   | OK254203 | - |
| H. suaveolens    | ELarsson 139-09 | Norway     | MK602734              | MK602734 | -   | -   | -   | -   |
| H. suaveolens    | ELarsson 8-14 | Sweden    | MK602735              | MK602735 | -   | -   | -   | -   |
| H. suaveolens    | SSvantesson877 | Norway     | MK602736              | -   | -   | -   | -   | -   |
| H. subsuccosum   | SEW 55       | United States | AY569033            | -   | -   | -   | -   | -   |
| H. subsuccosum   | REB-10       | United States | IN135178            | -   | -   | -   | -   | -   |
| H. sulcatum      | Yuan 14521   | China     | MW579901              | MW579902 | MW579930 | -   | OK254202 | - |
| H. sulcatum      | Yuan 14649   | China     | MW579960              | MW579901 | MW579929 | -   | OK254201 | - |
| H. sulcatum      | Yuan 14660   | China     | MW579959              | MW579900 | MW579901 | -   | -   | -   |
| Hydnumellum sp.1 | Shi 164      | China     | -                      | MW579896 | -   | -   | -   | -   |
| Hydnumellum sp.2 | Yuan 14387   | China     | MW579970              | MW579908 | MW579934 | -   | -   | -   |
| Hydnumellum sp.3 | Yuan 14388   | China     | MW579971              | -   | -   | -   | -   | -   |
| Hydnumellum sp.4 | Wang 295     | China     | MW579972              | -   | -   | -   | -   | -   |
| Hydnumellum sp.5 | Yuan 14594   | China     | MW579973              | MW579909 | MW579935 | -   | OK254205 | - |
| H. yunnanense    | Yuan 14386   | China     | MW579962              | MW579903 | -   | -   | OK254199 | - |
| H. yunnanense    | Yuan 14396   | China     | MW579963              | MW579904 | -   | -   | OK254200 | - |

(Continued)
Table 1 (Continued)

| Species         | Specimen no. | Locality     | GenBank accession no. |
|-----------------|--------------|--------------|-----------------------|
|                 |              |              | ITS                   |
|                 |              |              | nrLSU                 |
|                 |              |              | nSSU                  |
|                 |              |              | RPB1                  |
|                 |              |              | RPB2                  |
| *H. underwoodii*| REB-358      | United States| JN135189              |
| *H. underwoodii*| REB-50       | United States| KC571781              |
| *H. versipellis*| EBendiksen164-07 | Norway      | MK602770            |
| *H. versipellis*| RGCarlsson13-057 | Sweden      | MK602771            |
| *Sarcodon aspratus*| -          | -            | DQ448877             |
| *S. aspratus*    | -            | -            | AF335110             |
| *S. imbricatus*  | JRova 1408929 | Sweden       | MK602746            |
| *S. imbricatus*  | ELarssen 384-10 | Norway      | MK602747            |
| *S. imbricatus*  | SSvantesson355 | Norway      | MK602748            |
| *S. scabripes*   | REB-351      | United States| JN135191             |
| *S. scabripes*   | FCME:23240   | Mexico       | EU293829             |
| *S. squamosus*   | ELarssen 248-12 | Sweden      | MK602767            |
| *S. squamosus*   | OF177452     | Norway       | MK602768            |
| *S. squamosus*   | OF295554     | Norway       | MK602769            |
| *S. quercinofibulatus* | JC-20090718.2 | Italy     | JX271818            |
| *S. leucopus*    | OF296099     | Norway       | MK602755            |
| *S. leucopus*    | OF296944     | Norway       | MK602756            |

New sequences are shown in bold.

University (BJFC). Macro-morphological descriptions were based on field notes and laboratory measurements. The microscopic measures used in this study were followed by Sun et al. (2020, 2022) under a light microscope (Nikon Eclipse E 80i microscope, Nikon, Tokyo, Japan). Microscopic characteristics, measurements, and drawings were made from slide preparations stained with Cotton Blue and Melzer's reagent, following Liu et al. (2021a). The following abbreviations were used: IKI = Melzer's reagent, IKI– = neither amyloid or dextrinoid, KOH = 5% potassium hydroxide, CB = Cotton Blue, CB += cyanophilous, CB– = acyanophilous, L = mean spore length (arithmetic average of all spores), W = mean spore width (arithmetic average of all spores), Q = variation in the L/W ratios between the specimens studied, and n = number of spores measured from given number of specimens. A field Emission Scanning Electron Microscope (FESEM) Hitachi SU-8010 (Hitachi, Ltd., Tokyo, Japan) was used to photograph the ornamentation of the basidiospores, and the materials were studied at up to 2,200 times magnification, according to Song et al. (2021, 2022).

DNA extraction, polymerase chain reaction amplification, and sequencing

The CTAB rapid plant genome extraction kit DN14 (Aidlab Biotechnologies, Beijing, China) was used to acquire total genomic DNA from dried specimens according to the manufacturer's instructions with some modifications (Sun et al., 2022). ITS4 and ITS5 were used as primers for the internal transcribed spacer (ITS), LR0R and LR7 were used for the large subunit of nuclear ribosomal RNA gene (nLSU), NS1/NS4 were used for the small subunit of nuclear ribosomal RNA gene (nSSU), and 5F/7Cr were used to the second largest subunit of RNA polymerase II (RPB2) gene. The Polymerase Chain Reaction (PCR) procedure for ITS was as follows: initial denaturation at 95°C for 3 min, followed by 35 cycles at 94°C for 40 s, 56°C for 45 s, and 72°C for 1 min, and a final extension of 72°C for 10 min. The PCR procedure for nLSU and nSSU was as follows: initial denaturation at 94°C for 1 min, followed by 35 cycles at 94°C for 30 s, 50°C for 1 min, and 72°C for 1.5 min, and a final extension of 72°C for 10 min. The PCR process for RPB2 was as follows: initial denaturation at 94°C for 2 min, 9 cycles at 94°C for 45 s, 60°C for 45 s, followed by 36 cycles at 94°C for 45 s, 53°C for 1 min, 72°C for 90 s, and a final extension of 72°C for 10 min. The PCR products were purified and sequenced at the Beijing Genomics Institute, China, with the same primers. The newly generated sequences were deposited at GenBank. All sequences analyzed in this study were deposited at GenBank and are listed in Table 1.

Phylogenetic analyses

The new sequences generated in this study were combined with the sequences downloaded from GenBank and are listed in Table 1. Amaurodon aquicoeruleus Agerer and A. viridis (Alb. and Schwein.) J. Schröt were used as the outgroups, according
| Species          | Distribution in China                                                                 | Ecological habits                                      | Alt.  | Pileal surface (when fresh) | Spines color (when fresh) | Basidiospores (µm)                  | References            |
|------------------|----------------------------------------------------------------------------------------|--------------------------------------------------------|-------|-----------------------------|----------------------------|------------------------------------|-----------------------|
| *H. atrorubrum*  | Yunnan Province on the ground of Fagaceous forest                                      |                                                        | 2100 m| light brown to dark ruby     | white to dark brown         | (4.1–)4.5–6 × (3.2–)3.9–5.1(–6)  | Mu et al., 2021       |
| *H. atrospinosum*| Qinghai Province on the ground of *Picea* forest                                       |                                                        | 2800 m| light orange to yellowish brown | dark violet                 | (4–)4.1–5.1(–5.5) × (3–)3.3–3.9(–4) | Mu et al., 2021       |
| *H. bomiense*    | Xizang Autonomous Region on the ground with moss of Fagaceous forest                   |                                                        | 2760 m| grayish yellow, brown to dark brown | white to brown             | (4–)4.1–5.1(–5.2) × (3–)3.3–4.5(–4.8) | Mu et al., 2021       |
| *H. brunneocarum*| Liaoning Province on the ground of Fagaceous forest or mixed forest                    |                                                        | 400 m | brownish orange to brownish red | golden yellow to light brown | (4–)4.1–5.1(–5.2) × (3.1–)3.2–4.6(–4.8) | Mu et al., 2021       |
| *H. caeruleum*   | Xingjiang Autonomous Region on the ground of *Picea* forest                            |                                                        | 1900 m| pastel yellow to dark blonde | orange-white to dark brown  | (4.9–)5–6(–6.1) × (4–)4.1–4.9(–5)  | Mu et al., 2021       |
| *H. chocolatum*  | Sichuan Province on the ground of mixed forest                                         |                                                        | 3000 m| dark brown to fuscous         | brown to grayish brown      | 4–5(–5.8) × (4.5–)5–6             | This study            |
| *H. coactum*     | Yunnan Province on the ground of Fagaceae forest                                       |                                                        | 1600–2000 m| reddish-brown to dark brown | white to yellowish-white | (5.1–)3.7–7(–7.1) × (4.6–)4.7–5.9(–6) | Mu et al., 2020       |
| *H. concentricum*| Yunnan Province on the ground of forest dominated by trees of *Pinus* and *Quercus*   |                                                        | 3000–3500 m| light brown, pastel red, reddish-brown to grayish brown | fawn to reddish brown            | (3.2–)3.5–5 × (3.5–)4–5(–5.2) | This study            |
| *H. cussipileatum*| Yunnan Province on the ground of forest dominated by trees of *Pinus* and *Quercus*   |                                                        | 3525 m| reddish brown to grayish brown | grayish brown to fuscous    | 4–5.5 × 4–6 (–6.5)                | This study            |
| *H. fibulatum*   | Liaoning Province on the ground of *Quercus* forest                                     |                                                        | 740 m | light brown to dark brown     | pinkish white to brown      | (4.2–)4.4–5.8(–6) × (4–)4.1–4.9(–5.1) | Mu et al., 2021       |
| *H. grunulosum*  | Sichuan Province on the ground of *Acer* and *Cryptomeria* mixed forest               |                                                        | 1175 m| light yellow, light brown to grayish brown | grayish orange to dark brown when dry | (4–)4.1–5.1(–5.3) × (3.2–)3.4–4.7(–4.9) | Mu et al., 2021       |
| *H. grosselepidotum* | Yunnan Province on the ground of Fagaceae forest                                     |                                                        | 2000 m| pale orange to dark ruby      | white to pale yellow        | (5–)3.5–6.6(–6.6) × (4–)4.1–5.9(–6)  | Mu et al., 2020       |
| *H. inflatum*    | Yunnan Province on the ground of Fagaceae forest                                       |                                                        | 1580 m| grayish orange to brown       | white to golden brown       | (4–)3.2–5(–5.1) × (3–)3.8–4.3(–5)  | Mu et al., 2021       |
| *H. lidongensis* | Yunnan Province on the ground of Fagaceae forest                                       |                                                        | 2400 m| light brown to brown          | grayish-orange to brown     | (4–)4.1–6(–6.1) × (3.9–)3–4.5(–5.1) | Mu et al., 2020       |
| *H. melanocarpum*| Sichuan Province on the ground of mixed forest                                         |                                                        | 4090 m| vinaceous brown               | brown                      | (3.5–)3.8–5.1 × 4.5–5.5(–6)        | This study            |
| *H. peckii*      | Xizang Autonomous Region on the ground of *Pinus* mixed forest                         |                                                        | 2760 m| white to light orange         | brownish orange             | (4.1–)4.2–5(–5.1) × (3.8–)3.9–4.4(–4.6) | Mu et al., 2021       |
| *H. radiatum*    | Yunnan Province on the ground of forest dominated by *Pinus armandii* and *Rhododendron* or *Pinus* and *Quercus* |                                                        | 2400–2700 m| dark brown, fuscous to black | dark brown                 | 3–4.5(–5) × (3.5–)4–5           | This study            |

(Continued)
TABLE 2 (Continued)

| Species                      | Distribution in China | Ecological habits                      | Basidiospores (µm) | References |
|-----------------------------|-----------------------|----------------------------------------|--------------------|------------|
| *H. rubidofuscum*           | Liaoning Province on the ground of Quercus forest | 700 m pastel red to dark magenta       | 4–5 (4.1–5.1) × 4.5–5.3 (4.7–5.8) | Mu et al., 2021 |
| *H. spongiosipes*           | Liaoning Province on the ground of Quercus forest | 400 m pale orange to dark brown        | 5.1–6.1 (5.2–6.2) × 4.8–5.8 (4.9–6.1) | Mu et al., 2021 |
| *H. squamulosum*            | Xizang Autonomous Region on the ground with moss of Picea mixed forest | 2760 m dark brown                    | 4.1–5.1 (4.2–5.2) × 3.8–4.8 (3.9–5.0) | Mu et al., 2021 |
| *H. sulcatum*               | Liaoning Province on the ground of Quercus forest | 740 m brown                            | 4.1–5.1 (4.2–5.2) × 3.8–4.8 (3.9–5.0) | Mu et al., 2021 |
| *H. yunnanense*             | Yunnan Province on the ground | 2358 m grayish red to dark brown       | 5.1–6.1 (5.2–6.2) × 4.8–5.8 (4.9–6.1) | Mu et al., 2021 |

to Mu et al. (2021). Sequences were aligned by MAFFT v.7 with the G-INS-I option (Katoh and Standley, 2013) and manually adjusted in BioEdit v. 7.0.9. (Hall, 1999). Alignments were spliced in Mesquite v. 3.2. (Maddison and Maddison, 2017). The partition homogeneity test (PHT) (Farris et al., 1994) of the four-gene dataset was tested by PAUP v. 4.0b10 (Swofford, 2002) under 1,000 homogeneity replicates. The best-fit evolutionary model was selected with AIC (Akaike Information Criterion) using ModelTest 2.3 (Guindon and Gascuel, 2003; Darriba et al., 2012). Phylogenetic analyses were carried out according to the previous studies (Cui et al., 2019; Liu et al., 2022a).

Maximum parsimony (MP) analyses were applied to the combined datasets. The construction was performed in PAUP∗ version 4.0b10 (Swofford, 2002). All characters were equally weighted and gaps were treated as missing data. Trees were inferred using the heuristic search option with TBR branch swapping and 1,000 random sequence additions. Max trees were set to 5,000, branches of zero length were collapsed, and all parsimonious trees were saved. Clade robustness was assessed using a bootstrap analysis with 1,000 replicates (Felsenstein, 1985). Descriptive tree statistics of tree length (TL), consistency index (CI), retention index (RI), rescaled consistency index (RC), and homoplasy index (HI) were calculated for each maximum parsimonious tree generated. RAxML-HPC2 was used to construct the maximum likelihood (ML) analyses with the GTR+gamma model. All model parameters were estimated by the program, and only the best ML tree from all searches was kept. The ML bootstrap values were performed using rapid bootstrapping with 1,000 replicates.

MrModeltest 2.3 (Posada and Crandall, 1998; Nylander, 2004) was used to determine the best-fit evolution model for each dataset for Bayesian inference (BI). BI was calculated using MrBays 3.1.2 with four Markov chains running for two runs from random starting trees for one million generations, and trees were sampled every 100 generations (Ronquist and Huelsenbeck, 2003). The first 25% of the sampled trees were discarded as burn-in and a majority rule consensus tree of all remaining trees was calculated. All trees were viewed in FigTree v. 1.4.2.

Results

Phylogeny

The combined ITS + nLSU dataset included 257 sequences from 156 specimens representing 76 taxa. The dataset had an aligned length of 2,605 characters, including gaps (1,202 characters for ITS, 1,403 characters for nLSU), of which 1,527 characters were constant, 122 were variable and parsimony-uninformative, and 956 were parsimony-informative. Maximum parsimony analysis yielded 12 equally parsimonious trees (TL = 5,489, CI = 0.355, RI = 0.798,
RC = 0.283, HI = 0.645). The best model for the combined ITS + nLSU sequences dataset estimated and applied in the Bayesian analysis was the GTR + I + G model. Bayesian and ML analysis resulted in a topology similar to that of MP analysis. Bayesian analysis has an average standard deviation of split frequencies = 0.005071. Only the ML tree was provided in Figure 1, and the MP bootstrap values (≥75%), ML bootstrap values (≥75%), and BPP (≥0.95) were shown at the nodes.

The combined ITS + nLSU + nSSU + RPB2 dataset included 312 sequences from 156 specimens representing 76 taxa. The dataset had an aligned length of 4,639 characters, including gaps (1,181 characters for ITS, 1,399 characters for nLSU, 986 characters for nSSU, and 1,073 characters for RPB2), of which 3,168 characters were constant, 186 were variable and parsimony-uninformative, and 1,285 were parsimony-informative. Maximum parsimony analysis yielded 15 equally parsimonious trees (TL = 6,171, CI = 0.392, RI = 0.800, RC = 0.313, HI = 0.608). The best model for the combined ITS + nLSU + nSSU + RPB2 sequences dataset estimated and applied in the Bayesian analysis was the GTR + I + G model. Bayesian and ML analysis resulted in a topology similar to that of MP analysis. Bayesian analysis has an average standard deviation of split frequencies = 0.007966. Only the ML tree was provided in Figure 2, and the MP bootstrap values (≥75%), ML bootstrap values (≥75%), and BPP (≥0.95) were shown at the nodes.

Taxonomy

**Hydnellum chocolatum** B. K. Cui and C. G. Song, sp. nov. (Figures 3A,B, 4A,B, 5).

Mycobank no.: 846115

*Diagnosis:* Differs from others by its fibrillose, spongy to tomentose pileal surface in chocolate color.

*Type:* CHINA. Sichuan Province, Jiuzhaigou County, on the ground of the mixed forest, elev. 2,600 m, 19 September 2020, Bao-Kai Cui, Cui 18543 (holotype, BJFC 035406).

*Etymology:* chocolatum (Lat.) refers to the chocolate-colored pileal surface.

*Fruiting body:* Basidiomata annual, eccentrically stipitate, single to concrescent, and odorless when fresh. The pileus is circular to irregular, with irregular folds in the middle, and up to 7.4 cm in diam and 0.7 cm thick at the center. Pileal surface is chocolate to fuscous when fresh, becoming grayish brown upon drying, azonate, fibrillose to spongy at the center, and tomentose near the margin, with radially aligned stripes toward the margin; margin white to light brown when fresh, becoming grayish brown upon drying, up to 7 mm wide. Context is brown to vinaceous gray upon drying, corky to fragile, and up to 3 mm thick. Spines are soft, brown to grayish brown when fresh, becoming grayish brown upon drying, fragile, and up to 5 mm long. Stipe is cylindrical and glabrous, surface layer is dark brown to vinaceous gray, and inner layer is grayish brown, and up to 3.8 cm long and 0.9 cm in diam.

*Hyphal structure:* Hyphal system monomitic; generative hyphae with simple septa; all the hyphae IKI–, CB–; tissues turned to olive-green or black in KOH.

*Context:* Generative hyphae grayish brown, thick-walled, branched, regular arranged, 2.5 to 6 µ m in diam.

*Spines:* Generative hyphae clay-buff, slightly thick-walled, occasionally branched, regular arranged, 2 to 4.5 µ m in diam. Cystidia and cystidioles are absent. Basidia clavate, bearing four sterigmata (2–4 µ m long) and a basal simple septum, 32–45 × 5–7 µ m; basidioles similar to basidia in shape, but slightly smaller.

*Stipe:* Generative hyphae clay-buff to grayish brown, slightly thick-walled, rarely branched, interwoven in the surface layer, regularly arranged in the inner layer, and 2 to 4 µ m in diam.

*Sporae:* Basidiospores subglobose to globose, hyaline, thick-walled, echinate, IKI–, CB– (4.5–5)–6 × 4–5(–5.8) µ m, L = 5.2 µ m, W = 4.7 µ m, Q = 1–1.25 (n = 60/2, without the ornamentation).

*Additional specimen (paratype) examined:* CHINA. Sichuan Province, Jiuzhaigou County, on the ground of the mixed forest, elev. 2,600 m, 19 September 2020, Bao-Kai Cui, Cui 18543 (BJFC 035404).

*Ecological habits:* Hydnellum chocolatum was collected in Southwest China under a plateau humid climate. It grows on the moist ground of the mixed forest, with well-watered bryophytes.

**Hydnellum concentricum** B. K. Cui and C. G. Song, sp. nov. (Figures 3C,D, 4C,D, 6).

Mycobank no.: 846116

*Diagnosis:* Differs from other Hydnellum species by its zonate pileal surface, thin context, short stipe, and presence of both simple septa and clamp connections in generative hyphae of spines.

*Type:* CHINA. Yunnan Province, Lijiang City, Yulong County, Jihe, Laojun Mountain, Jiushijulongtan, on the ground of forest dominated by trees of Pinus sp. and Quercus sp., elev. 2,800 m, 15 September 2018, Bao-Kai Cui, Cui 17017 (holotype, BJFC 030316).

*Etymology:* concentricum (Lat.) refers to the concentric bands on the pileal surface.

*Fruiting body:* Basidiomata annual, centrally stipitate, single, and odorless when fresh. Pileus infundibuliform, and up to 3.2 cm in diam and 0.4 cm thick at the center. Pileal surface is light brown, pastel red, reddish-brown to grayish brown when fresh, becoming brown to grayish brown upon drying, zonate, glabrous, with radially aligned stripes; margin fawn to orange-brown when fresh, becoming fawn upon drying, and up to 0.8 cm wide. Context is grayish brown upon drying, fragile, and up to 1 mm thick. Spines are soft, fawn to reddish-brown when fresh, grayish brown upon drying, fragile, and up to 3 mm long. Stipe cylindrical, glabrous, surface layer honey yellow to grayish
brown upon drying, inner layer grayish brown upon drying; and up to 1.8 cm long and 0.5 cm in diam.

**Hyphal structure:** Hyphal system monomitic; generative hyphae in context and stipe with simple septa, generative hyphae in spines mostly with simple septa, occasionally with clamp connections; all the hyphae IKI−, CB−; tissues turned to olive-green or black in KOH.

**Context:** Generative hyphae clay-buff to grayish brown, slightly thick-walled, branched, regularly arranged, and 2 to 6 µm in diam.

**Spines:** Generative hyphae clay-buff, thin-walled, occasionally branched, occasionally with clamp connections, regularly arranged, and 2 to 4.5 µm in diam. Cystidia and cystidioles are absent. Basidia clavate, bearing four sterigmata (2–4 µm long) and a basal simple septum, 22–48 × 5–7 µm; basidiospores are similar to basidia in shape but slightly smaller.

**Stipe:** Generative hyphae clay-buff, slightly thick-walled, rarely branched, interwoven in the surface layer, regularly arranged in the inner layer, and 2 to 4.5 µm in diam.

**Spores:** Basidiospores subglobose to ellipsoidal, hyaline, thin-walled, echinulate, IKI−, CB−; tissues turned to olive-green or black in KOH.

**Additional specimen (paratype) examined:** CHINA. Yunnan Province, Shangri-La, on the ground of forest dominated by...
FIGURE 2

Maximum likelihood tree of the Hydnellum species based on the combined ITS + nLSU + nSSU + RPB2 sequences data. Branches are labeled with parsimony bootstrap values equal to or higher than 75%, ML bootstrap values equal to or higher than 75%, and Bayesian posterior probabilities equal to or higher than 0.95. Bold names = New species.

trees of *Pinus yunnanensis*, elev. 3,200 m, 17 September 2018, Bao-Kai Cui, Cui 17098 (BJFC 030398).

Ecological habits: *Hydnellum concentricum* was collected in Southwest China, under a plateau monsoon climate. It grows on the moist ground of a forest dominated by trees of *Pinus yunnanensis*.

*Hydnellum crassipileatum* B. K. Cui and C. G. Song, sp. nov. (Figures 3E,F, 4E,F, 7).

MycoBank no.: 846117

**Diagnosis:** Differs from other *Hydnellum* species by its thick pileus with reddish brown to grayish brown pileal surface.

**Type:** CHINA. Yunnan Province, Lijiang City, Yulong County, Jiuhe, Laojun Mountain, Jiushijiulongtan, on the ground of forest dominated by trees of *Pinus* sp. and *Quercus* sp., elev. 2,800 m, 15 September 2018, Bao-Kai Cui, Cui 17021 (holotype, BJFC 030320).

**Etymology:** *crassipileatum* (Lat.) refers to the thick pileus.

**Fruiting body:** Basidiomata annual, eccentrically stipitate, single, and odorless when fresh. Pileus circular to elliptical, up to 5.5 cm in diam, and 0.5 cm thick at the center. Pileal surface is reddish-brown to grayish brown, becoming grayish brown upon drying, up to 6 mm wide. Context light grayish-brown upon drying, up to 5 mm thick. Spines soft, grayish brown to fuscous when fresh, fuscous to black upon drying, up to 4 mm long. Stipe cylindrical, grayish brown, surface layer grayish-brown, inner layer grayish brown to fuscous; up to 4.8 cm long, and 1.9 cm in diam.

**Hyphal structure:** Hyphal system monomitic; generative hyphae with simple septa; all the hyphae IKI–, CB–; tissues turned to olive-green or black in KOH.

**Context:** Generative hyphae clay-buff, thick-walled, occasionally branched, regularly arranged, and 2.5 to 5 µm in diam.

**Spines:** Generative hyphae clay-buff, thick-walled, occasionally branched, more or less regularly arranged, and 2.5 to 4 µm in diam. Cystidia and cystidioles are absent.
FIGURE 3
Basidiomata of Hydnellum species. (A) H. chocolatum (paratype, Cui 18543), (B) H. chocolatum (holotype Cui 18545), (C,D) H. concentricum (holotype, Cui 17017), (E,F) H. crassipileatum (paratype, Cui 17019), (G) H. melanocarpum (paratype, Cui 18557), and (H) H. melanocarpum (paratype, Cui 18559), (I,J) H. radiatum (holotype, Cui 17130) Scale bars: 2 cm.
FIGURE 4
Scanning Electron Microscope (SEM) of basidiospores of *Hydnellum* species. (A,B) *H. chocolatum*, (C,D) *H. concentricum*, (E,F) *H. crassipileatum*, (G,H) *H. melanocarpum*, and (I,J) *H. radiatum*. Scale bars: 1.5 µm.

Basidia clavate, bearing four sterigmata (2.5–3.5 µm long) and a basal simple septum, 14–31 × 5–7 µm; basidioles similar to basidia in shape, but slightly smaller.

Stipe: Generative hyphae clay-buff, slightly thick-walled, rarely branched, interwoven in the surface layer, regularly arranged in the inner layer, and 2.5 to 5 µm in diam.

Spores: Basidiospores subglobose to ellipsoidal, hyaline, thin-walled, echinulate, IKI–, CB–, 4–6(–6.5) × 4–5.5 µm, \( L = 5.6 \) µm, \( W = 4.5 \) µm, \( Q = 1–1.38 \) (\( n = 60/2 \), without the ornamentation).

Additional specimen (paratype) examined: CHINA. Yunnan Province, Lijiang City, Yulong County, Jiuhe, Laojun Mountain.
FIGURE 5
Microscopic structures of *H. chocolatum* (drawn from Cui 18545). (A) Basidiospores, (B) Basidia and basidioles, (C) Hyphae from context, (D) Hyphae from spines, (E) Hyphae from the inner layer of stipe, and (F) Hyphae from the surface layer of stipe.

Jiushijulongtan, on the ground of forest dominated by trees of *Pinus* and *Quercus*, elev. 2,800 m, 15 September 2018, Bao-Kai Cui, Cui 17019 (BJFC 030318).

Ecological habits: *Hydnellum crassipileatum* was collected in Southwest China, under a plateau monsoon climate. It grows on the ground of a moist forest dominated by trees of *Pinus* and *Quercus*.

*Hydnellum melanocarpum* B. K. Cui and C. G. Song, sp. nov. (Figures 3G,H, 4G,H, 8).

MycoBank no.: 846118

Diagnosis: Differs from other *Hydnellum* species by its vinaceous brown to black pileus with spongy pileal surface, and the presence of both simple septa and clamp connections in generative hyphae of spines.

Type: CHINA. Sichuan Province, Jiuzhaigou County, Jiuzhaigou Reverse, on the ground of the mixed forest, elev. 2,500 m, 20 September 2020, Bao-Kai Cui, Cui 18556 (holotype, BJFC 035417).

Etymology: *melanocarpum* (Lat.) refers to the vinaceous brown to black pileus.
**FIGURE 6**
Microscopic structures of *H. concentricum* (drawn from Cui 17017). (A) Basidiospores, (B) Basidia and basidioles, (C) Hyphae from context, (D) Hyphae from spines, (E) Hyphae from the inner layer of stipe, and (F) Hyphae from the surface layer of stipe.

**Fruiting body**: Basidiomata annual, centrally or eccentrically stipitate, single to concrecent, and odorless when fresh. Pileus is circular to irregular, up to 4.8 cm in diam, and 0.7 cm thick at the center. Pileal surface is vinaceous brown to black when fresh and becoming grayish brown upon drying, azonate, and glabrous to spongy at the center; margin cream, clay-buff, to orange-brown when fresh, light vinaceous gray at the lower tip, and becoming grayish brown to fuscous upon drying, and up to 0.6 cm wide. Spines are soft, brown when fresh, grayish brown to black upon drying, fragile, and up to 4 mm long. Context is grayish brown upon drying, fragile, and up to 3 mm thick. Stipe is cylindrical, glabrous, and grayish brown; and up to 2.6 cm long and 0.8 cm in diam.

**Hyphal structure**: Hyphal system monomitic; generative hyphae in context and stipe with simple septa, generative
Microscopic structures of *H. crassipileatum* (drawn from Cui 17021). (A) Basidiospores, (B) Basidia and basidioles, (C) Hyphae from context, (D) Hyphae from spines, (E) Hyphae from the inner layer of stipe, and (F) Hyphae from the surface layer of stipe.

Hyphae in spines mostly with simple septa, occasionally with clamp connections; all the hyphae IKI–, CB–; tissues turned to olive green in KOH.

**Context:** Generative hyphae clay-buff to grayish brown, thick-walled, branched, regularly arranged, and 2 to 4 μm in diam.

**Spines:** Generative hyphae clay-buff, thin-walled, occasionally branched, regularly arranged, and 2 to 3.5 μm in diam. Cystidia and cystidioles are absent. Basidia clavate, bearing four sterigmata (1.5–3 μm long) and a basal simple septum, 18–38 × 5–7 μm; basidioles similar to basidia in shape, but slightly smaller.
Microscopic structures of *H. melanocarpum* (drawn from Cui 18556). (A) Basidiospores, (B) Basidia and basidioles, (C) Hyphae from context, (D) Hyphae from spines, (E) Hyphae from the inner layer of stipe, and (F) Hyphae from the surface layer of stipe.

**Stipe:** Generative hyphae clay-buff, slightly thick-walled, rarely branched, interwoven in the surface layer, regularly arranged in the inner layer, and 2 to 4 μm in diam.

**Spores:** Basidiospores subglobose, hyaline, thin-walled, echinulate, IKI−, CB−, 4.5–5.5(–6) × (3.5–)3.8–5.1 μm, \( L = 5 \mu m \), \( W = 4.6 \mu m \), \( Q = 1–1.25 \) (\( n = 90/3 \), without the ornamentation).

**Additional specimens (paratypes) examined:** CHINA. Sichuan Province, Jiuzhaigou County, Jiuzhaigou Nature Reserve, on the ground of the mixed forest, elev. 2,500 m, 20 September 2020, Bao-Kai Cui, Cui 18557 (BJFC 035418) and Cui 18559 (BJFC 035420).

**Ecological habits:** *Hydnum melanocarpum* was collected in Southwest China, under a plateau monsoon climate. It grows on
the ground of the mixed forest, in well-watered bryophytes, and its roots are often interspersed with pine needles.

*Hydnellum radiatum* B. K. Cui and C. G. Song, sp. nov. (Figures 3I,J, 4I,J, 9).

MycoBank no.: 846120

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**Diagnosis:** Differs from other *Hydnellum* species by its radially aligned stripes on pileal surface, grayish brown context, and short stipe.

**Type:** CHINA. Yunnan Province, Lanping County, Tongdian, Jianganchang, on the ground of forest dominated by

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**FIGURE 9**

Microscopic structures of *H. radiatum* (drawn from Cui 17130). (A) Basidiospores, (B) Basidia and basidioltes, (C) Hyphae from context, (D) Hyphae from spines, (E) Hyphae from the inner layer of stipe, and (F) Hyphae from the surface layer of stipe.
Pinus armandii and Rhododendron, elev. 2,480 m, 18 September 2018, Bao-Kai Cui, Cui 17130 (holotype, BJFC 030430).

Etymology: radiatum (Lat.) refers to the radially aligned stripes on the pileal surface.

Fruiting body: Basidiomata annual, eccentrically stipitate, single, and odorless when fresh. Pileus is subcircular, plicate, and up to 2.9 cm in diam and 0.5 cm thick at the center. Pileal surface is dark brown, fuscous to black when fresh and becoming fuscous to black upon drying, azonate, fibrillosse, and with strong radially aligned stripes; margin white, cream to light brown when fresh, becoming grayish brown upon drying, and up to 0.3 cm wide. Context is grayish brown upon drying, tough, and up to 3 mm thick. Spines are soft, fuscous to black when fresh, grayish brown upon drying, fragile, and up to 3 mm long. Stipe is cylindrical, glabrous, surface layer fuscous to black upon drying, inner layer grayish brown upon drying, and up to 4 cm long and 1 cm in diam.

Hyphal structure: Hyphal system monomitic; generative hyphae with simple septa; all the hyphal IKI–, CB–; tissues of stipe with strong radially aligned stripes; margin white, cream to light brown when fresh, becoming grayish brown upon drying, and up to 2.9 cm in diam and 0.5 cm thick at the center. Stipe is cylindrical, glabrous, surface layer fuscous to black upon drying, inner layer grayish brown upon drying, and up to 4 cm long and 1 cm in diam.

Context: Generative hyphae clay-buff, thick-walled, branched, regularly arranged, and 2 to 5.5 μ m in diam.

Spines: Generative hyphae clay-buff, thick-walled, occasionally branched, regularly arranged, and 2 to 3.5 μ m in diam. Cystidia and cystidioloi are absent. Basidia clavate, bearing four sterigmata (1.5–4 μ m long) and a basal simple septum, 14–21 × 3–4 μ m; basidioles similar to basidia in shape, but slightly smaller.

Stipe: Generative hyphae clay-buff, thick-walled, rarely branched, interwoven in both the surface layer and the inner layer, and 2 to 5 μ m in diam.

Spores: Basidiospores subglobose to ellipsoidal, hyaline, thin-walled, echinulate, IKI–, CB–; tissues of pileus and spines turned to olive green in KOH, tissues of stipe without reaction.

Hyphal system monomitic; generative hyphae with simple septa; all the hyphal IKI–, CB–; tissues of stipe with strong radially aligned stripes; margin white, cream to light brown when fresh, becoming grayish brown upon drying, and up to 0.3 cm wide. Context is grayish brown upon drying, tough, and up to 3 mm thick. Spines are soft, fuscous to black when fresh, grayish brown upon drying, fragile, and up to 3 mm long. Stipe is cylindrical, glabrous, surface layer fuscous to black upon drying, inner layer grayish brown upon drying, and up to 4 cm long and 1 cm in diam.

Ecological habitats: Hydnellum radiatum was collected in Southwest China, under a plateau monsoon climate. It grows on the ground of the forest dominated by trees of Pinus yunnanensis, in well-watered bryophytes, and its roots are often interspersed with pine needles.

Key to species of Hydnellum from China:

(1) Pileal surface scaled.................................................................2
(1) Pileal surface not scaled...........................................................3
(2) Pileal surface pale orange to dark ruby............................................................... H. grosselepidotum
(2) Pileal surface differently colored............................................................... H. lidongensis
(3) Pileus subinfundibuliform to infundibuliform.................4
(3) Pileus differently shaped...............................................................8
(4) Pileal surface glabrous............................. H. concentricum
(4) Pileal surface not glabrous............................... H. melanocarpum
(5) Pileal surface brownish orange to brownish red........... H. brunneorubrum
(5) Pileal surface differently colored.................................6
(6) Pileal surface light brown to dark ruby...................... H. atrorubrum
(6) Pileal surface differently colored.................................7
(7) Pileus and spines grayish red.............................. H. yunnanense
(7) Pileus and spines differently colored.......................... H. bomiense
(8) Context tissue becoming blue-green in KOH.................... H. peckii
(8) Context tissue differently colored in KOH....................9
(9) Spines dark violet.............................................................. H. atrospinosum
(9) Spines differently colored...................................................10
(10) Clamp connections present..................................................11
(10) Clamp connections absent...............................................13
(11) Pileal surface pastel yellow to dark blonde.................... H. caeruleum
(11) Pileal surface differently colored.................................12
(12) Clamp connections present in spines............................11
(12) Clamp connections absent in spines.............................12
(13) Pileal surface zonate...........................................................14
(13) Pileal surface azonate.............................................................16
(14) Pileal surface pastel red to dark magenta.................... H. squamulosum
(14) Pileal surface differently colored.................................15
(15) Pileal surface glabrous to scupose when fresh........ H. rubidofuscum
(15) Pileal surface scabrous to fibrous when fresh........ H. sulcatum
(16) Pileal surface with radially aligned stripes.................... H. fibulatum
(16) Pileal surface without radially aligned stripes..............17
(17) Spines fuscous to black....................................................... H. radiatum
(17) Spines brown to grayish brown.............................. H. chocoatrum
(18) Spines white to yellowish-white.......................... H. coatum
(18) Spines differently colored.................................17
(19) Context grayish orange...................................................... H. granulosum
(19) Context differently colored.................................20
(20) Pileal surface reddish brown to grayish brown........... H. crassipileatum
(20) Pileal surface differently colored.............................21
Stipe light brown………………………….. H. inflatum
Stipe orange white, pale orange, sunburn to cognac….. H. inflatum
H. inflatum [Harrison, 1964].

In H. cumulatum ×umber pileus, wider basidia (20 µm) can be distinguished by its vinaceous buff, hessian brown to burnt grayish brown pileal surface; Hydnellum spongiosipes differs by its thick pileus with the reddish brown to grayish brown pileal surface; Hydnellum spongiosipes can be distinguished by its orange white to pale orange pileus and longer basidiospores [6–7 × 5–6 µm in H. spongiosipes vs. (4.5–)5–6 × 4–5(–5.8) µm in H. chocolatum, Baird et al., 2013].

Our phylogenetic analyses showed that Hydnellum concentricum was sister to H. squamulosum Y. H. Mu and H. S. Yuan (Figures 1, 2). The two species were both described in Southwest China, and share the annual, solitary to gregarious basidiomata, pastel red pileus, and reddish-brown spines (Mu et al., 2021). However, H. squamulosum differs from H. concentricum by its floccose to woolly, squamulose pileal surface and smaller basidiospores [4.1–5 × 3.3–4.1 µm in H. squamulosum vs. (3.5–)4–5(–5.2) × (3.2–)3.5–5 µm in H. concentricum, Mu et al., 2021].

Hydnellum melanocarpum is closely related to Hydnellum ferrugineum (Fr.) P. Karst. In our phylogenetic analyses (Figures 1, 2). However, H. ferrugineum differs from H. melanocarpum by its pale orange to burnt umber pileus, and larger basidiospores [5–6(–7) × 5–6 µm in H. ferrugineum vs. 4.5–5.5(–6) × (3.5–)3.8–5.1 µm H. melanocarpum, Baird et al., 2013].

Hydnellum radiatum resembles H. cumulatum in having similar colored spines, which have close phylogenetic relationship (Figures 1, 2). However, H. cumulatum can be distinguished by its vinaceous buff, hessian brown to burnt umber pileus, wider basidia (20 × 5–7 µm in H. cumulatum vs. 14–21 × 3–4 µm), and larger basidiospores [4–5.5 × 4–5 µm in H. cumulatum vs. (3.5–)4–5 × 3–4.5(–5) µm in H. radiatum, Harrison, 1964].

**Discussion**

The genus *Hydnellum* is easy to recognize in Bankeraceae by its coryx to woody pileus with crowded spines, but identification among the species in *Hydnellum* is difficult due to the quite similar morphological features. The main morphological characters of each species in *Hydnellum* from China were summarized in Table 2. The morphological differences between five new species were emphasized here briefly.

*Hydnellum chocolatum* was clustered with *H. crassipileatum* and *H. spongiosipes* (Peck) Pouzar in our phylogenetic analyses (Figures 1, 2). Morphologically, *H. chocolatum* resembles *H. crassipileatum* and *H. spongiosipes* in having single to concrescent basidiomata. However, *H. chocolatum* can be distinguished by its tomentose and azonate pileal margin, and longer basidia (32–45 × 5–7 µm); *H. crassipileatum* differs by its thick pileus with the reddish brown to grayish brown pileal surface; *Hydnellum spongiosipes* can be distinguished by its orange white to pale orange pileus and longer basidiospores [6–7 × 5–6 µm in *H. spongiosipes* vs. (4.5–)5–6 × 4–5(–5.8) µm in *H. chocolatum*, Baird et al., 2013].

In our phylogenetic analyses, Mu et al., 2021. However, *H. ferrugineum* can be distinguished by its pale orange to burnt umber pileus, and longer basidiospores [32–45 × 5–7 µm in *H. radiatum*]. However, the two species were both described in the genus *Hydnellum* in 2013. However, *H. mellifolium* differs by its thick pileus with the reddish brown to grayish brown pileal surface; *Hydnellum spongiosipes* can be distinguished by its orange white to pale orange pileus and longer basidiospores [6–7 × 5–6 µm in *H. spongiosipes* vs. (4.5–)5–6 × 4–5(–5.8) µm in *H. chocolatum*, Baird et al., 2013].

**Data availability statement**

The datasets presented in this study can be found in online repositories. The names of the repository/repositories

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2. https://www.ncbi.nlm.nih.gov/protein
and accession number(s) can be found below: https://www.ncbi.nlm.nih.gov/genbank/, ON603638-ON603665 and https://www.ncbi.nlm.nih.gov/genbank/, ON605658-ON605669.

Author contributions

B-KC designed the research. B-KC, Y-FS, SL, T-MX, D-MW, NG, and C-GS prepared the samples. C-GS, SL, and T-MX conducted the molecular experiments and analyzed the data. C-GS, Y-FS, D-MW, NG, and B-KC drafted the manuscript. All authors read and agreed to the published version of the manuscript.

Funding

This research was supported by the National Natural Science Foundation of China (Nos. 31870008 and U2003211) and Beijing Forestry University Outstanding Young Talent Cultivation Project (No. 2019Q03016).

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Acknowledgments

We express our gratitude to Yu-Cheng Dai (Beijing Forestry University, China) for his help during field collections.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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