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A Contribution to the Knowledge of *Hydnum* (Hydnaceae, Cantharellales) in China, Introducing a New Taxon and Amending Descriptions of Five Known Species

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Abstract: *Hydnum* (Hydnaceae, Cantharellales), one of the edible ectomycorrhizal mushrooms, is of considerable ecological and economic importance. Although previous studies have focused on the genus in China, the diversity still remains incompletely understood. In the present study, in addition to the known species from China being reviewed, six phylogenetic species from the country were described/redescribed, which included a new species: *H. erectum*, and five known taxa: *H. cremeoalbum*, *H. minus*, *H. orientalbidum*, *H. tenuistipitum*, and *H. treui*; *H. treui* is new to China. Detailed descriptions, color photographs of fresh basidiomata, and line drawings of microstructures of them are presented. A key to the accepted species of *Hydnum* in China is also provided.

Keywords: molecular phylogeny; morphology; new taxon; taxonomy

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1. Introduction

Hydnum L. (Hydnaceae, Cantharellales), with the type species *H. repandum* L., is morphologically characterized by its white to brownish-orange stipitate basidiomata with spinous hymenophore, smooth, hyaline, thin-walled, globose, ovoid to ellipsoidal basidiospores, and clavate to suburniform, stichic basidia with one to eight sterigmata [1–8]. It is a genus, forming ectomycorrhizal associations with a variety of host plants including members of the Fagales, Pinaceae, Malvaceae, Dipterocarpaceae, Salicaceae, and Myrtaceae, which plays an important role in maintaining the biodiversity of forest ecosystems [1,9,10]. In addition to the ecological value, species of *Hydnum* also contain polyphenolic compounds with pharmacological effects such as antioxidant and antimicrobial activities [9,11]. Moreover, they are edible and have been collected and consumed by humans for centuries [12].

When Linnaeus established *Hydnum* in 1753, it included all species of mushroom-forming fungi with a spinose hymenophore [1,9]. Molecular phylogenetic analyses suggested that spinose hymenophore has independently evolved many times in distant taxa [13]; thus, many species previously included in *Hydnum* have been moved to other genera, such as *Hericium* Pers., *Phellodon* P. Karst., *Sarcodon* Quél. ex P. Karst. [14]. Up to now, *Hydnum* s.s. has been divided into five subgenera: *Alba* Niskanen & Liimat., *Brevispina* T. Cao & H. S. Yuan, *Hydnum* L., *Pallida* Niskanen & Liimat., and *Rufescentia* Niskanen & Liimat. [1,15]. Within subg. *Hydnum*, two sections, viz. *Hydnum* L. and *Olympica* Niskanen

& Liimat. are included; subg. *Rufescentia* also includes two sections: *Magnorufescentia* Niskanen & Liimat. and *Rufescentia* Niskanen & Liimat; sect. *Rufescentia* currently includes three subsections: *Mulsicoloria* Niskanen & Liimat., *Rufescentia* Niskanen & Liimat., and *Tenuiformia* Niskanen & Liimat. [1].

Species diversity of *Hydnum* was abundant, approximately 60 species of the genus having been described from throughout the world [1,5,9,11,12,16–19]. In China, species of the genus have also received attention from mycologists. Earlier, only 3 taxa of *Hydnum*, viz. *H. repandum*, *H. repandum* var. *album*, and *H. rufescens* Pers., were reported in the country [15,20,21]. Then, Feng et al. recognized 18 phylogenetic species of the genus [9]. Two recent studies indicated that there are 19 species confirmed to be distributed in China [15,22].

Previous studies indicated that *Hydnum* species were mainly found in temperate regions of the world; few taxa were reported from subtropical/tropical forests [1,4,9,12,23–30]. It is well-known that subtropical/tropical China is a biodiversity hotspot, and with more field investigations in the region, more species of the genus will be uncovered. Recently, several collections of *Hydnum* were made from subtropical/tropical China, and these specimens were studied using morphological and molecular phylogenetic analyses, aiming to (i) describe new taxa and uncover more species of *Hydnum* in China; (ii) amend descriptions of some *Hydnum* species; (iii) provide an overview the *Hydnum* species in China.

2. Materials and Methods

2.1. Morphological Studies

The studied specimens were collected from Hainan, Hunan, and Zhejiang Provinces in China and deposited in the Fungal Herbarium of Hainan Medical University (FHMU), Haikou City, Hainan Province, China. Fresh specimens were used to make field records and digital photographs. Color documentation of fresh materials followed Kornerup and Wanscher [31]. Observations and measurements of microscopic features were made in 5% KOH solution and stained with 1% Congo Red [4]. Sections of the pileipellis were taken from the pileus between the center and margin. The number of measured basidiospores is presented as n/m/p, where "n" represents the total number of basidiospores measured from "m" basidiomata of "p" collections. Dimensions of basidiospores were presented in the form (a–) b–e–c (–d), where the range b–c contains at least 90% of the measured values (5th to 95th percentile), "a" and "d" are the extreme values, and "e" refers to the average length/width of basidiospores. Q refers to the length/width ratio of basidiospores; Qm refers to the average Q of basidiospores and is presented with standard deviation [32,33]. The analyses of basidiospore size were constructed using SPSS Statistics Version 17.0 [34]. The terms referring to the size of basidioma were based on Bas [35].

2.2. Molecular Procedures

Total genomic DNA was obtained with the Plant Genomic DNA Kit (KANGWEI Company, Taizhou, China) from materials dried with silica gel, according to the manufacturer's instructions. The primer pairs used for amplification were: LR0R/LR5 [36,37] for the nuclear ribosomal large subunit RNA (28S) and the nuclear rDNA region encompassing the internal transcribed spacers 1 and 2, along with the 5.8S rDNA (ITS), with ITS5/ITS4 [38]. PCR conditions followed the program of Zhang et al. [32]. PCR products were checked on 1% (*w*/*v*) agarose gels, and positive reactions with a bright single band were purified and directly sequenced using an ABI 3730xl DNA Analyzer (Guangzhou Branch of BGI, Guangzhou, China) with the same primers used for PCR amplifications [32,33]. DNA sequences were compiled by BioEdit [39] and then deposited in GenBank.

2.3. Dataset Assembly

Twenty-four DNA sequences (twelve of 28S and twelve of ITS) from thirteen specimens were newly generated. For the concatenated dataset, the sequences of 28S and ITS from the new collections were aligned with sequences of taxa of *Hydnum* from previous studies

and GenBank/UNITE (Table 1). Sequences of *H. elatum* Massee, *H.* sp. (FRI62832), *H.* sp. 17 BF-2016 (PDD93275, PDD98029, PERTH07830742, PERTH08072957, and GD1588), *H.* sp. 18 BF-2016 (PDD94968, GD1590, and GD1589), and *H.* sp. 19 BF-2016 (PERTH07608543, PERTH08018413, PERTH08091676, and PERTH08093865) were excluded from analyses due to the distinct genetic divergences of their ITS sequences, which was also noted by Feng et al., Niskanen et al., and Sugawara et al. [1,9,14]. *Sistotrema muscicola* (Pers.) S. Lundell was chosen as outgroup following Cao et al. [15]. To test for phylogenetic conflict between the two genes in the combined dataset, the phylogenetic trees based on 28S and ITS datasets were analyzed and conducted using the ML method to detect the topologies of genes used. The results of analyses showed that the different gene fragments were not in conflict. Then, the two datasets (28S and ITS) were aligned with MUSCLE v3.6 [40] and concatenated using Phyutility v2.2 for further analyses [41].

Table 1. Taxa, vouchers, locations, and GenBank/UNITE accession numbers of DNA sequences used in this study.

Taxon	Voucher	Locality	GenBank/UNITE Accession Nos.		References
			28S	ITS	
Hydnum aerostatisporum	BB 14.154	USA	—	KY800343	[18]
H. aerostatisporum	RAS071	USA	—	MH379885	[4]
H. albertense	H T. Niskanen 11-354	Canada	—	KX388664	[1]
H. albidum	10640TJB	USA	—	MH379883	[4]
H. alboaurantiacum	RAS186	USA	—	MH379955	[4]
H. alboaurantiacum	RAS208	USA	—	MH379937	[4]
H. alboluteum	TNS-F-36545	Japan	—	LC621797	[14]
H. alboluteum	TUMH 63987	Japan	—	LC621801	[14]
H. alboluteum	TUMH 63988	Japan	—	LC621802	[14]
H. alboluteum	TUMH 63989	Japan	—	LC621803	[14]
H. alboluteum	TUMH 63990	Japan	—	LC621804	[14]
H. alboluteum	TUMH 63992	Japan	—	LC621805	[14]
H. albomagnum	AFTOL-ID 471	USA	AY700199	DQ218305	[42]
H. albomagnum	RAS231	USA	—	MH379943	[4]
"H. albomagnum"	IFP 019480	Hunan, central China	MW979536	MW980550	[15]
"H. albomagnum"	IFP 019481	Hunan, central China	MW979537	MW980551	[15]
H. albopallidum	TUMH 63997	Japan	LC717904	LC621807	[14]
H. albopallidum	TUMH 63998	Japan	—	LC621808	[14]
H. albopallidum	TUMH 63999	Japan	—	LC621809	[14]
H. berkeleyanum	CAL 1656	India	NG_070500	NR_158533	[43]
H. berkeleyanum	HKAS77834	Hunan, SC China	KU612667	KU612525	[9]
H. berkeleyanum	IFP 019484	China	MW979538	MW980552	[15]
H. boreorepandum	H T. Niemela 1679	Finland	—	KX388658	[1]
H. boreorepandum	H 6003711	Finland	—	KX388657	[1]
H. boreorepandum	TUMH 64005	Japan	LC717880	LC621814	[14,44]

Table 1. *Cont.*

Taxon	Voucher	Locality	GenBank/UNITE Accession Nos.		References
			28S	ITS	
H. boreorepandum	TUMH 64006	Japan	LC717881	LC621815	[14,44]
H. brevispinum	IFP 019464	Hunan, central China	MW979559	MW980578	[15]
H. brevispinum	IFP 019465	Hunan, central China	MW979560	MW980579	[15]
H. canadense	H T. Niskanen 09-006	Canada	—	KX388681	[1]
H. cremeoalbum	GDGM87013	Guangdong, southern China	OR947135	OR947126	[22]
H. cremeoalbum	GDGM93011	Hubei, central China	OR947129	OR947110	[22]
H. cremeoalbum	TUMH60740	Japan	—	AB906678	[5]
H. cremeoalbum	HKAS92345	Chongqing, SW China	KU612676	KU612619	[9]
H. cremeoalbum	TUMH 64024	Japan	LC717912	LC621823	[14,44]
H. cremeoalbum	TUMH 64019	Japan	—	LC621820	[14]
H. cremeoalbum	TUMH 64026	Japan	—	LC621825	[14]
H. cremeoalbum	**N.K. Zeng954 (FHMU2404)**	**Hainan, southern China**	**OQ656791**	**—**	**Present study**
H. cremeoalbum	**N.K. Zeng2511 (FHMU1631)**	**Hainan, southern China**	**OQ656792**	**OQ656784**	**Present study**
H. crocidens	PERTH08072965	Australia	KU612685	KU612630	[9]
H. crocidens	PERTH08095981	Australia	KU612684	KU612631	[9]
H. cuspidatum	RAS246	USA	—	MH379944	[4]
H. cuspidatum	RAS205	USA	—	MH379936	[4]
H. erectum	**gui0024 (FHMU7689)**	**Zhejiang, eastern China**	**OR722669**	**OR722666**	**Present study**
"*H. ellipsosporum*"	HMJAU5985	Jilin, NE China	—	KU612602	[9]
H. ellipsosporum	HKAS93254	Germany	—	KU612604	[9]
"*H. ellipsosporum*"	HKAS93255	Germany	—	KU612605	[9]
"*H. ellipsosporum*"	HKAS56491	Germany	—	KU612603	[9]
"*H. ellipsosporum*"	Os5579	Germany	—	AY817138	[11]
H. ellipsosporum	H T. Niskanen 12-036	Finland	—	KX388671	[1]
H. ellipsosporum	FD3281	Switzerland	KX086217	KX086215	Unpublished
H. ferruginescens	MH16005	USA	—	MH379905	[4]
H. ferruginescens	RAS229	USA	—	MH379942	[4]
H. flabellatum	IFP 019459	Liaoning, NE China	MW979556	MW980575	[15]
H. flavidocanum	IFP 019460	Yunnan, SW China	MW979545	MW980559	[15]
H. flavidocanum	IFP 019461	Yunnan, SW China	MW979546	MW980560	[15]
H. ibericum	BIO:Fungi:12330	Spain	—	HE611086	[17]
H. ibericum	MA-fungi 3457	Spain	—	AJ547879	[12]

Table 1. *Cont.*

Taxon	Voucher	Locality	GenBank/UNITE Accession Nos.		References
			28S	ITS	
H. itachiharitake	TUMH 64032	Japan	LC717905	LC621829	[14,44]
H. itachiharitake	TUMH 64028	Japan	—	LC621827	[14]
H. itachiharitake	TUMH 64033	Japan	—	LC621830	[14]
H. jussii	H 6003709	Finland	—	KX388665	[1]
H. jussii	IFP 019485	Xinjiang, NW China	MW979539	MW980553	[15]
H. jussii	IFP 019486	Xinjiang, NW China	MW979540	MW980554	[15]
H. longibasidium	IFP 019462	Hunan, central China	MW979541	MW980556	[15]
H. longibasidium	IFP 019463	Hunan, central China	MW979542	MW980555	[15]
H. longipes	GDGM82458	Yunnan, SW China	—	OR947121	[22]
H. magnorufescens	HMJAU4677	Russia	—	KU612550	[9]
H. magnorufescens	161209	Slovenia	KU612669	KU612549	[9]
H. magnorufescens	TO HG2818	Italy	—	KC293545	[16]
H. melitosarx	GDGM84518	Sichuan, SW China	OR947136	OR947117	[22]
H. melitosarx	H T. Niskanen 11-056	USA	—	KX388683	[1]
H. melitosarx	K 176869	UK	—	KX388685	[1]
H. melleopallidum	SMI356	Canada	—	FJ845406	[14]
H. microcarpum	GDGM87902	Guangdong, southern China	OR947134	OR947116	[22]
H. microcarpum	GDGM87902-1	Guangdong, southern China	—	OR947115	[22]
H. minospororufescens	TUMH 64041	Japan	—	LC621837	[14]
H. minospororufescens	TUMH 64043	Japan	—	LC621838	[14]
H. minospororufescens	TUMH 64044	Japan	—	LC621839	[14]
H. minus	TUMH60737	Japan		AB906675	[5]
H. minus	IFP 019482	Hunan, central China	MW979543	MW980557	[15]
H. minus	IFP 019483	Hunan, central China	MW979544	MW980558	[15]
H. minus	TUMH 64050	Japan	LC717910	LC621842	[14,44]
H. minus	TUMH 63123	Japan	—	LC377881	[14]
H. minus	TUMH 64046	Japan	—	LC621840	[14]
H. minus	N.K. Zeng2819 (FHMU1798)	Yunnan, SW China	KY407528	KY407533	[45]
H. minus	**N.K. Zeng1062 (FHMU2408)**	**Hainan, southern China**	**OQ656793**	**OQ656785**	**Present study**
H. minus	**N.K. Zeng1067 (FHMU7603)**	**Hainan, southern China**	**—**	**OQ656786**	**Present study**
H. mulsicolor	LJU GIS 1336	Slovenia	—	AJ547885	[12]

Table 1. *Cont.*

Taxon	Voucher	Locality	GenBank/UNITE Accession Nos.		References
			28S	ITS	
H. mulsicolor	REB-341	USA	—	JX093560	[46]
"H. mulsicolor"	TUMH 63094	Japan	LC717911	LC377892	[19,44]
"H. mulsicolor"	TUMH 63078	Japan	—	LC377890	[19]
H. mulsicolor	TUMH 64009	Japan	—	LC621843	[14]
H. neorepandum	H T. Niskanen 10-095	Canada	—	KX388659	[1]
H. neorepandum	H T. Niskanen 10-086	Canada	—	KX388660	[1]
H. olympicum	H T. Niskanen 09-134	USA	—	KX388661	[1]
H. olympicum	SAT-10-208-05	USA	—	MT955159	Unpublished
H. oregonense	HVM61	USA	—	KF879509	[47]
H. oregonense	PNW-MS g2010502h1-09	USA	—	AJ534972	[12]
H. orientalbidum	GDGM93480	Chongqing, SW China	OR947127	OR947108	[22]
H. orientalbidum	GDGM91301	Zhejiang, eastern China	OR947130	OR947111	[22]
H. orientalbidum	TUMH 62998	Japan	LC717908	LC377875	[19,44]
H. orientalbidum	TNS-F-35220	Japan	—	LC621845	[14]
H. orientalbidum	TNS-F-3783	Japan	—	LC621846	[14]
H. orientalbidum	TUMH 62997	Japan	—	LC377874	[14]
H. orientalbidum	**N.K. Zeng5307 (FHMU6327)**	**Hainan, southern China**	**OQ656794**	**OQ656787**	**Present study**
H. orientalbidum	**N.K. Zeng5308 (FHMU6361)**	**Hainan, southern China**	**OQ656795**	**OQ656788**	**Present study**
H. orientalbidum	**N.K. Zeng5309 (FHMU3153)**	**Hainan, southern China**	**OQ656796**	**OQ656789**	**Present study**
H. ovoideisporum	BIO:Fungi 12683	Spain	—	NR_119818	[48]
H. ovoideisporum	71106	Slovenia	—	KU612536	[9]
H. pallidocroceum	IFP 019466	Xinjiang, NW China	MW979554	MW980568	[15]
H. pallidocroceum	IFP 019467	Xinjiang, NW China	MW979555	MW980569	[15]
H. pallidomarginatum	IFP 019468	Yunnan, SW China	MW979552	MW980566	[15]
H. pallidomarginatum	IFP 019469	Yunnan, SW China	MW979553	MW980567	[15]
H. pinicola	GDGM93020	Hubei, central China	OR947128	OR947109	[22]
H. pinicola	GDGM83047	Yunnan, SW China	OR947137	OR947119	[22]
H. pinicola	TUMH 64000	Japan	—	LC621810	[14]
H. pinicola	TUMH 64002	Japan	—	LC621811	[14]
H. pinicola	TUMH 64003	Japan	—	LC621812	[14]
H. pinicola	TUMH 64004	Japan	—	LC621813	[14]

Table 1. *Cont.*

Taxon	Voucher	Locality	GenBank/UNITE Accession Nos.		References
			28S	ITS	
H. quebecense	H T. Niskanen 10-064	Canada	—	KX388662	[1]
H. quebecense	CN9	USA	—	MH379881	[4]
H. repando-orientale	TUMH60745	Japan	—	AB906683	[5]
H. repando-orientale	TUMH 62860	Japan	LC717900	LC377883	[19,44]
H. repando-orientale	TUMH 64069	Japan	LC717903	LC621873	[14,44]
H. repandum	KR9177	Germany	—	KU612575	[9]
H. repandum	HKAS93253	Germany	—	KU612581	[9]
H. repandum	031209C	Slovenia	—	KU612576	[9]
H. repandum	031209A	Slovenia	KU612655	KU612574	[9]
"*H. repandum*"	HKAS54416	Jilin, NE China	—	KU612583	[9]
"*H. repandum*"	HKAS92333	Sweden	—	KU612582	[9]
"*H. repandum*"	420526MF0925	Hubei, central China	MH141377	—	Unpublished
H. repandum	H 6003710	Finland	—	NR_164553	[1]
"*H. rufescens*"	HKAS92339	Jilin, NE China	KU612658	KU612537	[9]
H. rufescens	HKAS92338	Heilongjiang, NE China	KU612659	KU612538	[9]
"*H. rufescens*"	HKAS82529	Tibet, SW China	KU612657	KU612541	[9]
"*H. rufescens*"	HKAS92337	Sweden	KU612656	KU612539	[9]
H. rufescens	H 6003708	Finland	—	KX388688	[1]
H. rufescens	H T. Niemela 7839	Estonia	—	KX388656	[1]
H. sinorepandum	GDGM82445	Yunnan, SW China	OR947139	OR947122	[22]
H. sinorepandum	GDGM82382	Yunnan, SW China	OR947141	OR947124	[22]
H. slovenicum	LJU GIS 1338	Slovenia	—	AJ547870	[12]
H. slovenicum	LJU GIS 1340	Slovenia	—	AJ547884	[12]
H. sp.	F1110834	Costa Rica	—	KU612598	[9]
H. sp.	F1104787	USA	—	KU612606	[9]
H. sp.	FRI62832	Malaysia	—	KU612625	[9]
H. sp.	HKAS57385	Yunnan, SW China	—	KU612601	[9]
H. sp.	HKAS61337	Hunan, central China	KU612644	KU612597	[9]
H. sp.	HKAS82411	Taiwan, SE China	KU612668	KU612607	[9]
H. sp.	TM070	Canada	DQ898744	—	[3]
H. sp.	wi1A4spel	Taiwan, SE China	—	KC679833	Unpublished
H. sp.	wi8T4spel	Taiwan, SE China	—	KC679834	Unpublished
H. sp.	231109	Slovenia	KU612660	KU612545	[9]
H. sp.	F1187537	Canada		KU612544	[9]
H. sp.	HKAS92340	Heilongjiang, NE China	KU612661	KU612543	[9]
H. sp.	HKAS56128	Yunnan, SW China	—	KU612526	[9]

Table 1. *Cont.*

Taxon	Voucher	Locality	GenBank/UNITE Accession Nos.		References
			28S	ITS	
H. sp.	HKAS56881	Yunnan, SW China	—	KU612530	[9]
H. sp.	HKAS57475	Yunnan, SW China	KU612666	KU612528	[9]
H. sp.	HKAS61795	Heilongjiang, NE China	KU612665	KU612531	[9]
H. sp.	HKAS77834	Yunnan, SW China	KU612667	KU612525	[9]
H. sp.	HKAS74602	Yunnan, SW China	—	KU612532	[9]
H. sp.	F1125199	USA	—	KU612534	[9]
H. sp.	F1188749	USA	KU612663	KU612535	[9]
H. sp.	F1186911	USA	KU612662	KU612548	[9]
H. sp.	HKAS82508	Tibet, SW China	KU612670	KU612546	[9]
H. sp.	HKAS45769	Tibet, SW China	—	KU612547	[9]
H. sp.	HKAS55319	Yunnan, SW China	—	KU612590	[9]
H. sp.	HKAS51088	Yunnan, SW China	—	KU612587	[9]
H. sp.	HKAS78334	Guangdong, southern China	—	KU612589	[9]
H. sp.	HKAS55410	Yunnan, SW China	KU612654	KU612596	[9]
H. sp.	HKAS55449	Yunnan, SW China	—	KU612594	[9]
H. sp.	HKAS82558	Sichuan, SW China	—	KU612595	[9]
H. sp.	F1188765	USA	KU612653	KU612599	[9]
H. sp.	HKAS55327	Yunnan, SW China	KU612682	KU612568	[9]
H. sp.	HKAS56789	Yunnan, SW China	KU612680	KU612571	[9]
H. sp.	HKAS82410	Taiwan, SE China	KU612679	KU612573	[9]
H. sp.	HKAS93261	Yunnan, SW China	KU612681	KU612567	[9]
H. sp.	F1185236	USA	—	KU612600	[9]
H. sp.	HKAS93258	Hainan, southern China	KU612677	KU612618	[9]
H. sp.	HKAS92345	Chongqing, SW China	KU612676	KU612619	[9]
H. sp.	HKAS57714	Yunnan, SW China	KU612673	KU612617	[9]
H. sp.	HKAS58838	Yunnan, SW China	KU612675	KU612616	[9]
H. sp.	HKAS55325	Yunnan, SW China	—	KU612613	[9]
H. sp.	HKAS93259	Yunnan, SW China	KU612683	KU612612	[9]
H. sp.	HKAS92336	Yunnan, SW China	—	KU612614	[9]
H. sp.	HKAS52807	Yunnan, SW China	—	KU612609	[9]
H. sp.	HKAS92350	Guizhou, SW China	KU612672	KU612610	[9]
H. sp.	HKAS92347	Chongqing, SW China	KU612652	—	[9]
H. sp.	HKAS92349	Guizhou, SW China	KU612671	—	[9]
H. sp.	TUMH 64099	Japan	—	LC621899	[14]
H. sp.	TUMH 64100	Japan	—	LC621900	[14]

Table 1. *Cont.*

Taxon	Voucher	Locality	GenBank/UNITE Accession Nos.		References
			28S	ITS	
H. sphaericum	IFP 019470	Hunan, central China	MW979549	MW980563	[15]
H. sphaericum	IFP 019471	Hunan, central China	MW979551	MW980565	[15]
H. sphaericum	IFP 019472	Hunan, central China	MW979550	MW980564	[15]
H. subalpinum	TUMH 64013	Japan	LC717888	LC717913	[44]
H. subalpinum	TUMH 64016	Japan	LC717891	LC621871	[14,44]
H. subalpinum	TUMH 64017	Japan	LC717892	LC621872	[14,44]
H. subalpinum	TNS-F-85326	Japan	LC717885	LC621866	[14,44]
H. subcremeoalbum	TU110688	Papua New Guinea	—	UDB013289 *	[1]
"H. subberkeleyanum"	TNS-F-19323	Japan	—	LC621879	[14]
"H. subberkeleyanum"	TUMH 62863	Japan	—	LC377889	[14]
"H. subberkeleyanum"	TUMH 64075	Japan	—	LC621881	[14]
"H. subberkeleyanum"	TUMH 64081	Japan	—	LC621882	[14]
H. subconnatum	RAS235	USA	—	MH379930	[4]
H. subconnatum	RAS169	USA	—	MH379916	[4]
H. submulsicolor	H T. Niskanen 10-132	Canada	—	KX388682	[1]
H. subolympicum	DAOM:A. Voitk 12.09.02.av12	Canada	—	MH174257	[1]
H. subovoideisporum	H 6003707	Finland	—	NR_158494	[1]
H. subrufescens	H T. Niskanen 10-154	Canada	—	KX388649	[1]
H. subtilior	RAS180	USA	—	MH379918	[4]
H. subtilior	TENN 073034	USA	—	NR_164029	[4]
H. tangerinum	IFP 019473	Hunan, central China	MW979561	MW980580	[15]
H. tangerinum	IFP 019474	Hunan, central China	MW979562	MW980581	[15]
H. tangerinum	IFP 019475	Hunan, central China	MW979563	MW980582	[15]
H. tenuistipitum	IFP 019476	Hunan, central China	MW979557	MW980576	[15]
H. tenuistipitum	IFP 019477	Hunan, central China	MW979558	MW980577	[15]
H. tenuistipitum	**N.K. Zeng7540 (FHMU7644)**	**Hunan, central China**	**OQ913756**	**OQ913759**	**Present study**
H. tenuistipitum	**N.K. Zeng7555 (FHMU7636)**	**Hunan, central China**	**OQ913757**	**OQ913760**	**Present study**
H. tenuistipitum	**N.K. Zeng7558 (FHMU7642)**	**Hunan, central China**	**OQ913758**	**OQ913761**	**Present study**
H. tomaense	TUMH 64086	Japan	LC717907	LC621885	[14,44]

Table 1. *Cont.*

Taxon	Voucher	Locality	GenBank/UNITE Accession Nos.		References
			28S	ITS	
H. tomaense	TUMH 64085	Japan	—	LC621884	[14]
H. tomaense	TUMH 64087	Japan	—	LC621886	[14]
H. tottoriense	TUMH 64090	Japan	—	LC621889	[14]
H. tottoriense	TUMH 64091	Japan	—	LC621890	[14]
H. tottoriense	TUMH 64092	Japan	—	LC621891	[14]
H. treui	TU110403	Papua New Guinea	—	UDB013043 *	[1]
H. treui	**N.K. Zeng8373 (FHMU7690)**	**Hainan, southern China**	**OR722670**	**OR722667**	**Present study**
H. treui	**N.K. Zeng8374 (FHMU7691)**	**Hainan, southern China**	**OR722671**	**OR722668**	**Present study**
H. umbilicatum	CORT:012241	USA	—	MH379890	[4]
"*H. umbilicatum*"	HKAS92335	USA	KU612678	KU612608	[9]
"*H. umbilicatum*"	TUMH 63128	Japan	LC717909	LC377891	[19,44]
H. umbilicatum	TUMH 64093	Japan	—	LC621893	[14]
H. umbilicatum	TUMH 64094	Japan	—	LC621894	[14]
H. umbilicatum	TUMH 64098	Japan	—	LC621898	[14]
H. vagabundum	CLO4985	USA	—	MH379909	[4]
H. vagabundum	CORT:014461	USA	—	MH379949	[4]
H. ventricosum	IFP 019478	Liaoning, NE China	MW979547	MW980561	[9]
H. ventricosum	IFP 019479	Liaoning, NE China	MW979548	MW980562	[9]
H. vesterholtii	BIO:Fungi:10429	Spain	—	HE611084	[9]
H. vesterholtii	BIO:Fungi:10452	Spain	—	HE611085	[9]
H. vesterholtii	BIO:Fungi:12904	France	—	HE611087	[9]
"*H. vesterholtii*"	HKAS56213	Yunnan, SW China	—	KU612554	[9]
"*H. vesterholtii*"	HKAS55399	Yunnan, SW China	—	KU612555	[9]
"*H. vesterholtii*"	HKAS57047	Yunnan, SW China	—	KU612558	[9]
"*H. vesterholtii*"	HKAS58734	Yunnan, SW China	—	KU612559	[9]
"*H. vesterholtii*"	HKAS51086	Yunnan, SW China	KU612650	KU612557	[9]
"*H. vesterholtii*"	HKAS92341	Shaanxi, NW China	KU612647	KU612562	[9]
"*H. vesterholtii*"	HKAS92342	Yunnan, SW China	KU612646	KU612564	[9]
"*H. vesterholtii*"	HKAS92343	Sichuan, SW China	KU612648	KU612563	[9]
"*H. vesterholtii*"	HKAS92344	Heilongjiang, NE China	KU612649	KU612556	[9]
"*H. vesterholtii*"	HKAS77884	Hunan, central China	KU612645	KU612565	[9]
"*H. vesterholtii*"	HKAS56489	Germany	—	KU612561	[9]
"*H. vesterholtii*"	HKAS92351	Guizhou, SW China	KU612651	—	[9]

Table 1. *Cont.*

Taxon	Voucher	Locality	GenBank/UNITE Accession Nos.		References
			28S	ITS	
H. washingtonianum	UBC F-32538	Canada	—	MF954990	Unpublished
H. washingtonianum	WTU:014341	USA	—	MH379846	[4]
H. zongolicense	GO-2010-142a	Mexico	—	KC152121	[1]
Sistotrema muscicola	taxon:154757	Finland	AJ606041	AJ606041	[49]
S. muscicola	KHL 11721	Finland	AJ606040	AJ606040	[49]

New sequences are shown in bold; SW: Southwestern, NE: Northeastern, NW: Northwestern, SE: Southeastern. * UNITE accession numbers.

2.4. Phylogenetic Analyses

The combined nuclear dataset (28S + ITS) was analyzed with maximum likelihood (ML) and Bayesian Inference (BI). Maximum likelihood tree generation and bootstrap analyses were performed with the program RAxML 7.2.6, running 1000 replicates combined with an ML search. Bayesian analysis with MrBayes 3.1, implementing the Markov Chain Monte Carlo (MCMC) technique and parameters predetermined with MrModeltest 2.3, was performed [32,33]. The best-fit likelihood model for 28S and ITS was GTR + I + G and GTR + I + G, respectively. Bayesian analysis of the combined nuclear dataset (28S + ITS) was run for 45 million generations, and the average deviation of split frequencies was 0.005618. Trees sampled from the first 25% of generations were discarded as burn-in, and Bayesian posterior probabilities (PP) were then calculated for a majority consensus tree of the retained Bayesian trees [32,33].

3. Results

3.1. Molecular Data

The combined dataset (28S + ITS) consisted of 255 taxa with 1454 nucleotide sites, and the alignment was submitted to TreeBASE (S31163). The phylogram with branch lengths generated from RAxML and support values (BS and PP) are shown in Figure 1. The topologies of phylogenetic trees generated from ML and BI analyses were identical, although statistical support for some branches showed slight differences.

Existing molecular data indicated that the Chinese collections of *Hydnum* were grouped into 35 isolated lineages (Figure 1). A total of six lineages (16, 19, 22, 25, 32, and 35), including our new specimens, were identified. Lineage 16, with strong statistical support (BS = 97%, PP = 0.99), was comprised of the holotype (IFP 019476) and one specimen (IFP 019477) of *H. tenuistipitum* T. Cao & H.S. Yuan, three new collections (FHMU7644, FHMU7636, and FHMU7642) from central China, and three unidentified collections (HKAS56789, HKAS55327, and HKAS93261); lineage 19, with high statistical support (BS = 81%, PP = 0.99), included the holotype (TUMH 60740) of *H. cremeoalbum* Liimat. & Niskanen, two new specimens (FHMU2404 and FHMU1631) from southern China, four collections (HKAS92345, TUMH 64026, TUMH 64019, and TUMH 64024) identified as *H. cremeoalbum*, two specimens (IFP 019480 and IFP 019481) identified as *H. albomagnum* Banker, and one unidentified collection (HKAS93258) from southern China; lineage 22, with high statistical support (BS = 92%, PP = 1), was comprised of the holotype (TU110403) of *H. treui* Tedersoo, Liimat. & Niskanen, and two new collections (FHMU7690 and FHMU7691) from southern China; lineage 25, with strong statistical support (BS = 100%, PP = 1), included the holotype (TUMH 60737) and six collections (TUMH 63123, TUMH 64046, TUMH 64050, IFP 019482, FHMU1798, and IFP 019483) of *H. minus* Yanaga & N. Maek, and two new specimens (FHMU7603 and FHMU2408) from southern China; lineage 32, with high statistical support (BS = 94%, PP = 1), included one new specimen (FHMU7689) from eastern China, and one collection (HKAS92351) identified as *H. vesterholtii*; lineage 35, with strong statistical support (BS = 98%, PP = 1), included the holotype (TUMH 62998)

and three specimens (TNS-F-35220, TNS-F-3783, and TUMH 62997) of *H. orientalbidum* R. Sugaw. & N. Endo, three new collections (FHMU6327, FHMU3153, and FHMU6361) from southern China, and three unidentified collections (HKAS52807, HKAS92350, and HKAS92349) from China (Figure 1).

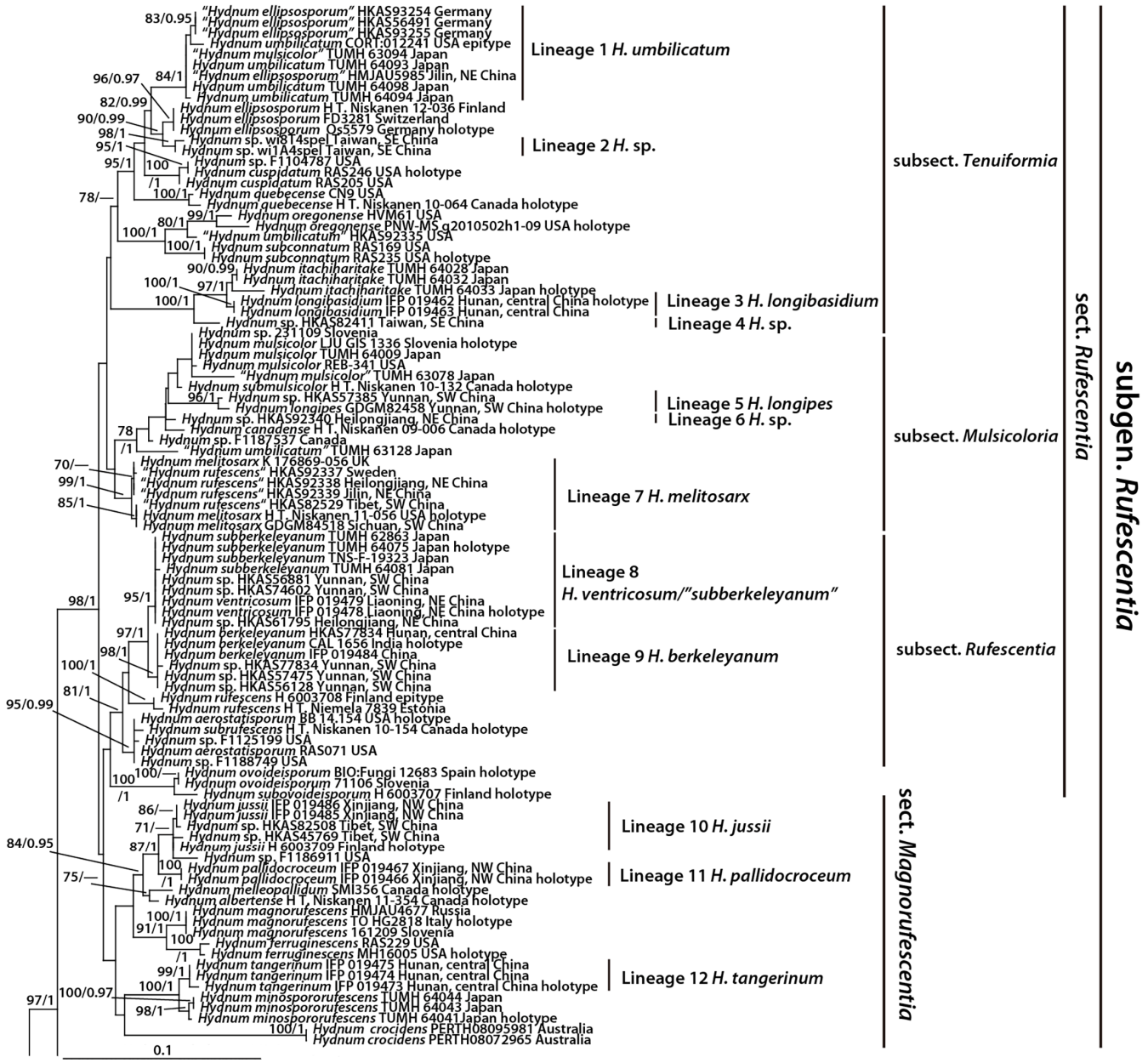

Figure 1. *Cont.*

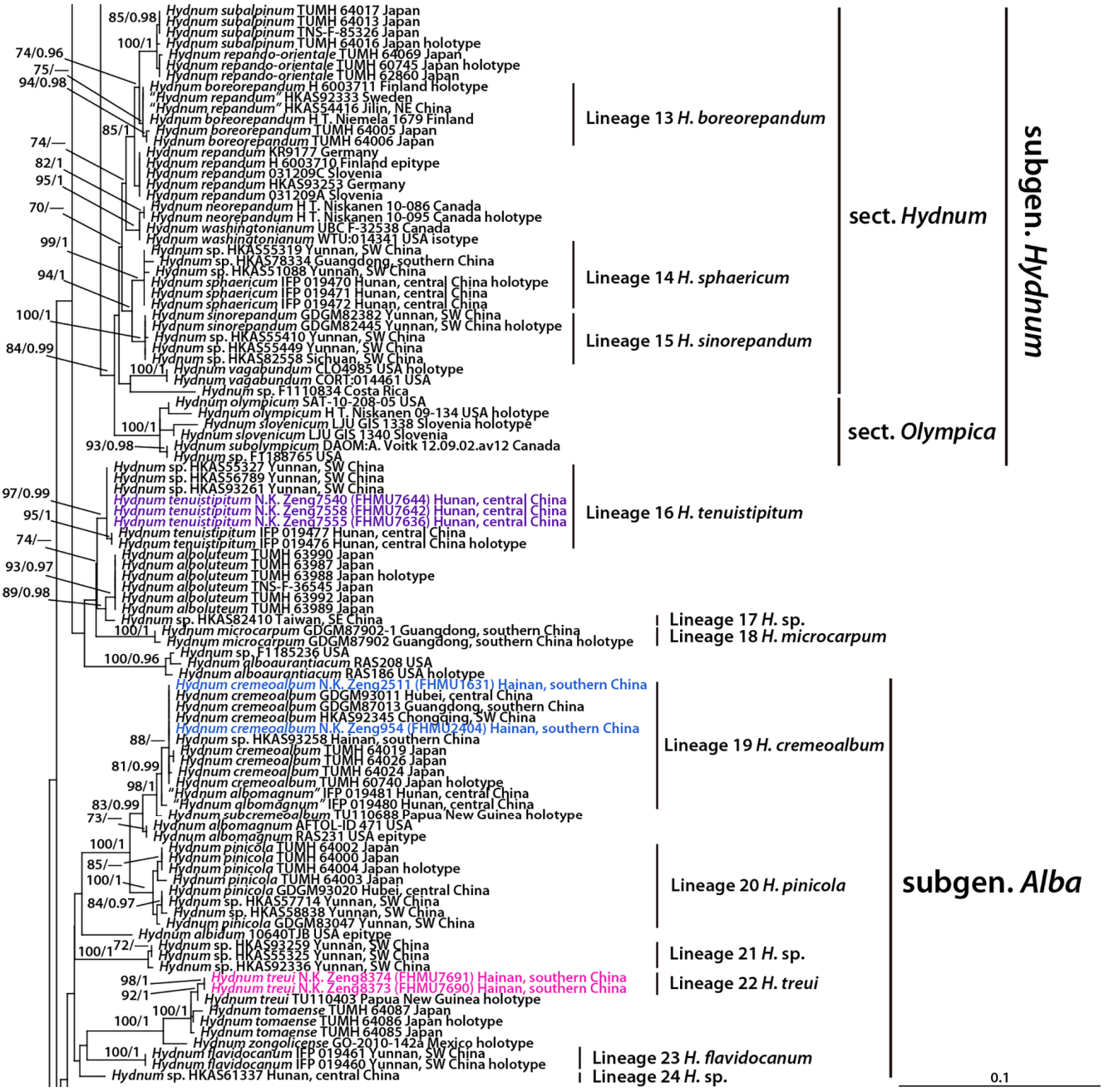

Figure 1. *Cont.*

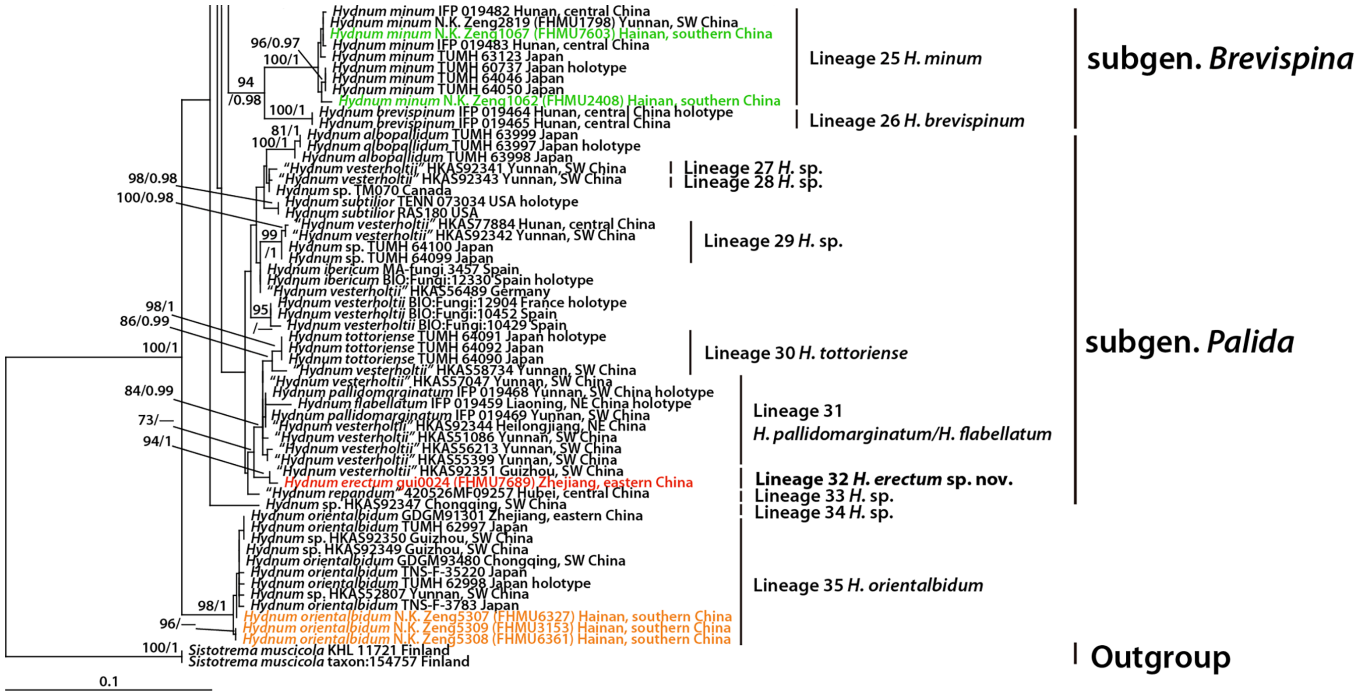

Figure 1. A phylogram of *Hydnum* inferred from a two-locus (28S and ITS) dataset using RAxML. BS (≥70%) and PP (≥0.95) are indicated above the branches. Newly generated sequences are in color; SW: Southwestern, NE: Northeastern, NW: Northwestern, SE: Southeastern.

3.2. Taxonomy

Hydnum cremeoalbum Liimat. & Niskanen, Mycologia 110 (5): 896, 2018. (Figure 2a,b and Figure 3).

MycoBank: MB 553875.

Description—*Basidiomata* medium to large-sized, usually branched, sometimes fused with the pileus of the same branch, solitary to gregarious, and fleshy. *Pileus* 6–9 cm in diameter, round to reniform, irregular when old, becoming somewhat infundibuliform or slightly wavy; surface dry, smooth to irregularly rugged, glabrous, cream white to pale cream (2A2–3) or cream (3A3), whitish (2A1); margin entire and decurved when young, straight to slightly waved in age, white (2A1) to pale cream (2A3); context approximately 4 mm thick, white (2A1), unchanging in color when injured. *Hymenophore* hydnoid, spines approximately 4 mm long, shortest near the pileus margin, slightly decurrent to decurrent, subulate to cylindrical, acute, straight, solitary, crowded, cream white to pale cream (1A2–2A2), pale yellowish-brown (2A5–3A5). *Stipe* 4–6 × 1.3–2 cm, central or eccentric, cylindrical to subcylindrical, robust, sometimes branched, slightly incurved, solid; surface dry, glabrous, whitish (1A1) to cream white (1A2), pale yellow (2A4). *Odor* not distinctive.

Basidiospores [40/6/2] 4.5–5.2–5.5 (–6) × 3–4.1–4.5 µm, Q = 1.11–1.29–1.43 (–1.83), Qm = 1.29 ± 0.13, subglobose to broadly ellipsoid or ovoid, slightly thick-walled (up to 1 µm), inamyloid, smooth, hyaline in KOH. *Basidia* 22–30 × 3.5–6.5 µm, subcylindric, clavate to suburniform, slightly inflated at the apex, slightly thin-walled (up to 0.5 µm), yellowish in KOH; sterigmata 1–5, somewhat curving. *Cystidia* absent. *Pileipellis* a cutis, composed of subcylindric hyphae measuring 2–8 µm wide, interwoven to subparallel, and yellowish in KOH; terminal hyphae 16–38 × 2–5.5 µm, thin-walled (less than 5 µm), slightly inflated at the apex or septum. *Clamp connections* present in all tissues.

Habitat—Gregarious on the ground in forests dominated by fagaceous trees.

Known distribution—Japan, southern China (Hainan and Guangdong Provinces), and central China (Hubei Province); probably found in Hunan Province and Chongqing Municipality (Figure 1).

Figure 2. Basidiomata of *Hydnum* species. (**a**,**b**) *Hydnum cremeoalbum* (**a**) from FHMU2404; (**b**) from FHMU1631); (**c**,**d**) *Hydnum erectum* (FHMU7689, holotype); (**e**,**f**) *Hydnum minus* (**e**) from FHMU2408; (**f**) from FHMU7603); (**g**,**h**) *Hydnum orientalbidum* (**g**) from FHMU6327; (**h**) from FHMU6361; (**i**,**j**) *Hydnum tenuistipitum* (**i**) from FHMU7642; (**j**) from FHMU7636); (**k**,**l**) *Hydnum treui* (**k**) from FHMU7690; (**l**) from FHMU7691. Scale bars = 1 cm. Photographs by N.K. Zeng.

Specimens examined—CHINA. Yunnan Province: Kunming City, elev. 1950 m, 27 July 2011, N.K. Zeng954 (FHMU2404); Hainan Province: Yinggeling of Hainan Tropical Rainforest National Park, elev. 650 m, 3 August, 2015, N.K. Zeng2511 (FHMU1631).

Notes—*Hydnum cremeoalbum* was originally described from Japan [1], then recently reported from Guangdong and Hubei Provinces, China [22]. In the present study, it was also found to be distributed in Hainan and Yunnan Provinces of China. The species is characterized by a cream white to cream, infundibuliform, and large pileus, a robust and branched stipe, a decurrent hymenophore, long spines (up to 4 mm), subglobose to ovoid basidiospores, and association with fagaceous trees. In addition, intraspecific variations of *H. cremeoalbum* were observed; for example, the Japanese specimens have smaller basidiomata (pilei 3–7 cm diameter), non-branched stipitis, and larger basidiospores measuring 5–7 × 3.5–5.5 μm [1].

Hydnum erectum N.K. Zeng, H.Z. Qin, W.F. Lin & L.G. Hu, sp. nov. (Figure 2c,d and Figure 4).

MycoBank: MB 851242.

Etymology: Latin "*erectum*" refers to the pileipellis, composed of mostly erect hyphae.

Diagnosis: Differs from other species of *H.* subgen. *Pallida* through a creamy yellow to pale salmon, velutinate pileus, basidia inflated in the center, and a trichodermal pileipellis mostly composed of erect hyphae.

Holotype: China. Zhejiang Province: Qingyuan County, Zuoxi Town, Yinjiang Village, elev. 800 m, 15 August 2023, gui0024 (FHMU7689). GenBank accession numbers: 28S = OR722669, ITS = OR722666.

Description—*Basidiomata* small, solitary, concrescent, and fleshy. *Pileus* 3.5–4.5 cm in diameter, convex to plano-convex, and shallowly raised in the center; surface irregularly bumpy, dry, velutinate, creamy yellow (3A3–4) to pale salmon (1A2–2A2), darker in the center; margin entire, incurved, and slightly creamy yellow (1A2–3) to whitish (1A1). Context approximately 5 mm thick in the center of the pileus, fleshy, and white (2A1), unchanging in color when injured. *Hymenophore* hydnoid, spines 1–2 mm long, shortest near the pileus margin and stipe, non-decurrent to slightly decurrent, subulate to cylindrical, acute, straight to slightly curving, white to pale salmon (1A2). *Stipe* 2.5–3 × 1.2–1.5 cm, central, subcylindrical, solid, and branched; surface dry, smooth, white to slightly salmon (1A2). *Odor* is not distinctive.

Basidiospores [20/1/1] 6.5–7.33–8 × 5.5–6.68–7.5 (–8) μm, Q = 1–1.1–1.25 (–1.27), Qm = 1.1 ± 0.09, globose, subglobose to broadly ellipsoid, slightly thick-walled (up to 1 μm), smooth, and hyaline in KOH. *Basidia* 22–40 × 5–12 μm, subcylindric to subclavate, often inflated in the center or vertex, slightly thick-walled (up to 1 μm), colorless in KOH, and most contained fine granular inclusions, sometimes with large guttules; sterigmata 2–4, up to 8 μm long, and 2 μm wide at the base, somewhat curving. *Cystidia* absent. *Pileipellis* a trichoderm, mostly composed of erect hyphae measuring 3–12 μm wide, subcylindric, and hyaline to yellowish in KOH; terminal hyphae 29–75 × 1.5–4 μm, slender, subcylindric to subclavate, slightly thick-walled (up to 1 μm), and slightly inflate at the apex or septum. *Clamp connections* present in all tissues.

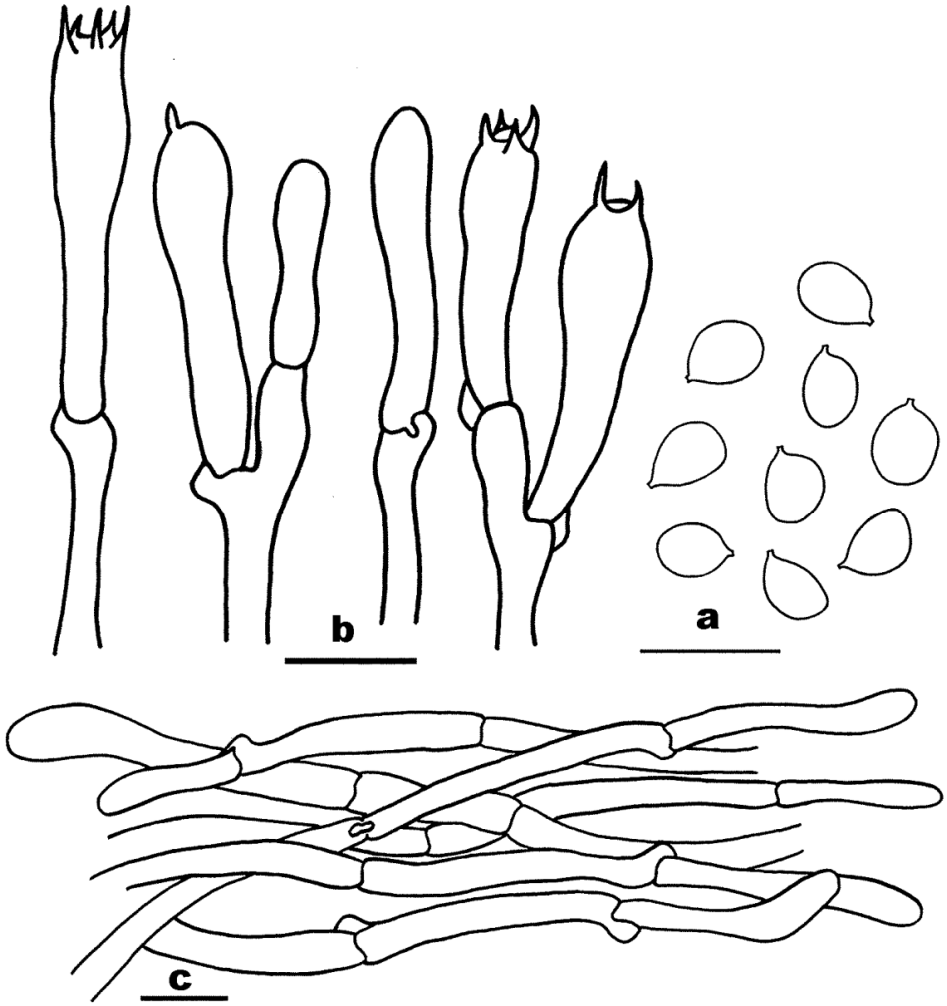

Figure 3. Microscopic features of *Hydnum cremeoalbum* (FHMU1631). (**a**) Basidiospores. (**b**) Basidia. (**c**) Pileipellis. Scale bars = 10 μm. Drawings by Y.Z. Zhang.

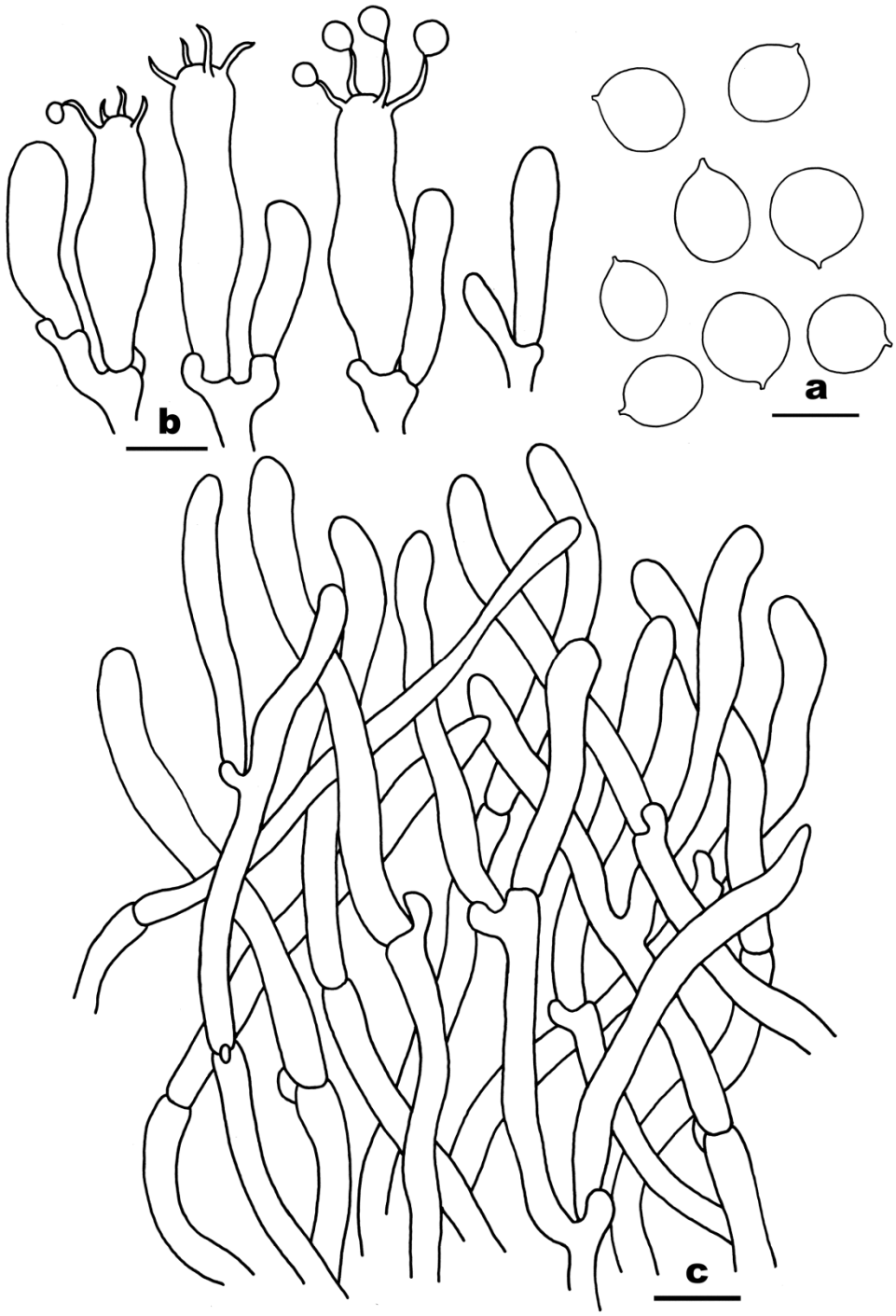

Figure 4. Microscopic features of *Hydnum erectum* (FHMU7689, holotype). (**a**) Basidiospores. (**b**) Basidia. (**c**) Pileipellis. Scale bars = 10 μm. Drawings by H.Z. Qin.

Habitat—Solitary and concrescent on the ground in forests dominated by fagaceous trees.

Known distribution—Eastern China (Zhejiang Province); probably also found in southwestern China (Guizhou Province) (Figure 1).

Notes—In China, *H. erectum* was misidentified as *H. vesterholtii* [9]; however, the latter has an ocher and slightly hygrophanous pileus, usually depressed in the center, a velutinous stipe often staining ocher when handled, presence of a citric odor, longer basidia measuring 42–68 μm, and a cutis-trichoderm pileipellis [17]. Morphologically, *H. erectum* is also similar to some members of subgen. *Pallida*, viz., *H. albopallidum* R. Sugaw. & N.

Endo, *H. flabellatum* T. Cao & H. S. Yuan, *H. pallidomarginatum* T. Cao & H. S. Yuan, and *H. tottoriense* R. Sugaw. & N. Endo. However, *H. albopallidum* has a white and glabrous pileus turning pale ocher to ocher early when bruised, a vimineous stipe staining pale yellow to pale ocher when bruised, larger basidiospores measuring 8–9.5 × 7–8 µm, a mixocutis pileipellis, and grows under a mixed forest of *Abies* Mill., *Betula* L., and *Tsuga* (Endl.) Carrière [14]; *H. flabellatum* differs from *H. erectum* by having a flabelliform to semicircular, glabrous pileus, often with some brownish orange scales, a stipe staining orange-white when injured, larger basidiospores measuring 8.5–9.5 × 6.5–7.8 µm, a pileipellis composed of subparallel hyphae, and association with trees of Pinaceae [15]; *H. pallidomarginatum* has a pale orange and glabrous pileus, an orange-white stipe staining brownish when bruised, broadly ellipsoid and larger basidiospores measuring 8.2–9.8 × 6.5–7.8 µm, longer basidia (32–65 µm), and a pileipellis composed of interwoven hyphae [15]; *H. tottoriense* differs from *H. erectum* by having a glabrous and pale yellow pileus slowly staining ocher to brownish orange when handled, longer spines (up to 6 mm), larger basidiospores measuring 7.5–9.5 × 6.5–8.5 µm, and a mixocutis pileipellis [14].

Hydnum minus Yanaga & N. Maek., Mycoscience 56 (4): 435, 2015. (Figure 2e,f and Figure 5).

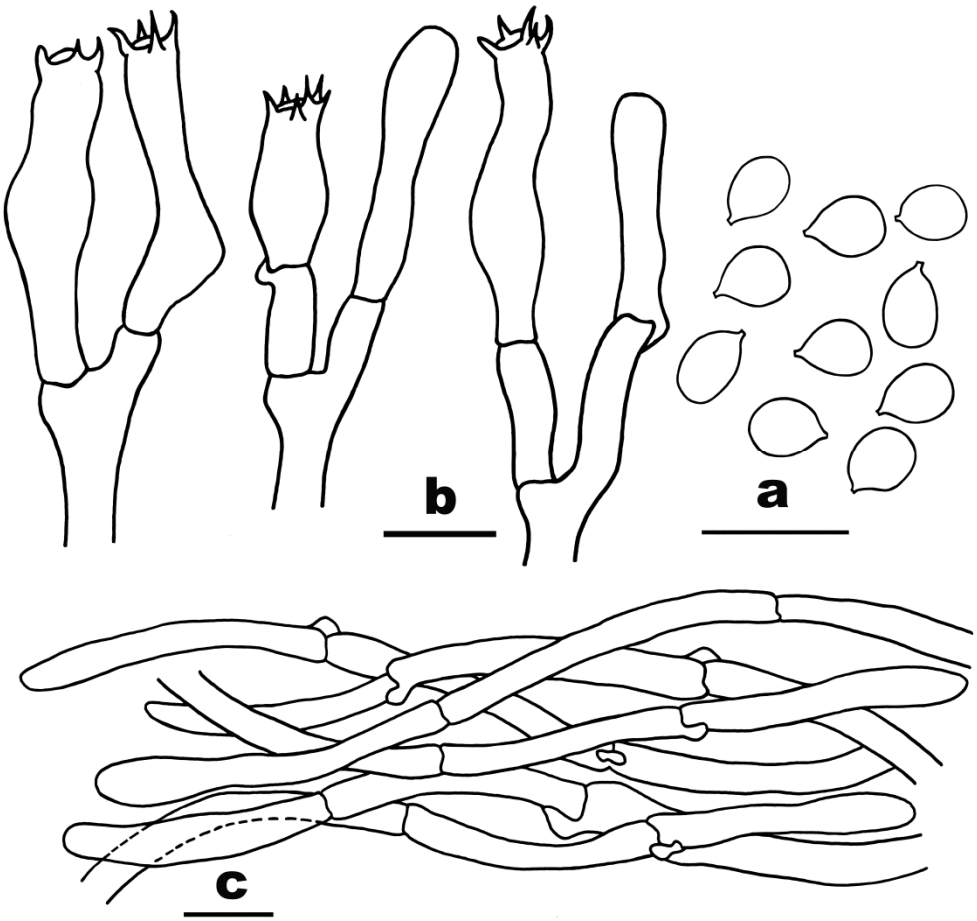

Figure 5. Microscopic features of *Hydnum minus* (FHMU2408). (**a**) Basidiospores. (**b**) Basidia. (**c**) Pileipellis. Scale bars = 10 µm. Drawings by Y.Z. Zhang.

MycoBank: MB 808762.

Description—*Basidiomata* small, gregarious, and sometimes fused, fleshy. *Pileus* 3–4.5 cm diameter, convex to plano-convex or irregular when young, then becoming plane, slightly umbilicate, or infundibuliform; surface dry, glabrous, smooth, white (2A1), cream white (2A2) to cream (3A3) when young, and pale brown (5B6–7) in age; margin entire to lobed, wavy, white (2A1) to cream white (2A2). Context 2–4 mm thick in the center of the

pileus, translucent or watery, white, and turning reddish-brown (6B6) to red (8B6) slowly when injured. *Hymenophore* hydnoid, spines 2–4 mm long, shortest near the pileus margin, slightly decurrent to decurrent, conical to cylindrical, adnate, crowded, white (1A1) to cream white (1A2). *Stipe* 2–6.5 × 0.2–1 cm, central or eccentric, cylindrical to subcylindrical, often incurved, solid when young, and hollow in age; surface dry, smooth, glabrous, white (2A1) to pale cream (2A2), turning pale brown (4A4–5B5) gradually when injured. *Odor* not distinctive.

Basidiospores [37/13/3] 4–4.72–5 × 3–3.68–4 µm, Q = 1.13–1.29–1.43 (–1.5), Qm = 1.29 ± 0.10, broadly ellipsoid to ellipsoid or ovoid, slightly thick-walled (up to 1 µm), smooth, and yellowish in KOH. *Basidia* 14–28 × 5–8 µm, clavate to subclavate, slightly thin-walled (up to 5 µm), and hyaline; sterigmata 3–6, up to 3.5 µm long, 1.5 µm wide at the base, somewhat curving. *Cystidia* absent. *Pileipellis* a cutis, composed of subcylindric hyphae measuring 4–10 µm wide, interwoven to subparallel, and yellowish in KOH; terminal hyphae 28–40 × 3–5 µm, slightly thin-walled (up to 5 µm), and slightly inflate at the apex or septum. *Clamp connections* present in all tissues.

Habitat—Gregarious on the ground in forests dominated by fagaceous trees.

Known distribution—Japan, southern China (Hainan Province), southwestern China (Yunnan Province), and central China (Hunan Province).

Specimens examined—CHINA. Hainan Province: Jianfengling of Hainan Tropical Rainforest National Park, elev. 850 m, 5 July 2012, N.K. Zeng1062, 1067 (FHMU2408, 7603); Yunnan Province: Wuding County, Gaoqiao Town, elev. 1980 m, 20 August 2016, N.K. Zeng2819 (FHMU1798).

Notes—*Hydnum minus* was originally described from Japan [5] and subsequently reported from Hunan Province, central China [15]. In the present study, it was also found to be distributed in Hainan and Yunnan Provinces of China. The species is characterized by a small, slightly umbilicate, cream-white pileus with a lobed to wavy margin, a translucent or watery, white context turning reddish-brown to red slowly when injured, long spines (up to 4 mm), a pale cream stipe turning pale brown gradually when injured, and broadly ellipsoid to ellipsoid basidiospores. In addition, intraspecific variations of *H. minus* were observed; for example, the Japanese specimens have smaller basidiomata (pilei 1–2.5 cm diameter) and shorter spines (0.5–1.7 mm) [5].

Hydnum orientalbidum R. Sugaw. & N. Endo, Mycologia 114 (2): 440, 2022. (Figure 2g,h and Figure 6).

MycoBank: MB 839853.

Description—*Basidiomata* very small to small, solitary to gregarious, sometimes fused, fleshy. *Pileus* 0.8–3 cm in diameter, convex to plano-convex, and shallowly depressed in the center; surface dry, glabrous, and smooth, creamy yellow (2A2–4A4) to pale orange (5A3–4), slightly darker in the center; margin entire, sometimes lobed, incurved, and sometimes wavy, white (1A1) to pale cream (1A2). Context 2–3 mm thick in the center of the pileus, fleshy, and white (2A1), unchanging in color when injured. *Hymenophore* hydnoid, spines 1–2 mm long, shortest near the pileus margin and stipe, usually decurrent, evenly distributed, crowded, subulate to cylindrical, acute, straight to slightly flexuous, solitary, and creamy yellow (2A4) to white (2A1). *Stipe* 1.5–3.5 × 0.4–1.2 cm, central, cylindrical to subcylindrical, slightly incurved or straight; surface dry, smooth, and white (2A1), sometimes with a creamy white (2A2) tone near the base. *Odor* not distinctive.

Basidiospores [60/13/3] 4.5–5.1–5.5 × 3.5–4.1–4.5 µm, Q = 1.11–1.24–1.43 (–1.57), Qm = 1.24 ± 0.09, ovoid to broadly ellipsoid, slightly thick-walled (up to 1 µm), inamyloid, smooth, colorless in KOH. *Basidia* 18–28 × 3–7 µm, subcylindric, subclavate to clavate, slightly thin-walled (up to 0.5 µm), hyaline; sterigmata 3–5, up to 3.5 µm long, somewhat curving. *Cystidia* absent. *Pileipellis* a cutis, composed of hyphae, interwoven to subparallel, 3.5–9 µm wide, yellowish in KOH; terminal hyphae 38–50 × 3–7 µm, cylindrical, thin-walled (less than 5 µm), and slightly inflate at the apex or septum. *Clamp connections* present in all tissues.

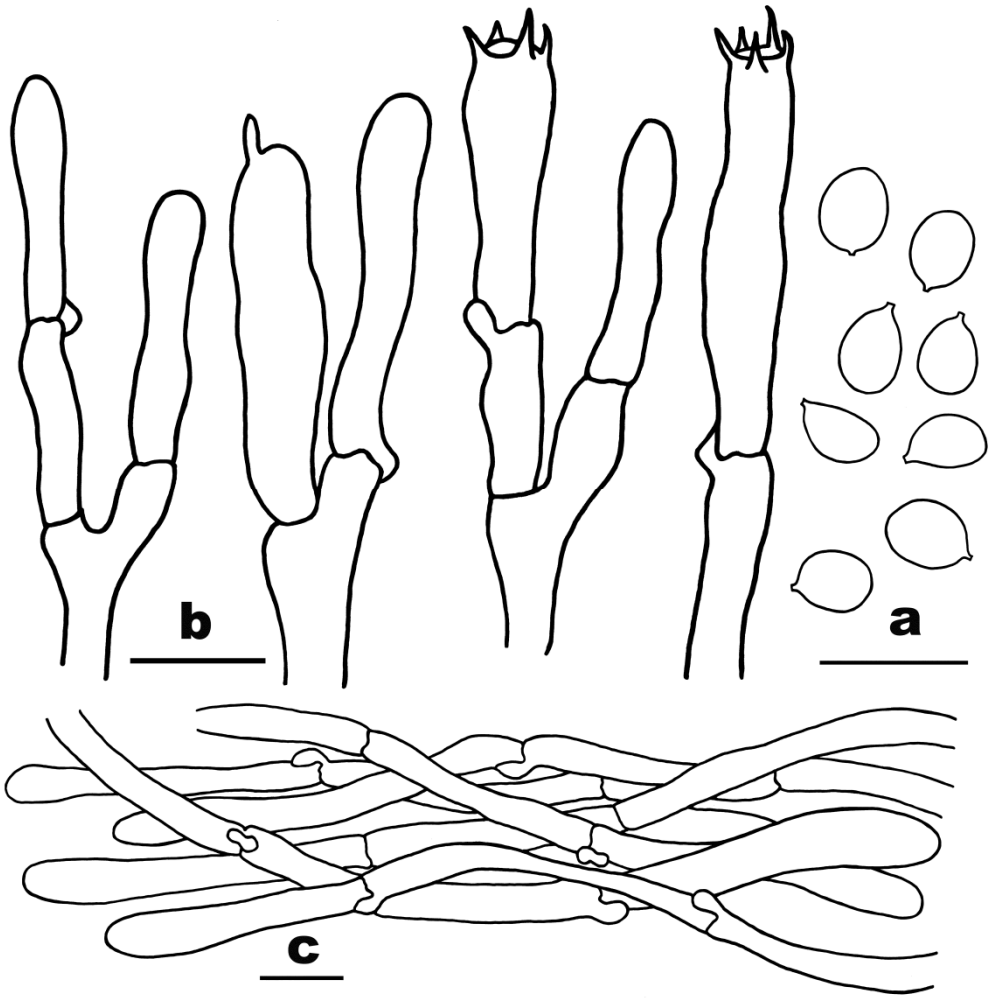

Figure 6. Microscopic features of *Hydnum orientalbidum* (FHMU3153). (**a**) Basidiospores. (**b**) Basidia. (**c**) Pileipellis. Scale bars = 10 μm. Drawings by Y.Z. Zhang.

Habitat—Solitary or gregarious on the ground in forests dominated by fagaceous trees.

Known distribution—Japan, southern China (Hainan Province), southwestern China (Sichuan Province and Chongqing Municipality), and eastern China (Zhejiang Province); probably found in Yunnan and Guizhou Provinces (Figure 1).

Specimens examined—CHINA. Hainan Province: Changjiang Li Autonomous County, Bawangling of Hainan Tropical Rainforest National Park, elev. 650 m, 28 July 2021, N.K. Zeng5307, 5308, 5309 (FHMU6327, 6361, 3153).

Notes—*Hydnum orientalbidum* was originally described from Japan [14] and subsequently reported from Sichuan and Zhejiang Provinces and Chongqing Municipality, China [22]. In the present study, it was also found to be distributed in Hainan, southern China. The species is characterized by a small, creamy yellow to pale orange pileus with a white margin, short spines, a white and short stipe, ovoid to broadly ellipsoid basidiospores, and association with fagaceous trees. In addition, intraspecific variations of *H. orientalbidum* were observed,; for example, the Japanese specimens have larger basidiomata (pilei up to 5.5 cm diameter) and longer spines (up to 6 mm) [14].

Hydnum tenuistipitum T. Cao & H.S. Yuan, Studies in Mycology 99 (no. 100121): 53, 2021. (Figure 2i,j and Figure 7).

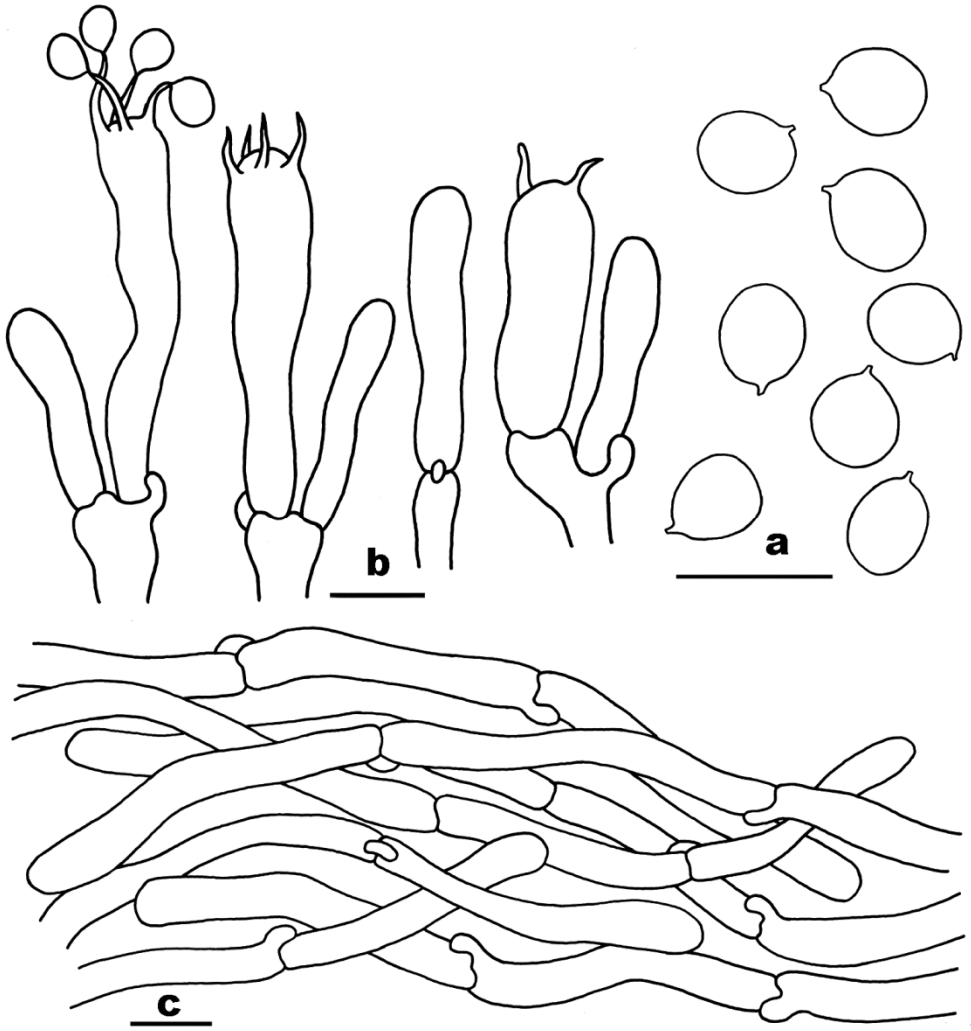

Figure 7. Microscopic features of *Hydnum tenuistipitum* (FHMU7644). (**a**) Basidiospores. (**b**) Basidia. (**c**) Pileipellis. Scale bars = 10 μm. Drawings by H.Z. Qin.

MycoBank: MB 839422.

Description—*Basidiomata* very small to small, solitary to gregarious, and sometimes fused, fleshy. *Pileus* 1–3 cm in diameter, plano-convex to slightly infundibuliform; surface smooth, dry, white (1A1) to creamy white (1A2–3); margin lobed, incurved to irregularly wavy, white (1A1) to creamy white (1A2–3). Context 1–3 mm thick in the center of the pileus, fleshy, and white (2A1), unchanging in color when injured. *Hymenophore* hydnoid, spines approximately 1 mm long, shortest near the pileus margin and stipe, decurrent to strongly decurrent, somewhat near the stipe base, crowded, subulate to cylindrical, acute, straight, somewhat adnate, white (1A1), creamy white (1A2–3) to yellowish-white (3A3–4). *Stipe* 1.5–3.5 × 0.4–1 cm, central, cylindrical to subcylindrical, solid, becoming hollow with age, slightly incurved or straight; surface dry, smooth, white (1A1) to cream white (1A2). *Odor* not distinctive.

Basidiospores [60/8/3] (5–) 5.5–6.28–7 × 4.5–5.62–6 (–7) μm, Q = 1–1.12–1.2 (–1.3), Qm = 1.12 ± 0.01, globose, subglobose to broadly ellipsoid, slightly thick-walled (up to 1 μm), smooth, and some contain granular contents, yellowish in KOH. *Basidia* 19–41 × 3–10 μm, subcylindric, clavate to subclavate, slightly thick-walled (up to 1 μm), and yellowish in KOH, most containing fine granular inclusions, sometimes with large guttules; sterigmata 2–5, up to 8 μm long, 2 μm wide at the base, somewhat curving. *Cystidia* absent. *Pileipellis* a cutis, interwoven to subparallel, 3–12 μm wide, and yellowish in KOH; terminal hyphae

30–65 × 4–6 μm, cylindrical, slightly thick-walled (up to 1 μm), and slightly inflate at the apex or septum. *Clamp connections* present in all tissues.

Habitat—Solitary or gregarious on the ground in forests dominated by *Pinus massoniana* Lamb.

Known distribution—Central China (Hunan Province); probably found in southwestern China (Yunnan Province) (Figure 1).

Specimens examined—CHINA, Hunan Province: Tongdao Dong Autonomous County, Longcheng Town, Ganxi Village, elev. 450 m, 10 April 2023, N.K. Zeng7540, 7555, 7558 (FHMU7644, 7636, 7642).

Notes—*Hydnum tenuistipitum* was originally described from Hunan Province, central China [15]. The species was redescribed based on our new collections, which is characterized by a small, creamy white pileus with a lobed margin, short spines (1 mm long), a strongly decurrent hymenophore, a short stipe unchanging in color when injured, globose to subglobose basidiospores, and association with *P. massoniana*. In addition, intraspecific variations of *H. tenuistipitum* were observed; for example, the collections cited by Cao et al. have orange-white pilei, longer stipitis (up to 6 cm) staining pale orange when injured, larger basidiospores measuring 6.8–7.2 × 5.5–6.5 μm, and longer basidia (up to 63 μm) [15].

Hydnum treui Tedersoo, Liimat. & Niskanen, Mycologia 110 (5): 897, 2018. (Figure 2k,l and Figure 8).

MycoBank: MB 553877.

Description—*Basidiomata* small to medium-sized, solitary to gregarious, usually fused, fleshy. *Pileus* 2.8–5.7 cm in diameter, convex to plano-convex or irregular, slightly infundibuliform; surface smooth, dry, unobviously ribbed, white (1A1) to creamy white (2A2–3A2); margin entire, incurved to slightly wavy, and white (1A1). Context 2–10 mm thick in the center of the pileus, fleshy, white to pinkish (5A2), unchanging in color when injured. *Hymenophore* hydnoid, spines 1–4 mm long, shortest near the pileus margin and stipe, nondecurrent to slightly decurrent, crowded, subulate to cylindrical, acute, straight, somewhat adnate, white (1A1) and creamy white (1A2) to yellowish (2A3). *Stipe* 1.6–2.6 × 0.8–1.3 cm, central, cylindrical to subcylindrical, slightly hollow to hollow; surface dry, smooth, white (1A1) to yellowish-white (1A4–5). *Odor* strong, sweetish, and fragrant.

Basidiospores [40/5/2] 6–6.44–7 (–7.5) × 5–5.88–6.5 (–7) μm, Q = 1–1.1–1.2 (–1.3), Qm = 1.1 ± 0.07, globose to subglobose, sometimes broadly ellipsoid, slightly thick-walled (up to 1μm), smooth, and yellowish in KOH. *Basidia* 21–59 × 6–10.5 μm, subcylindric, clavate to subclavate, slightly thick-walled (up to 1 μm), and colorless in KOH; sterigmata 2–4, up to 7 μm long, 2 μm wide at the base, somewhat curving. *Cystidia* absent. *Pileipellis* a cutis, interwoven to subparallel, 2–11 μm wide, and colorless in KOH; terminal hyphae 23–74 × 4–6 μm, cylindrical, slightly thick-walled (0.5–1 μm), and slightly inflate at apex or septum. *Clamp connections* present in all tissues.

Habitat—Solitary or gregarious on the ground in forests dominated by fagaceous trees.

Known distribution—Papua New Guinea and southern China (Hainan Province).

Specimens examined—CHINA. Hainan Province: Ledong County, Yinggeling of Hainan Tropical Rainforest National Park, elev. 650 m, 5 September, 2023, N.K. Zeng8373, 8374 (FHMU7690, 7691).

Notes—*Hydnum treui* was originally described from Papua New Guinea [1]. In the protologue, scant information on the morphological structures of the species was provided. Thus, *H. treui* was redescribed according to new specimens from China, which is characterized by a white to creamy white, unobviously ribbed pileus, the pinkish and thick context (up to 10 mm), long spines (up to 4 mm), the yellowish-white hymenophore, globose to subglobose basidiospores, and the presence of a fragrant odor.

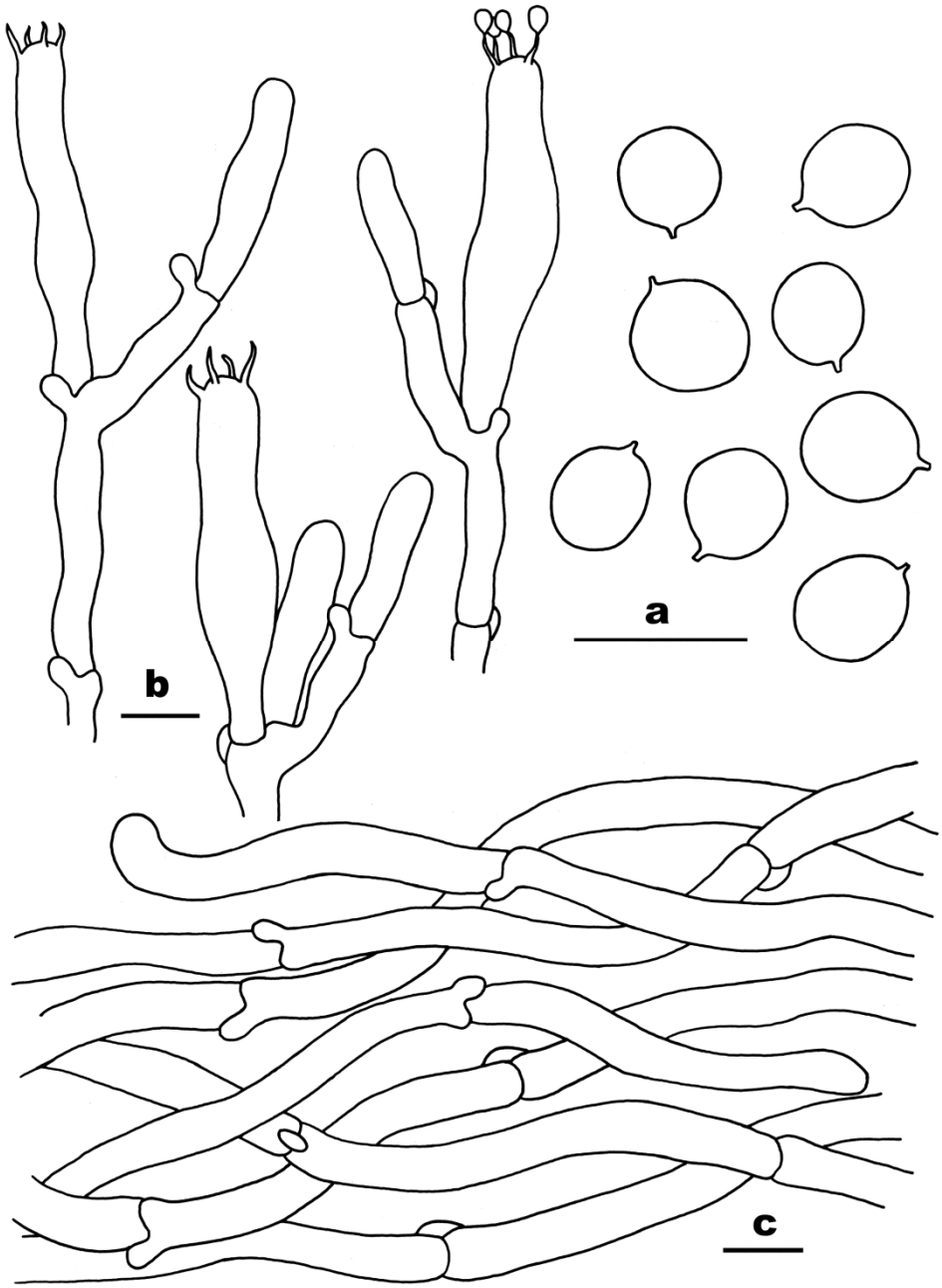

Figure 8. Microscopic features of *Hydnum treui* (FHMU7690). (**a**) Basidiospores. (**b**) Basidia. (**c**) Pileipellis. Scale bars = 10 μm. Drawings by H.Z. Qin.

Other known species from China

1. ***Hydnum brevispinum*** T. Cao & H.S. Yuan, Studies in Mycology 99 (no. 100121): 48, 2021.

MycoBank: MB 839417.

Holotype—Wei 10214 (IFP 019464) (Hunan Province, central China).

2. ***Hydnum flabellatum*** T. Cao & H.S. Yuan, Studies in Mycology 99 (no. 100121): 48, 2021.

MycoBank: MB 839414.

Holotype—Yuan 14708 (IFP 019459) (Liaoning Province, northeastern China).

3. ***Hydnum flavidocanum*** T. Cao & H.S. Yuan, Studies in Mycology 99 (no. 100121): 49, 2021.

MycoBank: MB 839415.

Holotype—Yuan 13903a (IFP 019460) (Yunnan Province, southwestern China).

4. *Hydnum longibasidium* T. Cao & H.S. Yuan, Studies in Mycology 99 (no. 100121): 49, 2021.

MycoBank: MB 839416.

Holotype—Wei10383 (IFP 019462) (Hunan Province, central China).

5. *Hydnum longipes* Ming Zhang & C.Q. Wang, Journal of Fungi, 10(2): 98, 2024.

Fungal Name: FN571736.

Holotype—GDGM82458 (Yunnan Province, southwestern China).

6. *Hydnum microcarpum* Ming Zhang, Journal of Fungi, 10(2): 98, 2024.

Fungal Name: FN571762.

Holotype—GDGM87902 (Guangdong Province, southern China).

7. *Hydnum pallidocroceum* T. Cao & H.S. Yuan, Studies in Mycology 99 (no. 100121): 50, 2021.

MycoBank: MB 839418.

Holotype—Yuan 14023 (IFP 019466) (Xinjiang Uygur Autonomous Region, northwestern China).

8. *Hydnum pallidomarginatum* T. Cao & H.S. Yuan, Studies in Mycology 99 (no. 100121): 51, 2021.

MycoBank: MB 839419.

Holotype—Yuan 13928a (IFP 019468) (Yunnan Province, southwestern China).

9. *Hydnum sinorepandum* Ming Zhang & C.Q. Wang, Journal of Fungi, 10(2): 98, 2024.

Fungal Name: FN571763.

Holotype—GDGM82445 (Yunnan Province, southwestern China).

10. *Hydnum sphaericum* T. Cao & H.S. Yuan, Studies in Mycology 99 (no. 100121): 51, 2021.

MycoBank: MB 839420.

Holotype—Wei10243 (IFP 019470) (Hunan Province, central China).

11. *Hydnum tangerinum* T. Cao & H.S. Yuan, Studies in Mycology 99 (no. 100121): 52, 2021.

MycoBank: MB 839421.

Holotype—Wei 10245 (IFP 019473) (Hunan Province, central China).

12. *Hydnum ventricosum* T. Cao & H.S. Yuan, Studies in Mycology 99 (no. 100121): 53, 2021.

MycoBank: MB 839423.

Holotype—Yuan 14536 (IFP 019478) (Liaoning Province, northeastern China).

4. Discussion

In previous studies, mycologists have paid much attention to species of *Hydnum* in North/Central America, Europe, and Australasia [1,4,9]. Twenty-two taxa have been confirmed from North America [1,4,9], fifteen species are recognized from Europe [1, 9,17], and ten taxa were found in Australasia [1,9]. Recently, the genus has received increasing attention in East Asia, where the species diversity of *Hydnum* in the area has been uncovered. Nine taxa were described as new from Japan: *H. alboluteum* R. Sugaw. & N. Endo, *H. albopallidum*, *H. itachiharitake* R. Sugaw. & N. Endo, *H. minosporoferufescens* R. Sugaw. & N. Endo, *H. orientalbidum*, *H. pinicola* R. Sugaw. & N. Endo, *H. subberkeleyanum*, *H. tomaense* R. Sugaw. & N. Endo., and *H. tottoriense* [14]. Additionally, high species diversity of *Hydnum* in China was also revealed, with thirteen taxa being described as new from the country: *H. brevispinum* T. Cao & H. S. Yuan, *H. flabellatum*, *H. flavidocanum* T. Cao & H. S. Yuan, *H. longibasidium* T. Cao & H. S. Yuan, *H. longipes* Ming Zhang & C.Q. Wang, *H. microcarpum* Ming Zhang, *H. pallidocroceum* T. Cao & H. S. Yuan, *H. pallidomarginatum*, *H. sinorepandum* Ming Zhang & C.Q. Wang, *H. sphaericum* T. Cao & H. S. Yuan, *H. tangerinum* T. Cao & H. S. Yuan, *H. tenuistipitum*, and *H. ventricosum* T. Cao & H. S. Yuan [15,22]. In the present study, 35 species-level lineages were identified (Figure 1). Among them,

one species is new to science, viz. *H. erectum* (lineage 32), and one is new to China, viz. *H. treui* (lineage 22).

Recent phylogenetic analyses of worldwide *Hydnum* samples have provided some new insights into the cloudy phylogeny and geography of this genus [9]. Our phylogenetic tree was constructed using two-locus DNA sequences (28S + ITS) with reliable sequences of already published species and those from new Chinese collections, which have contributed to our new knowledge of the genus. *Hydnum minus* was previously assigned to the subgen. *Alba* s. l. by Niskanen et al. [1], whereas our phylogenetic study indicated that *H. minus* is phylogenetically related to *H. brevispinum,* the type species of subgen. *Brevispina* [15], with 94% RAxML likelihood bootstrap (Figure 1). Moreover, *H. minus* is morphologically similar to *H. brevispinum* [15]. Therefore, *H. minus* was transferred to the subgen. *Brevispina* in the present study (Table 2). *Hydnum tenuistipitum* and *H. microcarpum* were previously clustered into the subgen. *Brevispina* [15,22]. However, our phylogenetic tree demonstrated that they are located in an isolated unidentified branch (Figure 1). Hence, *H. tenuistipitum* and *H. microcarpum* were removed from the subgen. *Brevispina* (Table 2). The subgenus classification of *H. tenuistipitum* and *H. microcarpum* needs to be further elucidated. It is worth noting that two Chinese collections (IFP 019480 and IFP 019481) were previously identified as *H. albomagnum* by Cao et al. [15]. However, our phylogenetic study showed that they clustered together with the holotype of *H. cremeoalbum,* forming a well-supported lineage (Figure 1: lineage 19). The two specimens are expected to be further identified by morphological studies.

Table 2. Subgenera, sections, subsections, and accepted species of *Hydnum* in China.

Subgenus	Section	Subsection	Species	Locality	References
Alba Niskanen & Liimat.	—	—	*H. cremeoalbum*	Japan	[5]
			H. flavidocanum	Yunnan, SW China	[15]
			H. pinicola	Japan	[14]
			H. treui	Papua New Guinea	[1]
Brevispina T. Cao & H. S. Yuan	—	—	*H. brevispinum*	Hunan, central China	[15]
			H. minus	Japan	[5]
Hydnum L.	*Hydnum* L.	—	*H. sinorepandum*	Yunnan Province, SW China	[22]
			H. sphaericum	Hunan, central China	[15]
Pallida Niskanen & Liimat.	—	—	*H. erectum*	Zhejiang, eastern China	Present study
			H. flabellatum	Liaoning, NE China	[15]
			H. pallidomarginatum	Yunnan, SW China	[15]
Rufescentia Niskanen & Liimat.	*Magnorufescentia* Niskanen & Liimat.	—	*H. pallidocroceum*	Xinjiang, NW China	[15]
			H. tangerinum	Hunan, central China	[15]
	Rufescentia Niskanen & Liimat.	*Mulsicoloria* Niskanen & Liimat.	*H. longipes*	Yunnan Province, SW China	[22]
			H. melitosarx	USA	[1]
		Rufescentia Niskanen & Liimat.	*H. ventricosum*	Liaoning, NE China	[15]
		Tenuiformia Niskanen & Liimat.	*H. longibasidium*	Hunan, central China	[15]

Table 2. *Cont.*

Subgenus	Section	Subsection	Species	Locality	References
—	—	—	*H. microcarpum*	Guangdong Province, southern China	[22]
			H. orientalbidum	Japan	[14]
			H. tenuistipitum	Hunan, central China	[15]

SW: Southwestern, NE: Northeastern, NW: Northwestern.

Our phylogenetic analysis also demonstrated that *H. subberkeleyanum* is a later synonym of *H. ventricosum* (Figure 1: lineage 8). Moreover, there are no essential morphological differences between the two taxa, judging from their protologues [14,15]. It is worth noting that the holotype of *H. pallidomarginatum* and the holotype of *H. flabellatum* grouped together without statistical support (Figure 1: lineage 31); their taxonomic relationship should be further assessed. In addition, although many section or subsection classifications of *Hydum* have been defined in this study, there is no sufficient support for many clades (Figure 1). Hence, more gene fragments (*TEF1* and *RBP2*) are needed to further construct molecular phylogenetic trees in the future.

Our phylogenetic study provided new perspectives into the geography of *Hydnum*. For example, *H. umbilicatum* is shared by East Asia, Europe, and North America [1,4]; *H. boreorepandum*, *H. melitosarx*, and *H. mulsicolor* occur in both East Asia and Europe [1,12,22]; *H. cremeoalbum*, *H. minus*, *H. orientalbidum*, *H. pinicola*, and *H. ventricosum* (synonymy: *H. subberkeleyanum*) are found in both China and Japan (Figure 1) [14,15,22]; *H. treui* is distributed in both tropical China and Papua New Guinea (Figure 1). It is worth noting that *H. jussii* and *H. vesterholtii* were reported to be distributed in China, according to previous studies [9,22]. However, they were just identified by molecular data; the specimens of the two species from China should be further studied morphologically in the future. Our phylogenetic tree also indicated that *H. berkeleyanum* and *H. umbilicatum* are probably distributed in China (Figure 1). Similarly, the Chinese collections of the two taxa should be further defined using morphological studies.

Therefore, *H. berkeleyanum*, *H. jussii*, *H. umbilicatum*, and *H. vesterholtii* were excluded in Table 2 and the key, and they should be further studied morphologically in the future.

5. Conclusions

In this study, a total of six *Hydnum* species from China are described, including a new species: *H. erectum* and five known taxa: *H. cremeoalbum*, *H. minus*, *H. orientalbidum*, *H. tenuistipitum*, and *H. treui*. Among them, *H. treui* is new to China. *Hydnum subberkeleyanum* is a later synonym of *H. ventricosum*; *H. minus* is confirmed to be a member of subgen. *Brevispina*.

Key to the Accepted Species of *Hydnum* in China	
1. Pileus white, pale cream, cream, yellowish-white, yellowish-grey	2
1. Pileus creamy yellow, pale orange, greyish orange, orange	11
2. Basidiomata medium to large, pileus > 5 cm diameter	3
2. Basidiomata small, pileus < 5 cm diameter	6
3. Distributed in sub-alpine regions, elevation > 3000 m, pileal context changing orange-white to pale orange when injured, basidiospores larger (8–9 × 6.5–7.5 µm)	*H. sinorepandum*
3. Distributed in subtropical/tropical regions, elevation < 2000 m, pileal context unchanging in color when injured, basidiospores smaller (up to 7 µm long and 6.5 µm wide)	4

Key to the Accepted Species of *Hydnum* in China	
4. Basidiospores larger (6–7 × 5–6.5 μm), basidia longer (21–59 μm), odor sweetish and fragrant	*H. treui*
4. Basidiospores smaller (up to 5.5 μm long and 4.5 μm wide), basidia shorter (up to 40 μm), odor indistinctive	5
5. Stipe cream white, branched, longer (4–6 cm), spines longer (>3 cm long)	*H. cremeoalbum*
5. Stipe white, not branched, shorter (2–3 cm), spines shorter (<3 cm long)	*H. pinicola*
6. Context unchanging in color when injured	7
6. Context turning red to reddish-brown when injured	*H.minus*
7. Pileus flabelliform to semicircular, with appressed brownish-orange scales, a distribution in temperate China	*H. flabellatum*
7. Pileus round, without scales, a distribution in subtropical China	8
8. Pileal surface turning brownish-orange to brownish red when injured	*H. microcarpum*
8. Pileal surface unchanging in color when injured	9
9. Basidiospores subglobose, pileipellis composed of frequently branched hyphae	*H. tenuistipitum*
9. Basidiospores broadly ellipsoid, pileipellis composed of occasionally to rarely branched hyphae	10
10. Pileal surface velutinate, pure white, spines shorter (0.2–0.8 mm), basidiospores smaller (5–5.8 × 3.8–4.8 μm)	*H. brevispinum*
10. Pileal surface glabrous, yellowish-white to yellowish-grey, spines longer (0.5–2 mm), basidiospores larger (7.2–8.8 × 5.5–6.5 μm)	*H. flavidocanum*
11. Pileipellis a cutis, composed of interwoven to subparallel hyphae	12
11. Pileipellis a trichoderm, composed of mostly erect hyphae	*H. erectum*
12. Basidiomata medium to large, pileus > 5 cm diameter	13
12. Basidiomata small, pileus < 5 cm diameter	14
13. Basidiospores subglobose, smaller (4.5–6 × 4–5 μm), spines clearly decurrent, pileal surface cream yellow, glabrous, stipe cream white, staining reddish when handled, a distribution in tropical China	*H. orientalbidum*
13. Basidiospores broadly ellipsoid, larger (7.2–8.8 × 5.8–7 μm), spines non-decurrent, pileal surface orange to brownish-orange, velutinate, stipe white, staining pale orange when handled, a distribution in subtropical China	*H. tangerinum*
14. Pileal surface changing to orange-white when injured, stipe longer (>5 cm long)	*H. longipes*
14. Pileal surface unchanging in color when injured, stipe shorter (<5 cm long)	15
15. Spines non-decurrent, a distribution in the gymnosperm forest	16
15. Spines subdecurrent to decurrent, a distribution in the angiosperm forest	18
16. Pileal context white, changing pale orange when injured, basidiospores larger (8–11 × 7–10 μm)	*H. melitosarx*
16. Pileal context yellowish-white, unchanging in color when injured, basidiospores smaller (up to 9.5 μm long and 8.5 μm)	17
17. Pileal surface orange-white to pale orange, stipe longer (3–5.5 cm), light yellow, unchanging in color when injured, basidiospores broadly ellipsoid (7.8–9.5 × 6–7.5 μm), basidia subcylindric or subclavate	*H. pallidocroceum*

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17. Pileal surface orange, stipe shorter (3–3.5 cm), orange-white, staining brownish when handled, basidiospores subglobose (8.2–9 × 7.5–8.5 μm), basidia fusiform to subcylindric, ventricose	*H. ventricosum*
18. Pileal surface glabrous, basidia shorter (up to 65 μm), stipe surface unchanging in color when handled, basidiospores broadly ellipsoid (Q = 1.2–1.28)	19
18. Pileal surface subglabrous to velutinate, basidia longer (up to 82 μm), stipe surface staining pale yellow when handled, basidiospores subglobose (Q = 1.09–1.13)	*H. longibasidium*
19. Pileus subglobose, pileal surface orange-white, stipe white, spines white, non-decurrent to subdecurrent	*H. sphaericum*
19. Pileus irregularly round to semicircular, or infundibuliform, pileal surface orange-white to pale orange, but pileal margin whitish (obviously lighter), stipe orange white to pale orange, spines orange white to pale orange, decurrent	*H. pallidomarginatum*

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References

1. Niskanen, T.; Liimatainen, K.; Nuytinck, J.; Kirk, P.; Ibarguren, I.O.; Garibay-Orijel, R.; Norvell, L.; Huhtinen, S.; Kytövuori, I.; Ruotsalainen, J.; et al. Identifying and naming the currently known diversity of the genus *Hydnum*, with an emphasis on European and North American taxa. *Mycologia* **2018**, *110*, 890–918. [CrossRef]
2. Agerer, R.; Kraigher, H.; Javornik, B. Identification of ectomycorrhizae of *Hydnum rufescens* on Norway spruce and the variability of the ITS region of *H. rufescens* and *H. repandum* (Basidiomycetes). *Nova Hedwig.* **1996**, *63*, 183–194.
3. Moncalvo, J.M.; Nilsson, R.H.; Koster, B.; Dunham, S.M.; Bernauer, T.; Matheny, P.B.; Porter, T.M.; Margaritescu, S.; Weiss, M.; Garnica, S.; et al. The cantharelloid clade: Dealing with incongruent gene trees and phylogenetic reconstruction methods. *Mycologia* **2006**, *98*, 937–948. [CrossRef] [PubMed]
4. Swenie, R.A.; Baroni, T.J.; Matheny, P.B. Six new species and reports of *Hydnum* (*Cantharellales*) from eastern North America. *MycoKeys* **2018**, *30*, 35–72. [CrossRef] [PubMed]
5. Yanaga, K.; Sotome, K.; Ushijima, S.; Maekawa, N. *Hydnum* species producing whitish basidiomata in Japan. *Mycoscience* **2015**, *56*, 434–442. [CrossRef]
6. Hall, D.; Stuntz, D.E. Pileate Hydnaceae of the Puget Sound area. I. White-spored genera: *Auriscalpium*, *Hericium*, *Dentinum* and *Phellodon*. *Mycologia* **1971**, *63*, 937–1098. [CrossRef]
7. Maas Geesteranus, R.A. *Hydnaceous Fungi of the Eastern Old World*; North-Holland Publishing Company: Amsterdam, The Netherlands, 1971; pp. 63–77.
8. Pine, E.M.; Hibbett, D.S.; Donoghue, M.J. Phylogenetic relationships of cantharelloid and clavaroid *Homobasidiomycetes* based on mitochondrial and nuclear rDNA sequences. *Mycologia* **1999**, *91*, 944–963. [CrossRef]

9. Feng, B.; Wang, X.H.; Ratkowsky, D.; Gates, G.; Lee, S.S.; Grebenc, T.; Yang, Z.L. Multilocus phylogenetic analyses reveal unexpected abundant diversity and significant disjunct distribution pattern of the Hedgehog Mushrooms (*Hydnum* L.). *Sci. Rep.* **2016**, *6*, 25586. [CrossRef] [PubMed]
10. Lee, S.S.; Watling, R.; Noraini-Sikin, Y. Ectomycorrhizal basidiomata fruiting in lowland forests of Peninsular Malaysia. *Bois Forêts Trop.* **2002**, *274*, 33–43.
11. Ostrow, H.; Beenken, L. *Hydnum ellipsosporum* spec. nov. (Basidiomycetes, Cantharellales)–ein Doppelgänger von *Hydnum rufescens* Fr. *Zeitschrift Für Mykologie* **2004**, *70*, 137–156.
12. Grebenc, T.; Martín, M.P.; Kraigher, H. Ribosomal ITS diversity among the European species of the genus *Hydnum* (Hydnaceae). *An. Jard. Bot. Madr.* **2009**, *66*, 121–132. [CrossRef]
13. Hibbett, D.S.; Pine, E.M.; Langer, E.; Langer, G.; Donoghue, M.J. Evolution of gilled mushrooms and puffballs inferred from ribosomal DNA sequences. *Proc. Natl. Acad. Sci. USA* **1997**, *94*, 12002–12006. [CrossRef] [PubMed]
14. Sugawara, R.; Maekawa, N.; Sotome, K.; Nakagiri, A.; Endo, N. Systematic revision of *Hydnum* species in Japan. *Mycologia* **2022**, *114*, 413–452. [CrossRef] [PubMed]
15. Cao, T.; Hu, Y.P.; Yu, J.R.; Wei, T.Z.; Yuan, H.S. A phylogenetic overview of the Hydnaceae (Cantharellales, Basidiomycota) with new taxa from China. *Stud. Mycol.* **2021**, *99*, 100121. [CrossRef]
16. Vizzini, A.; Picillo, B.; Ercole, E.; Voyron, S.; Contu, M. Detecting the variability of *Hydnum ovoideisporum* (Agaricomycetes, Cantharellales) on the basis of Italian collections, and *H. magnorufescens* sp. nov. *Mycosphere* **2012**, *4*, 32–44. [CrossRef]
17. Olariaga, I.; Grebenc, T.; Salcedo, I.; Martín, M.P. Two new species of *Hydnum* with ovoid basidiospores: *H. ovoideisporum* and *H. vesterholtii*. *Mycologia* **2012**, *104*, 1443–1455. [CrossRef]
18. Buyck, B.; Duhem, B.; Das, K.; Jayawardena, R.S.; Niveiro, N.; Pereira, O.L.; Prasher, I.B.; Adhikari, S.; Albertó, E.O.; Bulgakov, T.S.; et al. Fungal Biodiversity Profiles 21–30. *Cryptogam. Myco.* **2017**, *38*, 101–146. [CrossRef]
19. Sugawara, R.; Yamada, A.; Kawai, M.; Sotome, K.; Maekawa, N.; Nakagiri, A.; Endo, N. Establishment of monokaryotic and dikaryotic isolates of Hedgehog mushrooms (*Hydnum repandum* and related species) from basidiospores. *Mycoscience* **2019**, *60*, 201–209. [CrossRef]
20. Bi, Z.S.; Zheng, G.Y.; Li, T.H. *Macrofungus flora of Guangdong Province*; Guangdong Science and Technology Press: Guangzhou, China, 1994.
21. Zang, M.; Li, B.; Xi, J.X. *Fungi of Hengduan Mountains*; Science Press: Beijing, China, 1996.
22. Zhang, M.; Wang, C.; Bai, H.; Deng, W. A Contribution to the Phylogeny and Taxonomy of *Hydnum* (Cantharellales, Basidiomycota) from China. *J. Fungi* **2024**, *10*, 98. [CrossRef]
23. McNabb, R.F.R. Some new and revised taxa of New Zealand Basidiomycetes (Fungi). *N. Z. J. Bot.* **1971**, *9*, 355–370. [CrossRef]
24. Cooke, M.C. Australian fungi. *Grevillea* **1890**, *19*, 44–47.
25. Massee, G.E. Fungi exotici, XIX. *Bull. Misc. Inf. Kew.* **1914**, *1914*, 357–359.
26. Banker, H.J. A preliminary contribution to a knowledge of the Hydnaceae. *Bull. Torrey Bot. Club* **1901**, *28*, 199–222. [CrossRef]
27. Peck, C.H. Descriptions of new species of New York fungi. *Bull. N. Y. St. Mus. Nat. Hist.* **1887**, *1*, 5–24.
28. Peck, C.H. Report of the State Botanist (1901). *Ann. Rep. Reg. N. Y. St. Mus.* **1902**, *54*, 929–984.
29. Dai, Y.C. A revised checklist of corticioid and hydnoid fungi in China for 2010. *Mycoscience* **2011**, *52*, 69–79. [CrossRef]
30. Hongo, T.; Ueda, T. *Yamakei Field Books Kinoko*; Yama-Kei Publishers: Tokyo, Japan, 2006. (In Japanese)
31. Kornerup, A.; Wanscher, J.H. *Taschenlexikon der Farben. 3. Aufl.*; Muster-Schmidt Verlag: Göttingen, Germany, 1981; p. 242.
32. Zhang, Y.Z.; Liang, Z.Q.; Xie, H.J.; Wu, L.L.; Xue, R.; Zeng, N.K. *Cantharellus macrocarpus* (Cantharellaceae, Cantharellales), a new species from tropical China. *Phytotaxa* **2021**, *484*, 170–180. [CrossRef]
33. Zhang, Y.Z.; Lin, W.F.; Buyck, B.; Liang, Z.Q.; Su, M.S.; Chen, Z.H.; Zhang, P.; Jiang, S.; An, D.Y.; Zeng, N.K. Morphological and phylogenetic evidences reveal four new species of *Cantharellus* subgenus *Cantharellus* (Hydnaceae, Cantharellales) from China. *Front. Microbiol.* **2022**, *13*, 900329. [CrossRef]
34. Xie, H.J.; Tang, L.P.; Mu, M.; Fan, Y.G.; Jiang, S.; Su, M.S.; Liang, Z.Q.; Zeng, N.K. A contribution to knowledge of *Gyroporus* (Gyroporaceae, Boletales) in China: Three new taxa, two previous species, and one ambiguous taxon. *Mycol. Prog.* **2022**, *21*, 71–92. [CrossRef]
35. Bas, C. Morphology and subdivision of Amanita and a monograph of its section *Lepidella*. *Persoonia* **1969**, *5*, 285–573. [CrossRef]
36. Vilgalys, R.; Hester, M. Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several *Cryptococcus* species. *J. Bacteriol.* **1990**, *172*, 4238–4246. [CrossRef] [PubMed]
37. James, T.Y.; Kauff, F.; Schoch, C.; Matheny, P.B.; Hofstetter, V.; Cox, C.; Celio, G.; Gueidan, C.; Fraker, E.; Miadlikowska, J.; et al. Reconstructing the early evolution of the fungi using a six gene phylogeny. *Nature* **2006**, *443*, 818–822. [CrossRef] [PubMed]
38. White, T.J.; Bruns, T.; Lee, S.; Taylor, J.W. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenies. In *PCR Protocols: A Guide to Methods and Applications*; Academic Press: New York, NY, USA, 1990; pp. 315–322.
39. Hall, T.A. BioEdit: A user-friendly biological sequence alignment editor and analyses program for Windows 95/98/NT. *Nucleic Acids Symp. Ser.* **1999**, *41*, 95–98. [CrossRef]
40. Edgar, R.C. MUSCLE: Multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Res.* **2004**, *32*, 1792–1797. [CrossRef] [PubMed]
41. Smith, S.A.; Dunn, C.W. Phyutility: A phyloinformatics tool for trees, alignments andmolecular data. *Bioinformatics* **2008**, *24*, 715–716. [CrossRef] [PubMed]

42. Matheny, P.B.; Wang, Z.; Binder, M.; Curtis, J.M.; Lim, Y.W.; Nilsson, R.H.; Hughes, K.W.; Hofstetter, V.; Ammirati, J.F.; Schoch, C.L.; et al. Contributions of rpb2 and tef1 to the phylogeny of mushrooms and allies (Basidiomycota, Fungi). *Mol. Phylogenet. Evol.* **2007**, *43*, 430–451. [CrossRef] [PubMed]
43. Wang, X.H.; Das, K.; Horman, J.; Antonin, V.; Baghela, A.; Chakraborty, D.; Hembrom, M.E.; Nakasone, K.; Ortiz-Santana, B.; Vizzini, A.; et al. Fungal biodiversity profiles 51–60. *Cryptogam. Myco.* **2018**, *39*, 211–257. [CrossRef]
44. Sugawara, R.; Aoki, W.; Yamada, A.; Nakagiri, A.; Endo, N. Ecological speciation of Japanese hedgehog mushroom: *Hydnum subalpinum* sp. nov. is distinguished from its sister species *H. repando-orientale* by means of integrative taxonomy. *Mycol. Prog.* **2022**, *21*, 94. [CrossRef]
45. An, D.Y.; Liang, Z.Q.; Jiang, S.; Su, M.S.; Zeng, N.K. *Cantharellus hainanensis*, a new species with a smooth hymenophore from tropical China. *Mycoscience* **2017**, *58*, 438–444. [CrossRef]
46. Baird, R.; Wallace, L.E.; Baker, G.; Scruggs, M. Stipitate hydnoid fungi of the temperate southeastern United States. *Fungal Divers.* **2013**, *62*, 41–114. [CrossRef]
47. Moeller, H.V.; Peay, K.G.; Fukami, T. Ectomycorrhizal fungal traits reflect environmental conditions along a coastal California edaphic gradient. *FEMS Microbiol. Ecol.* **2014**, *87*, 797–806. [CrossRef] [PubMed]
48. Schoch, C.L.; Robbertse, B.; Robert, V.; Vu, D.; Cardinali, G.; Irinyi, L.; Meyer, W.; Nilsson, R.H.; Hughes, K.; Miller, A.N.; et al. Finding needles in haystacks: Linking scientific names, reference specimens and molecular data for Fungi. *Database* **2014**, *2014*, bau061. [CrossRef] [PubMed]
49. Nilsson, R.H.; Larsson, K.H.; Larsson, E.; Kõljalg, U. Fruiting body-guided molecular identification of root-tip mantle mycelia provides strong indications of ectomycorrhizal associations in two species of *Sistotrema* (Basidiomycota). *Mycol. Res.* **2006**, *110*, 1426–1432. [CrossRef] [PubMed]