

Article

Species Diversity of *Helvella lacunosa* Clade (Pezizales, Ascomycota) in China and Description of Sixteen New Species

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Abstract: *Helvella lacunosa* and its allies are widely distributed in the Northern Hemisphere and perform important functions in ecosystems. A comprehensive study on 101 collections of *Helvella lacunosa*, including those deposited in four Chinese fungaria or collected recently from 10 provinces, was conducted based on morphological and molecular characteristics. Phylogenies of “*Helvella lacunosa* clade” inferred from Hsp90, ITS, LSU, and TEF were reconstructed with 49 lineages recognized, of which 25 lineages occurred in China, and each represented an individual species. Sixteen new species were determined with detailed descriptions and illustrations. Two new Chinese records were reported. Species concepts and their distinctions in macro- and micro-features were discussed.

Keywords: Ascomycota; biodiversity; Helvellaceae; new species; phylogeny; taxonomy

1. Introduction

The *Helvella lacunosa* species complex (Helvellaceae, Pezizales) contains ascomycetous macrofungi having dark, saddle-shaped, lobed, or convex apothecia with sulcate or ribbed stipes. They are widely distributed in the Northern Hemisphere and perform important functions in ecosystems [1,2]. Some *Helvella* species are taken as precious and delicious food by local people in Shanxi and Xinjiang provinces of China.

The *Helvella* section *Lacunosae* was established by Dissing [3] to accommodate a group of operculate cup-fungi, including *H. lactea* Boud., *H. lacunosa* Afzel., *H. philonotis* Dissing, and *H. phlebophora* Pat. & Doass. The section was accepted by Weber [4] and Häffner [5] with *H. palustris* Peck and *H. sulcata* Afzel. added, which were treated as synonyms of *H. lacunosa* by Dissing [3]. Morphological features of the section include epigeous, stipitate, saddle-shaped or lobed apothecia; ribbed or lacunose stipes; a usually dark-colored hymenium surface; subcylindrical asci; filiform or clavate paraphyses; and ellipsoidal, hyaline, smooth, uniguttulate ascospores. Fragments of small subunit (SSU) and large subunit (LSU) ribosomal RNA genes were first adopted for pezizalean phylogenetic analyses in the 1990s [6] and were followed by subsequent studies [7–13]. Translation elongation factor 1- α (TEF) and other protein-coding genes were also applied to infer the phylogeny of this group of fungi [10,14–17]. As to *Helvella*, the internal transcribed spacer (ITS) and LSU phylogenies of *H. lacunosa* species complex were initially reported by Nguyen et al. [18]. And then, phylogenies of the genus based on a single gene, ITS or LSU, were reconstructed [2,19]. Hsp90 was introduced into the analysis of the genus and advocated as a primary DNA barcode [20]. Up to now, LSU is still the most popular locus to be used for species identification of the group, although its capacity is limited. Sequences of Hsp90 and ITS are usually lacking for some *Helvella* species, which creates barriers for species recognition. Our previous study [21] on the rib-stiped cupulate species of the genus tried to address this aspect.

Through the aid of molecular phylogenetics, species concepts of *Helvella* became well-established. A synopsis of the European species was accomplished by Skrede et al.

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[20], in which the monophyletic Clade C corresponded to the section containing *H. lacunosa* and its allies (as *Helvella lacunosa* clade). A total of 22 lineages were revealed in the clade based on multiple sequence analyses, and epi-/neo-types were designated for *H. atra* Oeder, *H. helvellula* (Durieu & Mont.) Dissing, *H. lacunosa*, *H. nigra* Bergeret, *H. pallescens* Schaeff., *H. phlebophora*, *H. queletiana* Sacc. & Traverso, and *H. sulcata*. Thereafter, nine additional species of *Helvella* were described from Spain [22], one from Mexico [23], and one from China [24], among which nine species belonged to this clade: *H. cystidiata* R.J. Xu et al., *H. fuscolacunosa* Skrede & T. Schumach., *H. hispanica* Skrede & T. Schumach., *H. iberica* Skrede & T. Schumach., *H. inexpectata* Skrede & T. Schumach., *H. jocatoi* F. Landeros et al., *H. neopallescens* Skrede & T. Schumach., *H. phlebophoroides* Skrede & T. Schumach., and *H. terricola* Skrede & T. Schumach.

In China, *H. lacunosa* was first recorded by Teng [25] from seven provinces, and then *H. atra*, *H. lacunosa*, *H. pallescens*, and *H. lactea* were listed by Tai [26]. More taxa of the clade were subsequently reported: *H. helvellula*, *H. lactea*, and *H. phlebophora* by Liu and Cao [27]; *H. philonotis* by Zhuang and Wang [28]; and *H. fusca* Gillet by Xu [29]. Recently, *H. cystidiata*, *H. pseudolacunosa* Q. Zhao & K.D. Hyde, *H. rugosa* Q. Zhao & K.D. Hyde, and *H. sublactea* Q. Zhao et al. were further discovered and described based on the Chinese materials [24,30,31]. A total of 13 species of the group were known in the country.

In connection with our current work on the family Helvellaceae of Flora Fungorum Sinicorum, extensive surveys of *Helvella* collections from different regions of China have been conducted. The results of a study on the species possessing cupulate apothecia with sulcate or ribbed stipes were previously reviewed [15]. In this work, members of *Helvella lacunosa* clade were investigated, and it turned out that species diversity of the clade is extremely high. The current research is a continuation towards the classification of the group based on multigene analysis.

2. Materials and Methods

2.1. Re-Examination and Collection of Samples

Collections of the *Helvella lacunosa* clade from China deposited in the following fungaria were re-examined: Herbarium Mycologicum Academiae Sinicae (HMAS), Herbarium of the Microbiology Institute of Guangdong (HMIGD), Herbarium of Mycological Institute of Jilin Agricultural University (HMJAU), and Mycological Herbarium of Chifeng University (CFSZ). Specimens recently collected from 10 cities, provinces, or administrative regions of China (Beijing, Fujian, Guizhou, Jiangsu, Jilin, Shanxi, Sichuan, Tibet, Yunnan, and Zhejiang) were also identified (Table 1). Morphological observations were conducted following the methods indicated in previous studies [21,32].

2.2. DNA Extraction, PCR Amplification and Sequencing

Well-preserved specimens were selected for DNA extraction using a Plant Genomic DNA Kit (DP305, TIANGEN Biotech, Beijing, China). Portions of the heat shock protein 90 (Hsp90), nuclear ribosomal DNA internal transcribed spacer (ITS), large subunit (LSU), and translation elongation factor 1- α (TEF) genes were amplified via PCR using the primer pairs H_hspf and H_hspr [20], ITS5 (or ITS3) and ITS4 [33], LROR and LR5 [34], and EF1-983F and EF1-1567R [35]. Products were purified and sequenced on an ABI 3730 DNA Sequencer (Applied Biosystems, Bedford, MA, USA).

2.3. Phylogenetic Analyses

In this study, newly generated forward and reverse sequences were assembled using Seqman v. 7.1.0 (DNASTAR Inc., Madison, WI, USA). The assembled sequences and those retrieved from GenBank are listed in Table 1. Four single-gene datasets and a multi-locus dataset were compiled. Sequences were aligned using MAFFT v. 7.221 [36] and then manually edited via BioEdit v. 7.1.10 [37] and MEGA v. 6.0.6 [38]. Maximum likelihood (ML) analyses were performed using RAxML-HPC2 [39] on XSEDE 8.2.12 on CIPRES Science

Gateway v. 3.3 [40] with the default GTRCAT model. Bayesian inference (BI) analyses were performed with MrBayes v. 3.2.5 [41]. Appropriate nucleotide substitution models and parameters were determined via Modeltest v. 3.7 [42]. The consensus trees were viewed in FigTree v. 1.3.1 (<http://tree.bio.ed.ac.uk/software/figtree/>, accessed on 1 September 2015). Two species of *Dissingia* served as outgroup taxa.

Table 1. Fungal species and sequences used in phylogenetic analyses.

Species	Voucher	Origin	Hsp90	ITS	LSU	TEF	Reference
<i>Helvella atra</i> Oeder 1770	O-255762 = H1055	Norway	MN692348	MN656170	MN655852	MN689304	[43]
	10865 = HMAS 290900	China: Tibet	OQ597592	OQ600286	OQ586677	OQ597533	This study
	11222 = HMAS 290901	China: Tibet	OQ597593	OQ600287	OQ586678	OQ597534	This study
	HMAS 83545	China: Xinjiang	OQ597594	n.a.	n.a.	OQ597535	This study
	HMAS 265533	China: Tibet	OQ597595	OQ600288	n.a.	OQ597536	This study
	HMJAU 27662	China: Inner Mongolia	OQ597596	OQ600289	OQ586679	n.a.	This study
<i>H. austrooccidentalis</i> X.C. Wang & W.Y. Zhuang, sp. nov.	11220 = HMAS 290902	China: Tibet	OQ597597	OQ600290	OQ586680	OQ597537	This study
	11223 = HMAS 290903, holotype	China: Tibet	OQ597598	OQ600291	OQ586681	OQ597538	This study
	ZRL20200655 = HMAS 290904	China: Sichuan	OQ597599	OQ600292	OQ586682	n.a.	This study
<i>H. borealis</i> X.C. Wang & W.Y. Zhuang, sp. nov.	3568 = HMAS 290905, holotype	China: Jilin	OQ597600	OQ600293	OQ586683	OQ597539	This study
	UC 1999199	USA: Minnesota	n.a.	n.a.	KC122796	n.a.	[18]
<i>H. cystidiata</i> R.J. Xu et al. 2022	HKAS 78941, holotype	China: Yunnan	n.a.	KX239839	KX239802	n.a.	[24]
	HKAS 74316	China: Yunnan	n.a.	KX239840	KX239803	n.a.	[24]
	HMAS 275836	China: Yunnan	OQ597601	OQ600294	n.a.	n.a.	This study
	HMJAU 52	China: Tibet	OQ597602	OQ600295	OQ586684	OQ597540	This study
	HMJAU 150	China: Tibet	OQ597603	OQ600296	OQ586685	OQ597541	This study
<i>H. dryophila</i> Vellinga & N.H. Nguyen 2013	UC 1999238 = MES218	USA: California	n.a.	KC122811	KC122772	n.a.	[18]
<i>H. fulva</i> X.C. Wang & W.Y. Zhuang, sp. nov.	10867 = HMAS 290906, holotype	China: Tibet	OQ597604	OQ600297	OQ586686	OQ597542	This study
<i>H. fusca</i> Gillet 1879	C-F-92122 = H305	Hungary	KY784415	n.a.	KY773101	n.a.	[20]
<i>H. fuscolacunosa</i> Skrede & T. Schumach. 2020	TRH12618 = H2883, holotype	Spain	MN598173	n.a.	MN644495	n.a.	[22]
<i>H. helvellula</i> (Durieu & Mont.) Dissing 1966	C-F-45507 = H278	France	KY784393	n.a.	KY773090	n.a.	[20]
<i>H. hispanica</i> Skrede & T. Schumach. 2020	O-F-256536 = H1023	Spain	MN598112	n.a.	MN644504	n.a.	[22]
<i>H. huangii</i> X.C. Wang & W.Y. Zhuang, sp. nov.	1414 = HMAS 290907	China: Beijing	OQ597605	OQ600298	OQ586687	OQ597543	This study
	HMAS 45031, holotype	China: Beijing	OQ597606	OQ600299	OQ586688	n.a.	This study
	HMJAU 3488	China: Jilin	OQ597607	OQ600300	OQ586689	OQ597544	This study
	CFSZ 2652	China: Inner Mongolia	OQ597608	n.a.	n.a.	n.a.	This study
<i>H. iberica</i> Skrede & T. Schumach. 2020	O-F256539 = H1018, holotype	Spain	MN598109	n.a.	MN644498	n.a.	[22]
<i>H. inexpectata</i> Skrede & T. Schumach. 2020	O-F-256540 = H1017	Spain	MN598192	n.a.	n.a.	n.a.	[22]
<i>H. jizushanica</i> X.C. Wang & W.Y. Zhuang, sp. nov.	11567 = HMAS 290908, holotype	China: Yunnan	OQ597609	OQ600301	OQ586690	OQ597545	This study

Species	Voucher	Origin	Hsp90	ITS	LSU	TEF	Reference
	HMAS 59718	China: Yunnan	OQ597610	OQ600302	OQ586691	n.a.	This study
<i>H. jocatoi</i> F. Landeros et al. 2021	CB08326 = MEXU 25760, holotype	Mexico	n.a.	KC016115	MH399851	n.a.	[18,23]
<i>H. juniperi</i> M. Filippa & Baiano 1999	H2973, holotype	Italy	MN598194	n.a.	n.a.	n.a.	[22]
<i>H. lactea</i> Boud. 1907	C-F-39379 = H374	Denmark	KY784473	n.a.	n.a.	n.a.	[20]
	CUP 52755, isotype of <i>H. astieri</i> Korf and Donadini	France	MK238676	n.a.	MK129270	n.a.	[44]
<i>H. lacunosa</i> Afzel. 1783	H407, epitype	Sweden	KY784503	n.a.	KY773152	n.a.	[20]
	O-255761 = H1041	Norway	MN692347	MN656169	MN655855	MN689302	[43]
	HKAS 87594, holotype of <i>H. pseudolacunosa</i> Q. Zhao and K.D. Hyde	China: Inner Mongolia	n.a.	KR493476	KT932629	n.a.	[30,45]
	HMAS 57959	China: Shanxi	OQ597611	n.a.	n.a.	n.a.	This study
	HMAS 61369	China: Shanxi	OQ597612	OQ600303	OQ586692	n.a.	This study
	HMAS 83536	China: Xinjiang	OQ597613	OQ600304	n.a.	OQ597546	This study
	HMAS 85622	China: Shanxi	OQ597614	OQ600305	n.a.	n.a.	This study
	HMAS 86534	China: Shanxi	OQ597615	OQ600306	OQ586693	OQ597547	This study
	HMAS 98364	China: Shanxi	OQ597616	n.a.	n.a.	n.a.	This study
	HMJAU 6816	China: Inner Mongolia	OQ597617	OQ600307	OQ586694	OQ597548	This study
	HMJAU 6817	China: Inner Mongolia	OQ597618	OQ600308	OQ586695	OQ597549	This study
	HMJAU 22359	Belarus	OQ597619	n.a.	n.a.	n.a.	This study
	HMJAU 23240	China: Inner Mongolia	OQ597620	OQ600309	OQ586696	OQ597550	This study
	ChenJQ 01 = HMAS 290909	China: Shanxi	OQ597621	n.a.	OQ586697	OQ597551	This study
<i>H. liui</i> X.C. Wang & W.Y. Zhuang, sp. nov.	HMAS 85725, holotype	China: Shanxi	OQ597622	OQ600310	n.a.	n.a.	This study
	XT13106	China: Hebei	n.a.	MF405782	n.a.	n.a.	[46]
<i>H. lobata</i> X.C. Wang & W.Y. Zhuang, sp. nov.	HaiY01 = HMAS 290910, holotype	China: Jiangsu	OQ597623	OQ600311	OQ586698	n.a.	This study
<i>H. magna</i> X.C. Wang & W.Y. Zhuang, sp. nov.	10861 = HMAS 290911	China: Tibet	OQ597624	OQ600312	OQ586699	OQ597552	This study
	10864 = HMAS 290912	China: Tibet	OQ597625	OQ600313	OQ586700	OQ597553	This study
	11790 = HMAS 290913	China: Yunnan	OQ597626	OQ600314	OQ586701	OQ597554	This study
	HMAS 60679, holotype	China: Gansu	OQ597627	OQ600315	OQ586702	OQ597555	This study
	HMAS 61724	China: Gansu	OQ597628	n.a.	OQ586703	n.a.	This study
	HMAS 66121	China: Gansu	OQ597629	OQ600316	OQ586704	OQ597556	This study
	HMAS 69594	China: Gansu	OQ597630	n.a.	n.a.	n.a.	This study
	HMAS 69595	China: Gansu	OQ597631	OQ600317	OQ586705	n.a.	This study
	HMAS 70345	China: Beijing	OQ597632	OQ600318	OQ586706	n.a.	This study
	HMAS 75848	China: Beijing	OQ597633	OQ600319	n.a.	n.a.	This study
<i>H. neopallescens</i> Skrede & T. Schumach. 2020	O-F-256550 = H1022, holotype	Spain	MN598111	n.a.	MN644500	n.a.	[22]
<i>H. nigra</i> Bergeret 1783	O-253345 = H063, epitype	Sweden	KY784227	n.a.	KY772947	KY772855	[20]
	UC 1999221	USA: New Hampshire	n.a.	KC122819	n.a.	n.a.	[18]
	HMAS 58374	Denmark	OQ597634	n.a.	n.a.	n.a.	This study
	HMAS 244000	UK	OQ597635	OQ600320	OQ586707	OQ597557	This study
	HMAS 262949	Italy	OQ597636	OQ600321	OQ586708	OQ597558	This study

Species	Voucher	Origin	Hsp90	ITS	LSU	TEF	Reference
<i>H. pallescens</i> Schaeff. 1774	O-66205 = H138, epitype	Norway	KY784271	n.a.	KY772988	KY772878	[20]
	HMAS 243999	UK	OQ597637	OQ600322	OQ586709	OQ597559	This study
<i>H. palustris</i> Peck 1883	O-253359 = H043	Norway	KY784214	n.a.	KY772933	KY772848	[20]
	HMAS 30755	China: Jilin	OQ597638	n.a.	n.a.	n.a.	This study
<i>H. parva</i> X.C. Wang & W.Y. Zhuang, sp. nov.	11559 = HMAS 290914, holotype	China: Yunnan	OQ597639	OQ600323	OQ586710	OQ597560	This study
<i>H. philonotis</i> Dissing 1964	O-255760 = H2110	Norway	MN692353	MN656182	MN655853	MN689303	[43]
	10695 = HMAS 290915	China: Tibet	OQ597640	OQ600324	OQ586711	OQ597561	This study
	HMAS 30756	China: Qinghai	OQ597641	n.a.	n.a.	n.a.	This study
	HMAS 51197	China: Sichuan	OQ597642	OQ600325	n.a.	n.a.	This study
	HMAS 262553	China: Tibet	OQ597643	OQ600326	n.a.	OQ597562	This study
	HMAS 264754	China: Tibet	OQ597644	OQ600327	OQ586712	OQ597563	This study
<i>H. phlebophora</i> Pat. & Doass. 1886	C-F-45405 = H273	Iceland	KY784388	n.a.	KY773087	n.a.	[20]
	HMAS 268001	China: Qinghai	OQ597645	OQ600328	OQ586713	OQ597564	This study
<i>H. phlebophoroides</i> Skrede & T. Schumach. 2020	O-F-256565 = H1031, holotype	Spain	MN598116	n.a.	MN644506	n.a.	[22]
<i>H. phlebophoropsis</i> X.C. Wang & W.Y. Zhuang, sp. nov.	HMAS 85654, holotype	China: Shanxi	OQ597646	OQ600329	n.a.	n.a.	This study
	HMAS 30757	China: Gansu	OQ597647	n.a.	n.a.	n.a.	This study
<i>H. plateata</i> X.C. Wang & W.Y. Zhuang, sp. nov.	11229 = HMAS 290916	China: Tibet	OQ597648	OQ600330	OQ586714	OQ597565	This study
	HMAS 270642, holotype	China: Tibet	OQ597649	OQ600331	OQ586715	OQ597566	This study
	11595 = HMAS 290917	China: Yunnan	OQ597650	OQ600332	OQ586716	OQ597567	This study
	ZRL20201123 = HMAS 290918	China: Sichuan	OQ597651	OQ600333	OQ586717	n.a.	This study
<i>H. queletiana</i> Sacc. & Traverso 1910	C-F-45303 = H403, neotype	Denmark	KY784499	n.a.	KY773151	n.a.	[20]
<i>H. ravidata</i> X.C. Wang & W.Y. Zhuang, sp. nov.	10682 = HMAS 290919, holotype	China: Sichuan	OQ597652	OQ600334	OQ586718	OQ597568	This study
	HMAS 61920	China: Hebei	OQ597653	OQ600335	OQ586719	n.a.	This study
<i>H. rugosa</i> Q. Zhao & K.D. Hyde 2015	HKAS 75442, holotype	China: Yunnan	n.a.	JX462575	KR493511	n.a.	[47]
	HKAS 87587	China: Yunnan	n.a.	KR493478	n.a.	MG980690	[48]
	11596 = HMAS 290920	China: Yunnan	OQ597654	OQ600336	OQ586720	OQ597569	This study
	ChenZH 31346 = HMAS 290921	China: Yunnan	OQ597655	OQ600337	OQ586721	OQ597570	This study
	HMJAU 37659	China: Yunnan	OQ597656	OQ600338	OQ586722	OQ597571	This study
	11291 = HMAS 290922	China: Tibet	OQ597657	OQ600339	OQ586723	OQ597572	This study
	Wu 5321 = HMAS 290923	China: Guizhou	OQ597658	OQ600340	OQ586724	OQ597573	This study
	HMAS 72111	China: Guizhou	OQ597659	OQ600341	n.a.	n.a.	This study
	Zhang 7455 = HMAS 290924	China: Fujian	OQ597660	OQ600342	OQ586725	OQ597574	This study
	HMAS 270927	China: Guangdong	OQ597661	OQ600343	OQ586726	OQ597575	This study
	HMAS 270956	China: Guangdong	OQ597662	OQ600344	OQ586727	OQ597576	This study
	HMAS 270961	China: Guangdong	OQ597663	OQ600345	OQ586728	OQ597577	This study
HMIGD 43032	China: Guangdong	OQ597664	OQ600346	OQ586729	OQ597578	This study	

Species	Voucher	Origin	Hsp90	ITS	LSU	TEF	Reference
	HMIGD 70298	China: Guangdong	OQ597665	OQ600347	OQ586730	OQ597579	This study
	HMIGD 70454	China: Guangdong	OQ597666	OQ600348	OQ586731	OQ597580	This study
	HMIGD 70469	China: Guangdong	OQ597667	n.a.	n.a.	n.a.	This study
	8021 = HMAS 290925	China: Jilin	OQ597668	MG846999	MG847045	MG847091	This study, [32]
	8023 = HMAS 290926	China: Jilin	OQ597669	OQ600349	OQ586732	OQ597581	This study
	8024 = HMAS 290927	China: Jilin	OQ597670	OQ600350	OQ586733	OQ597582	This study
<i>H. semiobruta</i> Donadini & Berthet 1976	C-F-45467 = H307	Spain	KY784417	n.a.	KY773102	n.a.	[20]
<i>H. sublactea</i> Q. Zhao et al. 2016	HKAS 69753 = Zhao 1032, holotype	China: Yunnan	n.a.	KT894825	KT894832	n.a.	[31]
	C-F-45434 = H400	Papua New Guinea	KY784497	n.a.	n.a.	n.a.	[20]
	8022 = HMAS 290928	China: Jilin	OQ597671	OQ600351	OQ586734	OQ597583	This study
	CFSZ 11221	China: Inner Mongolia	OQ597672	OQ600352	OQ586735	OQ597584	This study
	CFSZ 2041	China: Inner Mongolia	OQ597673	OQ600353	n.a.	n.a.	This study
	CFSZ 4790	China: Inner Mongolia	OQ597674	n.a.	OQ586736	n.a.	This study
	HMAS 33914	China: Beijing	OQ597675	n.a.	n.a.	n.a.	This study
	HMAS 33915	China: Beijing	OQ597676	n.a.	n.a.	n.a.	This study
	HMAS 33916	China: Beijing	OQ597677	n.a.	n.a.	n.a.	This study
	HMAS 85702	China: Jilin	OQ597678	n.a.	n.a.	n.a.	This study
<i>H. sulcata</i> Afzel. 1783	O-68095 = H152, epitype	Norway	KY784284	n.a.	KY773001	KY772882	[20]
<i>H. terricola</i> Skrede & T. Schumach. 2020	O-F256562 = H2978, holotype	Spain	MN598197	n.a.	n.a.	n.a.	[22]
	HMAS 38355	China: Xinjiang	OQ597679	OQ600354	n.a.	n.a.	This study
<i>H. varia</i> X.C. Wang & W.Y. Zhuang, sp. nov.	HMAS 131945	China: Yunnan	OQ597680	OQ600355	n.a.	n.a.	This study
	HMAS 186052	China: Yunnan	OQ597681	OQ600356	n.a.	n.a.	This study
	HMAS 270932, holotype	China: Guangdong	OQ597682	OQ600357	OQ586737	OQ597585	This study
	HMAS 270958	China: Guangdong	OQ597683	OQ600358	n.a.	OQ597586	This study
	Wu 345 = HMAS 290929	China: Guizhou	OQ597684	OQ600359	OQ586738	OQ597587	This study
	ZRL20150069 = HMAS 290930	China: Zhejiang	OQ597685	OQ600360	OQ586739	OQ597588	This study
	ZRL20191640 = HMAS 290931	China: Zhejiang	OQ597686	OQ600361	OQ586740	n.a.	This study
<i>H. vespertina</i> N.H. Nguyen & Vellinga 2013	UC 1999206	USA: California	n.a.	KC122847	KC122780	n.a.	[18]
	H102	USA: California	KY784245	n.a.	KY772963	n.a.	[20]
<i>H. vitrea</i> X.C. Wang & W.Y. Zhuang, sp. nov.	ZhangZH02 = HMAS 290932, holotype	China: Jiangsu	OQ597687	OQ600362	OQ586741	n.a.	This study
<i>H. vulgata</i> X.C. Wang & W.Y. Zhuang, sp. nov.	HMAS 53683, holotype	China: Hubei	OQ597688	OQ600363	OQ586742	n.a.	This study
	HMAS 85589	China: Jilin	OQ597689	OQ600364	n.a.	n.a.	This study
	HMIGD 25964	China: Jilin	OQ597690	OQ600365	OQ586743	OQ597589	This study

Species	Voucher	Origin	Hsp90	ITS	LSU	TEF	Reference
<i>H. yunnanensis</i> X.C. Wang & W.Y. Zhuang, sp. nov.	11785 = HMAS 290933, holotype	China: Yunnan	OQ597691	OQ600366	OQ586744	OQ597590	This study
	11789 = HMAS 290934	China: Yunnan	OQ597692	OQ600367	OQ586745	OQ597591	This study
<i>Helvella</i> sp. 1	O-253390 = H213	Japan	KY784334	n.a.	KY773045	n.a.	[20]
<i>Helvella</i> sp. 2	O-253391 = H461	Japan	KY784543	n.a.	n.a.	n.a.	[20]
<i>Helvella</i> sp. 3	O-253393 = H466	Japan	KY784547	n.a.	n.a.	n.a.	[20]
<i>Helvella</i> sp. 4	H104	USA: Massachusetts	KY784247	n.a.	KY772964	KY772869	[20]
<i>Helvella</i> sp. 5	C-F-92119 = H377	USA: Michigan	KY784476	n.a.	KY773139	n.a.	[20]
<i>Helvella</i> sp. 6	UC 1999237 = MES286	USA: California	n.a.	KC122810	KC122773	n.a.	[18]
<i>Dissingia leucomelaena</i> (Pers.) K. Hansen & X.H. Wang 2019	KH.06.01 = H115	USA: Massachusetts	KY784253	n.a.	KC012682	KC109207	[20,49]
	HMAS 61356	Sweden	MK652202	MK592137	n.a.	n.a.	[21]
<i>D. oblongispora</i> (Harmaja) T. Schumach. & Skrede 2019	O-166316 = H132	Norway	KY784265	n.a.	KY772983	MK113836	[20,44]
	HMAS 75147	China: Sichuan	MK652205	MK592140	n.a.	MK652162	[21]

GenBank accession numbers in bold indicating newly generated sequences.

3. Results

3.1. Molecular Phylogenies

Sequences from 49 species of the *Helvella lacunosa* clade and two outgroup taxa were investigated (Table 1). The characteristics of each dataset, e.g., the number of sequences included, alignment length, and numbers of variable and informative sites, are given in Table 2.

The four-locus dataset contained 135 sequences in an alignment with a length of 2652 base pairs (bp). A transversion model with invariable sites and gamma distribution (TVM+I+G) was selected by means of the Akaike information criterion as the best fit for Bayesian inference analysis. The phylogeny of this clade was reconstructed (Figure 1). A total of 46 *Helvella* lineages were recognized, and 25 of them consisted of Chinese materials. Nine lineages stood for the following known species: *H. atra*, *H. cystidiata*, *H. lacunosa*, *H. palustris*, *H. philonotis*, *H. phlebophora*, *H. rugosa*, *H. sublactea*, and *H. terricola*. The remaining 16 species represented undescribed taxa. The macro- and microscopic morphological characters of the undescribed species were given in Figures 2–5.

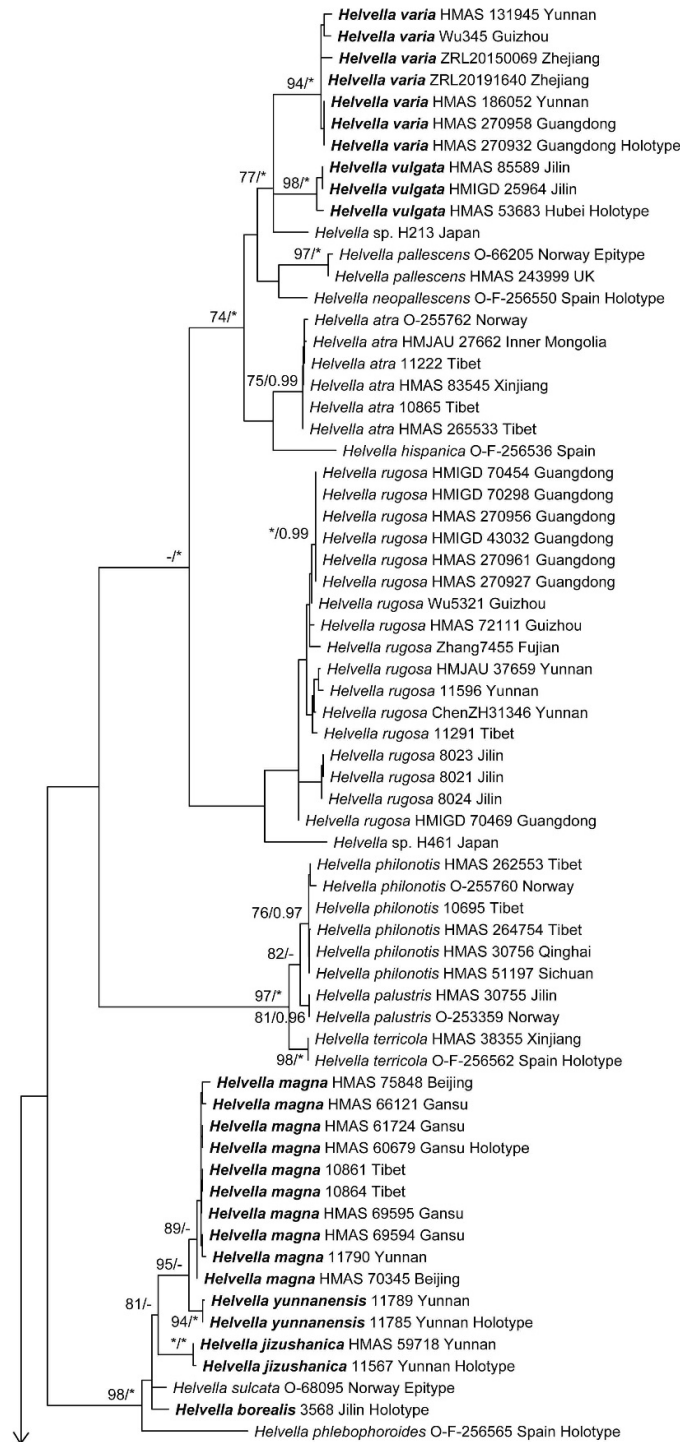
Table 2. Detailed characteristics of the phylogenetic analysis datasets.

Locus	No. of Seq.	Length of Alignment (bp)	No. of Variable Sites	No. of Parsimony-Informative Sites	Model for BI
Hsp90 + ITS + LSU + TEF	135	2652	857	709	TVM + I + G
Hsp90	135	240	68	60	
ITS	100	975	491	443	
LSU	105	874	154	106	
TEF	72	567	173	141	

Full name of the used model: TVM + I + G (transversion model with invariable sites and gamma distribution).

The phylogenies inferred from the individual gene datasets are shown in Figures S1–S4. Compared with the multi-locus phylogeny (Figure 1), three additional lineages were revealed in the ITS and LSU trees, representing *H. dryophila*, *H. jocatoidi*, and *Helvella* sp.

UC1999237. They clustered with *H. vespertina*, forming a subclade with high statistic supports (MLBP = 99% in Figure S2, MLBP = 98% in Figure S3). Additionally, they were all from North America. Hsp90 phylogeny showed less robust clustering support than the multi-locus or ITS ones (Figures 1 and S1). The TEF tree shared a similar topology with the four-locus and ITS phylogenies (Figure S4).



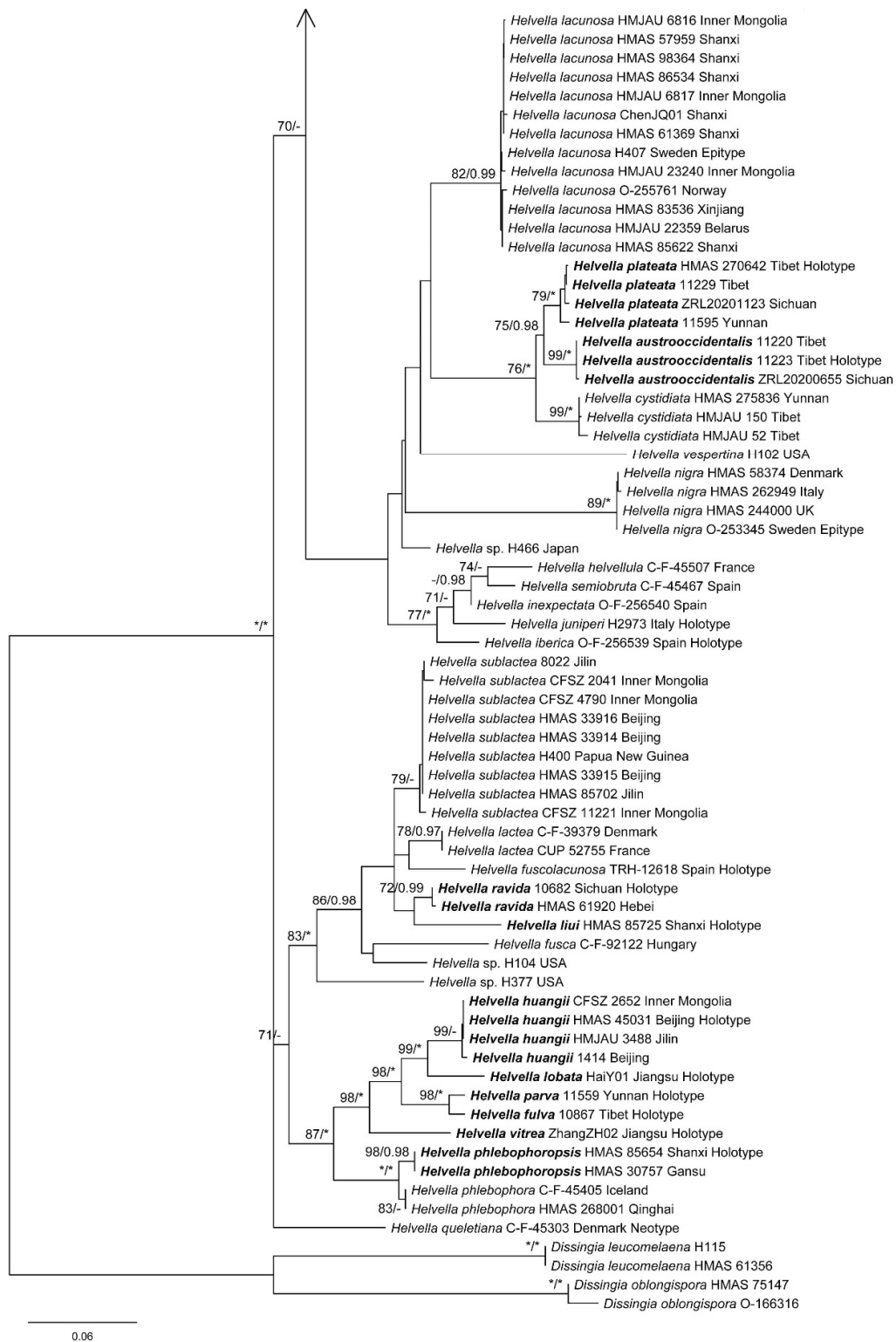


Figure 1. Maximum-likelihood phylogenetic tree of *Helvella lacunosa* clade inferred from combined Hsp90, ITS, LSU, and TEF1 dataset. Bootstrap values $\geq 70\%$ (left) and posterior probability values ≥ 0.95 (right) are indicated at nodes. Asterisk denotes 100% bootstrap or 1.00 posterior probability.

3.2. Taxonomy

3.2.1. New Species

Helvella austrooccidentalis X.C. Wang & W.Y. Zhuang, sp. nov. Figures 2A–C, 4D and 5(21–22)

Fungal Names: FN571317

Etymology: The specific epithet refers to geographic distribution of the species in southwestern China.

Typification: China, Tibet, Nyingchi City, Bayi District, Lulang Town, 29°46'3" N, 94°44'3" E, on rotten trunk, 23 September 2016, Xin-Cun Wang et al. 11223, HMAS 290903, holotype.

Apothecia saddle-shaped or lobed, stipitate, 3–4 cm diam. and 5.5–10 cm high when fresh, 1.6–2.5 cm diam. and 4.5–7 cm high when dry; margin revolute or attached to the stipe; hymenium surface undulate-rugose, greyish brown, dark brown to black when fresh, dark brown to black when dry; receptacle surface light brown to dark brown when dry, glabrous; stipe surface ribbed or lacunose, dirty white to yellow brown when fresh, yellow brown to light brown when dry, 3.5–5 × 0.2–0.7 cm when dry. Ectal excipulum of textura angularis, cells hyaline to yellow brown, outer cells 12–46.5 × 6–20 µm. Medullary excipulum of textura intricata, hyphae hyaline. Asci subcylindrical, tapering at base, eight-spored, 260–400 × 13–21 µm. Paraphyses filiform to clavate, septate, hyaline to yellow brown, 5–13 µm wide at apex and 2.5–4 µm below. Ascospores narrow ellipsoidal to ellipsoidal, hyaline, smooth, uniguttulate, 16–22 × 10.5–14.5 µm, Q = 1.5–1.65.

Additional specimens examined: China, Sichuan Province, Garzê Tibetan Autonomous Prefecture, Yajiang County, Gexigou National Nature Reserve, Hekou Town, Xiadu Village, 29°57'25" N, 100°57'35" E, Alt. 3241.56 m, on ground of mixed forest, Rui-Lin Zhao et al. ZRL20200655, HMAS 290904. Tibet, Nyingchi City, Bayi District, Lulang Town, 29°46'3" N, 94°44'3" E, on rotten trunk, 23 September 2016, Xin-Cun Wang et al. 11220, HMAS 290902.

Notes: This species was a sister of *H. cystidiata* and *H. plateata* (Figure 1). It differs from *H. cystidiata* in 3 bp for Hsp 90, 121 bp for ITS (112 bp in ITS1, 1 bp in 5.8S, and 8 bp in ITS2), 5 bp for LSU, and 4 bp for TEF; it differs from *H. plateata* in 1 bp for Hsp90, 105 bp for ITS (93 bp in ITS1, 1 bp in 5.8S, and 11 bp in ITS2), 4 bp for LSU, and 1 bp for TEF. Morphologically, it differs from *H. cystidiata* in yellow brown paraphysis apex and differs from *H. plateata* in lighter paraphysis color and broader ascospores (Table 3).

Table 3. Morphological comparisons among species of *Helvella lacunosa* clade.

Species	Specimen	Asci (µm)	Paraphyses Apex Width (µm)	Paraphyses Apex Color	Paraphyses Width (µm)	Paraphyses Color	Outer Cells (µm)	Ascospores (µm)	Mean of Q
<i>H. austrooccidentalis</i>	11223, holotype	260–333 × 14.5–21	6.5–13	yellow brown	2.5–4	hyaline to yellow brown	26.5–46.5 × 9–20	17–21 × 10.5–14.5	1.5
	ZRL20200655	313–400 × 13–17	3–6	yellow brown	2.5–3	yellow brown	12–26.5 × 6–10.5	16–22 × 10.5–12.5	1.65
<i>H. borealis</i>	3568, holotype	240–280 × 12–14.5	6.5–10.5	hyaline	3.5–5	hyaline	17–73 × 6.5–37	14.5–16 × 9–10.5	1.55
<i>H. cystidiata</i>	HKAS 78941, holotype	200–330 × 13–19	4–8	hyaline	3–5	hyaline	10–35 × 8–20	15–18.5 × 9–12	1.6
	HMAS 275836	326.5–346.5 × 14.5–20	4–8	hyaline to yellow brown	2.5–4	hyaline to yellow brown		17.5–20 × 10.5–13	1.6
	HMJAU 150	326.5–386.5 × 13.5–16	8–16	hyaline	2.5–4	hyaline to yellow brown	24–66.5 × 9.5–21	17–22 × 10.5–12.5	1.7
<i>H. fulva</i>	10867, holotype	280–346.5 × 13–21	5–9	hyaline to yellow brown	2.5–4	hyaline to yellow brown	26.5–33 × 8–13	17–20 × 10.5–12.5	1.6
<i>H. huangii</i>	HMAS 45031, holotype	213.5–280 × 13.5–18.5	5.5–8	hyaline	3.5–5.5	hyaline to yellow brown	26.5–36 × 8–18.5	17–20 × 11–13	1.5
	HMJAU 3488	246.5–320 × 14.5–18.5	4–5	hyaline	4–5	hyaline to yellow brown			
	CFSZ 2652	253–300 × 13.5–18.5	4.5–6.5	hyaline to yellow brown	2.5–4	hyaline to yellow brown	20–40 × 9–12	14.5–20 × 10.5–12.5	1.5
<i>H. jizushanica</i>	11567, holotype	246.5–320 × 13–18.5	6–8.5	hyaline	2.5	hyaline to yellow brown	17–46.5 × 10.5–29	16–21 × 10.5–12.5	1.6
<i>H. liui</i>	HMAS 85725, holotype	266.5–333 × 16–18.5	5–6.5	hyaline	3–4	hyaline	20–33 × 5–10.5	17–20 × 11–13	1.5
<i>H. lobata</i>	HaiY01, holotype	220–320 × 12–20	5–6.5	hyaline	2.5–4	hyaline to yellow brown	24–46.5 × 8–18.5	16–20 × 12–14.5	1.35
<i>H. magna</i>	10861	326.5–413 × 13–17	6.5–13	hyaline to yellow brown	2.5–6	hyaline to yellow brown	20–88 × 8–30.5	20–22.5 × 12–14.5	1.6
	11790	306.5–340 × 13–18.5	3–4	hyaline	2.5–3	hyaline			
	HMAS 60679, holotype	233–320 × 14.5–20	8–10	hyaline to yellow brown	4–5	hyaline to yellow brown	26.5–44 × 13–21	17–22.5 × 11–13	1.65
	HMAS 70345	280–320 × 13–18.5	5–8	hyaline to yellow brown	2.5–4	hyaline to yellow brown		15–21 × 10.5–16	1.35
<i>H. parva</i>	11559, holotype	226.5–266.5 × 13–17	6.5	hyaline	3.5–4	hyaline to yellow brown	20–53 × 6.5–20	17–18.5 × 10.5–12	1.6
<i>H. phlebophoropsis</i>	HMAS 85654, holotype	240–280 × 13–20	5–8	hyaline to yellow brown	2.5–4	hyaline to yellow brown	33–42.5 × 5–12	14.5–20 × 10.5–13	1.5
	HMAS 30757	246.5–266.5 × 13–20	4–6.5		4	hyaline to yellow brown	24–25 × 8–9	16.5–21 × 10.5–13	1.6
<i>H. plateata</i>	HMAS 270642, holotype	246.5–426.5 × 14.5–20	4–6.5	hyaline to yellow brown	2.5–4	hyaline to yellow brown	24–33 × 6.5–12	20–22.5 × 11–13	1.75
	11595	260–333 × 13–20	6.5–9	light brown to brown	2.5–5	light brown	26.5–46.5 × 9–21	18.5–23 × 11–12.5	1.75
	ZRL20201123	206.5–300 × 15–20	6.5–10.5	light brown to brown	3–5	light brown to brown	18.5–60 × 9–24	16–21 × 9–12.5	1.7
<i>H. ravidia</i>	10682, holotype	240–333 × 14.5–24	8–13	hyaline	4–4.5	hyaline	17–57 × 8–25	16–18.5 × 10.5–13	1.5
	HMAS 61920	253 × 14.5				hyaline to yellow brown		16–20 × 10.5–13	1.5
<i>H. varia</i>	HMAS 131945	230–300 × 13.5–22.5	5–8	hyaline to yellow brown	2.5–5	hyaline to yellow brown	14.5–40 × 9–21.5	16–20 × 10.5–13.5	1.5

Species	Specimen	Asci (μm)	Paraphyses Apex Width (μm)	Paraphyses Apex Color	Paraphyses Width (μm)	Paraphyses Color	Outer Cells (μm)	Ascospores (μm)	Mean of Q
	HMAS 270932, holotype	240–306.5 \times 14.5–17	4.5–8	hyaline to yellow brown	4	yellow brown		14.5–18.5 \times 12–14.5	1.25
	Wu 345	193–246.5 \times 14.5–18.5	5.5–8	hyaline	3.5–4.5	hyaline	21–46.5 \times 9–21	14.5–17.5 \times 9.5–12	1.5
	ZRL20150069		5.5–6.5	hyaline	2.5–4	yellow brown	17.5–41.5 \times 10.5–20	16–20 \times 10.5–12	1.6
<i>H. vitrea</i>	ZhangZH02, holotype	293–360 \times 16–21	5–8	hyaline	2.5–4.5	hyaline		14.5–18.5 \times 12–14	1.25
<i>H. vulgata</i>	HMAS 53683, holotype	260–293 \times 13–16	4.5–6.5	hyaline to yellow brown	2.5–4	hyaline to yellow brown	17–37 \times 6.5–17	16–20 \times 10.5–12	1.6
	HMIGD 25964	240–306.5 \times 12–17	4–6.5	hyaline	2.5–3	hyaline		15–20 \times 10.5–12	1.55
<i>H. yunnanensis</i>	11785	280–320 \times 13–20	5–8	hyaline	2.5–3	hyaline to yellow brown	16–36 \times 6.5–16	16–20 \times 10.5–13	1.5

Helvella borealis X.C. Wang & W.Y. Zhuang, sp. nov. Figures 3D and 5(9)

Fungal Names: FN571318

Etymology: The specific epithet refers to the geographic distribution of the species.

Typification: China, Jilin Province, Yanbian Korean Autonomous Prefecture, Dunhua City, Huangnihe National Nature Reserve, Donggou, 43°55'6" N, 128°18'57" E, Alt. 350 m, on rotten wood, 17 August 2000, Wen-Ying Zhuang and Yan-Hui Zhang 3568, HMAS 290905, holotype.

Apothecia saddle-shaped, stipitate, 0.4–1.5 cm diam. and 1–4 cm high when dry; margin revolute or attached to the stipe; hymenium surface undulate-rugose, dirty white to greyish white when fresh, yellow brown, red brown to dark brown when dry; receptacle surface buff when dry, glabrous; stipe surface sulcate, whitish when fresh, buff to yellow brown when dry, 2.3–5.5 cm when fresh, 0.7–3 × 0.2–0.5 cm when dry. Ectal excipulum of *textura angularis*, cells hyaline to light brown, outer cells 17–73 × 6.5–37 μm. Medullary excipulum of *textura intricata*, hyphae hyaline. Asci subcylindrical, tapering at base, eight-spored, 240–280 × 12–14.5 μm. Paraphyses filiform, septate, hyaline, 6.5–10.5 μm wide at apex and 3.5–5 μm below. Ascospores ellipsoidal, hyaline, smooth, uniguttulate, 14.5–16 × 9–10.5 μm, Q = 1.55.

Notes: *Helvella sulcata* was treated as a synonym of *H. lacunosa* by Dissing [3] and some subsequent researchers [5,50] but accepted as a separate species by Weber [4]. *Helvella borealis* has the closest relationship with *H. sulcata* (Figure 1), but differs in 1 bp for Hsp90, 3 bp for LSU, and 5 bp for TEF. Morphologically, *H. borealis* differs from *H. sulcata* in white or brown but not black hymenium, shorter asci (240–280 vs. 290–320 μm), broader paraphyses apex (6.5–10.5 vs. 5–6.5 μm), and narrower ascospores (9–10.5 vs. 10.5–13.2 μm) [22].

Helvella fulva X.C. Wang & W.Y. Zhuang, sp. Nov. Figures 2S, 4H and 5(19)

Fungal Names: FN571319

Etymology: The specific epithet refers to the hymenium color of the species.

Typification: China, Tibet, Nyingchi City, Mainling County, Lilong Town, Lilonggou, 29°2'23" N, 93°53'41" E, on soil, 14 September 2016, Xin-Cun Wang et al. 10867, HMAS 290906, holotype.

Apothecia saddle-shaped or lobed, stipitate, 1.6–3 cm diam. and 2.3–3.8 cm high when fresh; margin revolute or attached to the stipe; hymenium surface undulate-rugose, light brown when fresh, reddish brown to dark brown when dry; receptacle surface yellow brown when dry, glabrous; stipe surface sulcate, yellow brown to light brown when dry, 1–1.5 × 0.2–0.4 cm when dry. Ectal excipulum of *textura angularis*, cells hyaline, outer cells 24–46.5 × 8–18.5 μm. Medullary excipulum of *textura intricata*, hyphae hyaline. Asci subcylindrical, tapering at base, eight-spored, 280–346.5 × 13–21 μm. Paraphyses filiform to clavate, septate, hyaline to yellow brown, 5–9 μm wide at apex and 2.5–4 μm below. Ascospores ellipsoidal, hyaline, smooth, uniguttulate, 17–20 × 10.5–12.5 μm, Q = 1.6.

Notes: This species is a sister of *H. parva* (Figure 1), but differs in 1 bp in Hsp90, 14 bp for ITS (10 bp in ITS1 and 4 bp in ITS2), 3 bp for LSU, and 6 bp for TEF. Morphologically, it has longer asci and shorter outer ectal excipular cells than those of the latter (Table 3).

Helvella huangii X.C. Wang & W.Y. Zhuang, sp. nov. Figures 3C and 5(7–8)

Fungal Names: FN571321

Etymology: The specific epithet is named after the distinguished Chinese mycologist Nian-Lai Huang (1939.11–2022.09, Sanming Mycological Institute).

Typification: China, Beijing City, Mentougou District, Tanzhe Temple, 39°54'23" N, 116°1'54" E, on soil, 23 August 1982, Ru-Yong Zheng and Wen-Ying Zhuang ZC 8, HMAS 45031, holotype.

Apothecia saddle-shaped, stipitate, 0.7–1.5 cm diam. and 2–3.3 cm high when dry; margin revolute or attached to the stipe; hymenium surface undulate-rugose, yellow brown, red brown, light brown, dark brown or black when dry; receptacle surface yellow

brown, light brown to dark brown when dry, glabrous; stipe surface sulcate, buff, yellow brown to light brown when dry, 1.3–2.4 × 0.2–0.6 cm when dry. Ectal excipulum of textura angularis, cells hyaline to light brown, outer cells 20–40 × 8–18.5 µm. Medullary excipulum of textura intricata, hyphae hyaline. Asci subcylindrical, tapering at base, eight-spored, 213.5–320 × 13.5–18.5 µm. Paraphyses filiform, septate, hyaline to yellow brown, 4–8 µm wide at apex and 2.5–5.5 µm below. Ascospores ellipsoidal, hyaline, smooth, uniguttulate, 14.5–20 × 10.5–13 µm, Q = 1.5.

Additional specimens examined: China, Beijing City, Mentougou District, Tanzhe Temple, 39°54'23" N, 116°1'54" E, Alt. 400 m, on ground, 17 September 1996, Zheng Wang and Wen-Ying Zhuang 1414, HMAS 290907. Inner Mongolia Autonomous Region, Chifeng City, Bairin Left Banner, Yezhugou Village, 43°43'55" N, 119°21'38" E, 16 August 2005, Tie-Zhi Liu and Yu-Jun Gao, CFSZ 2652. Jilin Province, Changchun City, Jingyuetan National Forest Park, 43°46'41" N, 125°28'25" E, on the ground of broad-leaved forest, 15 August 2004, Jian-Rui Wang, HMJAU 3488.

Notes: The species is a sister of *H. lobata* (Figure 1) but differs from the latter in 1 bp for Hsp90, 49 bp for ITS (34 bp in ITS1 and 15 bp in ITS2), and 6 bp for LSU. Morphologically, it has narrower ascospores than that of the latter (Table 3).

Helvella jizushanica X.C. Wang & W.Y. Zhuang, sp. nov. Figures 2P and 5(16)

Fungal Names: FN571322

Etymology: The specific epithet refers to the type of locality of the fungus.

Typification: China, Yunnan Province, Dali Bai Autonomous Prefecture, Binchuan County, Jizu Mountain, 25°57'27" N, 100°23'34" E, on soil, 20 September 2017, Xin-Cun Wang et al. 11567, HMAS 290908, holotype.

Apothecia saddle-shaped, stipitate, 1.5 cm diam. and 5 cm high when fresh, 0.5–0.8 cm diam. and 1.5–3.5 cm high when dry; margin revolute or attached to the stipe; hymenium surface undulate-rugose, yellow brown to greyish brown when fresh, light brown or dark brown when dry; receptacle surface white, buff or yellow brown when dry, glabrous; stipe surface sulcate, buff to light brown when dry, 1–3 × 0.15–0.35 cm when dry. Ectal excipulum of textura angularis, cells hyaline, outer cells 17–46.5 × 10.5–29 µm. Medullary excipulum of textura intricata, hyphae hyaline. Asci subcylindrical, tapering at base, eight-spored, 246.5–320 × 13–18.5 µm. Paraphyses filiform to clavate, septate, hyaline to yellow brown, 6–8.5 µm wide at apex and 2.5 µm below. Ascospores ellipsoidal, hyaline, smooth, uniguttulate, 16–21 × 10.5–12.5 µm, Q = 1.6.

Additional specimen examined: China, Yunnan Province, Dali Bai Autonomous Prefecture, Binchuan County, Jizu Mountain, on soil, 8 August 1989, Yu-Chen Zong and Yu Li 176, HMAS 59718.

Notes: This species has close relationships with *H. magna* and *H. yunnanensis* (Figure 1). It differs from *H. magna* in 2 bp for Hsp90, 31 bp for ITS (16 bp in ITS1 and 15 bp in ITS2), 11 bp for LSU, and 3 bp for TEF; and from *H. yunnanensis* in 1 bp for Hsp90, 32 bp for ITS (15 bp in ITS1 and 17 bp in ITS2), 12 bp for LSU, and 2 bp for TEF. Morphologically, the ascumata of this species have a yellower tint than those of its allies.

Helvella liui X.C. Wang & W.Y. Zhuang, sp. nov. Figures 3I, 4F, 4I and 5(23)

Fungal Names: FN571323

Etymology: The specific epithet is named after the distinguished Chinese mycologist Bo Liu (1927.03–2017.07, Shanxi University).

Typification: China, Shanxi Province, Taiyue Mountain National Forest Park, on the ground of forest, 12 August 1985, Fu Du, MHSU 455 = HMAS 85725, holotype.

Apothecia saddle-shaped, stipitate, 0.7 cm diam. and 1 cm high when dry; margin revolute or attached to the stipe; hymenium surface undulate-rugose, orange brown when dry; receptacle surface yellow brown when dry, glabrous; stipe surface sulcate, yellow brown when dry, 0.5 × 0.15 cm when dry. Ectal excipulum of textura angularis, cells hyaline to yellow brown, outer cells 20–33 × 5–10.5 µm. Medullary excipulum of textura intricata, hyphae hyaline. Asci subcylindrical, tapering at base, eight-spored, 266.5–333 × 16–

18.5 μm . Paraphyses filiform, septate, hyaline, 5–6.5 μm wide at apex and 3–4 μm below. Ascospores ellipsoidal, hyaline, smooth, uniguttulate, 17–20 \times 11–13 μm , $Q = 1.5$.

Notes: This species is sister of *H. ravidia* (Figure 1) but differs from the latter in 4 bp for Hsp90 and 16 bp for ITS2. Although both of them have hyaline paraphyses, this species has narrower paraphyses and smaller outer ectal excipular cells than the latter (Table 3).

Helvella lobata X.C. Wang & W.Y. Zhuang, sp. nov. Figures 2Q–R and 5(20)

Fungal Names: FN571324

Etymology: The specific epithet refers to the lobed apothecia of this species.

Typification: China, Jiangsu Province, Nanjing City, Xuanwu District, Zijin Mountain, 32°4'17" N, 118°50'57" E, on soil, 30 May 2021, Ying Hai HaiY01, HMAS 290910, holotype.

Apothecia lobed, stipitate, 0.8 cm diam. and 2.8 cm high when dry; margin revolute or attached to the stipe; hymenium surface undulate-rugose, brown when fresh, dark brown to black when dry; receptacle surface greyish when fresh, whitish or blackish when dry, glabrous; stipe surface sulcate, whitish when fresh, yellow brown to light brown when dry, 2 \times 0.2–0.3 cm when dry. Ectal excipulum of *textura angularis*, cells hyaline to yellow brown, outer cells 24–46.5 \times 8–18.5 μm . Medullary excipulum of *textura intricata*, hyphae hyaline. Asci subcylindrical, tapering at base, eight-spored, 220–320 \times 12–20 μm . Paraphyses filiform, septate, hyaline to yellow brown, 5–6.5 μm wide at apex and 2.5–4 μm below. Ascospores ellipsoidal, hyaline, smooth, uniguttulate, 16–20 \times 12–14.5 μm , $Q = 1.35$.

Notes: This species is a sister of *H. huangii* (Figure 1). Their molecular and morphological distinctions were previously indicated in the notes of the latter.

Helvella magna X.C. Wang & W.Y. Zhuang, sp. nov. Figures 2D–F, 3F, 4E, 4G and 5(11–13)

Fungal Names: FN571326

Etymology: The specific epithet refers to the presence of large-sized ascomata of the species.

Typification: China, Gansu Province, Gannan Tibetan Autonomous Prefecture, Têwo County, Lazikou Town, Lazikou National Forest Park, 34°7'3" N, 103°53'51" E, Alt. 2050 m, on soil, 9 September 1992, Wen-Ying Zhuang and Xiao-Lan Mao 984, HMAS 60679, holotype.

Apothecia saddle-shaped or lobed and sometimes capitate, stipitate, 1.2–9 cm diam. and 3–8 cm high when fresh, 0.5–5 cm diam. and 1.5–6 cm high when dry; margin revolute or attached to the stipe; hymenium surface undulate-rugose, dark grey to black when fresh, greyish white, dirty grey, reddish brown, light brown, dark brown to black when dry; receptacle surface buff, yellow brown or blackish when dry, glabrous; stipe surface sulcate, dirty white, buff, yellow brown, reddish brown, light brown or dark brown when dry, 1–4 \times 0.15–2.4 cm when dry. Ectal excipulum of *textura angularis*, cells hyaline to yellow brown, outer cells 20–88 \times 8–30.5 μm . Medullary excipulum of *textura intricata*, hyphae hyaline. Asci subcylindrical, tapering at base, eight-spored, 280–415 \times 13–20 μm . Paraphyses filiform to clavate, septate, hyaline to yellow brown, 3–13 μm wide at apex and 2.5–6 μm below. Ascospores ellipsoidal to broad ellipsoidal, hyaline, smooth, uniguttulate, 15–22.5 \times 10.5–16 μm , $Q = 1.35$ –1.65.

Additional specimens examined: China, Beijing City, Mentougou District, Qingshui Town, Baihua Mountain National Nature Reserve, 39°49'39" N, 115°35'31" E, Alt. 1400 m, on soil, Wen-Ying Zhuang and Zheng Wang 1215, HMAS 70345; *ibid.*, Dongling Mountain, 40°1'1" N, 115°29'25" E, Alt. 1100 m, on soil, 20 August 1998, Zheng Wang 282, HMAS 75848. Gansu Province, Gannan Tibetan Autonomous Prefecture, Têwo County, Dianga Town, Dalonggou, Alt. 2600 m, on soil, 10 September 1992, Wen-Ying Zhuang and Xiao-Qing Zhang 1005, HMAS 69595; *ibid.*, Lazikou Town, Lazikou National Forest Park, 34°7'3" N, 103°53'51" E, Alt. 2000 m, on the ground of mixed forest, 9 September 1992, Mao-Lin Tian M6470, HMAS 66121; *ibid.*, Zhouqu County, Wuping Town, Shatan Forest Farm, 33°41'48" N, 104°10'14" E, Alt. 2400 m, on soil, 3 September 1992, Wen-Ying Zhuang

and Xiao-Qing Zhang 937, HMAS 69594; Longnan City, Huixian County, on soil, September 1992, Mao-Lin Tian M6510, HMAS 61724. Tibet, Nyingchi City, Mainling County, Wolong Town, 29°7'45" N, 93°41'59" E, on soil, 14 September 2016, Xin-Cun Wang et al. 10861, HMAS 290911; *ibid.*, 10864, HMAS 290912. Yunnan Province, Kunming City, Panlong District, Yeya Lake, 25°7'22" N, 102°51'36" E, on soil, 25 September 2017, Huan-Di Zheng et al. 11790, HMAS 290913.

Notes: This fungus is relatively common in China. Morphological variations were observed within species: some collections (HMAS 60679, 61724, and 66121) have large, rugose, and capitate apothecia and coarse and sulcate stipes, whereas others possess smaller non-capitate apothecia with somewhat slenderer stipes. It has close relationships with *H. jizushanica* and *H. yunnanensis* (Figure 1) but differs from *H. jizushanica* in 2 bp for Hsp90, 31 bp for ITS (16 bp in ITS1 and 15 bp in ITS2), 11 bp for LSU, and 3 bp for TEF; it differs from *H. yunnanensis* in 1 bp for Hsp90, 12 bp for ITS (7 bp in ITS1 and 5 bp in ITS2), 3 bp for LSU, and 1 bp for TEF. Collections having large capitate apothecia are easily distinguished from related species.

Helvella parva X.C. Wang & W.Y. Zhuang, sp. nov. Figures 2M, 3E, 4A and 5(10)

Fungal Names: FN571327

Etymology: The specific epithet refers to the small-sized ascomata of the species.

Typification: China, Yunnan Province, Dali Bai Autonomous Prefecture, Binchuan County, Jizu Mountain, 25°57'27" N, 100°23'34" E, on soil, 20 September 2017, Xin-Cun Wang et al. 11559, HMAS 290914, holotype.

Apothecia saddle-shaped or discoid, stipitate, 0.8–1 cm diam. and 2 cm high when fresh, 0.5 cm diam. and 1.1–1.2 cm high when dry; margin revolute or attached to the stipe; hymenium surface undulate-rugose, greyish when fresh, light brown to dark brown when dry; receptacle surface buff when dry, glabrous; stipe surface sulcate, greyish white when fresh, buff to light brown when dry, 0.8 × 0.1–0.2 cm when dry. Ectal excipulum of textura angularis, cells hyaline, outer cells 20–53 × 6.5–20 µm. Medullary excipulum of textura intricata, hyphae hyaline. Asci subcylindrical, tapering at base, eight-spored, 226.5–266.5 × 13–17 µm. Paraphyses filiform, septate, hyaline to yellow brown, 6.5 µm wide at apex and 3.5–4 µm below. Ascospores ellipsoidal, hyaline, smooth, uniguttulate, 17–18.5 × 10.5–12 µm, Q = 1.6.

Notes: This species was a sister to *H. fulva* (Figure 1). Their molecular and morphological differences were previously indicated in the notes of the latter.

Helvella phlebophoropsis X.C. Wang & W.Y. Zhuang, sp. nov. Figures 3J and 5(24–25)

Fungal Names: FN571328

Etymology: The specific epithet refers to its morphological similarity and phylogenetically close relationship with *H. phlebophora*.

Typification: China, Shanxi Province, Taiyue Mountain National Forest Park, 12 August 1985 Fu Du, MHSU 453 = HMAS 85654, holotype.

Apothecia discoid, stipitate, 0.5–1.2 cm diam. and 0.7–1.5 cm high when dry; margin revolute, attached to the stipe or not; hymenium surface undulate-rugose, dark brown to black when dry; receptacle surface dark brown to black when dry, glabrous; stipe surface ribbed, yellow brown to light brown when dry, 0.4–1.1 × 0.15–0.4 cm when dry. Ectal excipulum of textura angularis, cells hyaline to yellow brown, outer cells 24–42.5 × 5–12 µm. Medullary excipulum of textura intricata, hyphae hyaline. Asci subcylindrical, tapering at base, eight-spored, 240–280 × 13–20 µm. Paraphyses filiform, septate, hyaline to yellow brown, 4–8 µm wide at apex and 2.5–4 µm below. Ascospores ellipsoidal, hyaline, smooth, uniguttulate, 14.5–21 × 10.5–13 µm, Q = 1.5–1.6.

Additional specimen examined: China, Gansu Province, Tianshui City, Maiji District, Dongcha Town, Baiyanglin, 34°20'26" N, 106°31'0" E, on soil, 4 August 1958, Yu-Chuan Yang, 469, HMAS 30757.

Notes: It is a sister of *H. phlebophora* (Figure 1) but differs in 2 bp for Hsp90 and 2 bp for ITS2. Morphologically, it has wider asci (13–20 µm wide vs. 12–14 µm [3] or 12–15 µm

[4] wide) and larger ascospores ($14.5\text{--}21 \times 10.5\text{--}13 \mu\text{m}$ vs. $15\text{--}16 \times 9\text{--}10 \mu\text{m}$ [3] or $16\text{--}17.5 \times 11\text{--}12 \mu\text{m}$ [4]) than the latter.

Helvella plateata X.C. Wang & W.Y. Zhuang, sp. nov. Figures 2G–I, 3K and 5(26–28)

Fungal Names: FN571329

Etymology: The specific epithet refers to its location in the Qinghai–Tibet Plateau.

Typification: China, Tibet, Nyingchi City, Bayi District, Lulang Town, $29^{\circ}45'57''$ N, $94^{\circ}44'28''$ E, Alt. 3325 m, on rotten wood, 11 August 2013, Tie-Zheng Wei et al. 3655, HMAS 270642, holotype.

Apothecia saddle-shaped or lobed, stipitate, 0.8–2.7 cm diam. and 2.7–5 cm high when fresh, 0.4–1.6 cm diam. and 1.7–3.6 cm high when dry; margin revolute or attached to the stipe; hymenium surface undulate-rugose, light brown to black when fresh, dark brown to black when dry; receptacle surface light brown when dry, glabrous; stipe surface sulcate, light brown or dark brown when dry, $1.4\text{--}2.7 \times 0.15\text{--}0.8$ cm when dry. Ectal excipulum of *textura angularis*, cells hyaline to light brown, outer cells $18.5\text{--}60 \times 6.5\text{--}24 \mu\text{m}$. Medullary excipulum of *textura intricata*, hyphae hyaline. Asci subcylindrical, tapering at base, eight-spored, $206.5\text{--}426.5 \times 13\text{--}20 \mu\text{m}$. Paraphyses filiform to clavate, septate, hyaline to light brown, 4–10.5 μm wide at apex and 2.5–5 μm below. Ascospores narrow ellipsoidal, hyaline, smooth, uniguttulate, $16\text{--}23 \times 9\text{--}13 \mu\text{m}$, $Q = 1.7\text{--}1.75$.

Additional specimens examined: China, Sichuan Province, Garzê Tibetan Autonomous Prefecture, Batang County, Zhubalong Nature Reserve, $29^{\circ}38'20''$ N, $99^{\circ}7'57''$ E, Alt. 4274m, on soil, 18 August 2020, Xin-Yu Zhu and Ming-Zhe Zhang ZRL20201123, HMAS 290918. Tibet, Nyingchi City, Bayi District, Lulang Town, $29^{\circ}46'3''$ N, $94^{\circ}44'3''$ E, on soil, 23 September 2016, Xin-Cun Wang et al. 11229, HMAS 290916. Yunnan Province, Dali Bai Autonomous Prefecture, Binchuan County, Jizu Mountain, $25^{\circ}57'46''$ N, $100^{\circ}22'41''$ E, on soil, 21 September 2017, Xin-Cun Wang et al. 11595, HMAS 290917.

Notes: This species is a sister of *H. austrooccidentalis* and *H. cystidiata* (Figure 1). It differs from *H. cystidiata* in 2 bp for Hsp90, 61 bp for ITS (47 bp in ITS1, 2 bp in 5.8S, and 12 bp in ITS2), 2 bp for LSU, and 3 bp for TEF. The molecular distinction between *H. plateata* and *H. austrooccidentalis* was discussed in the notes of the latter. This species possesses very narrow ascospores compared with the others (Table 3).

Helvella ravidia X.C. Wang & W.Y. Zhuang, sp. nov. Figures 2N,O, 3H and 5(17–18)

Fungal Names: FN571330

Etymology: The specific epithet refers to color of the apothecia of this species.

Typification: China, Sichuan Province, Ngawa Tibetan and Qiang Autonomous Prefecture, Li County, Miyaluo Town, Jiabigou, $31^{\circ}37'32''$ N, $102^{\circ}50'23''$ E, Alt. 2850 m, on the ground of *Picea* sp. forest, 10 August 2016, Xin-Cun Wang 10682, HMAS 290919, holotype.

Apothecia saddle-shaped or lobed, stipitate, 1.2–2.1 cm diam. and 2.2–4.5 cm high when dry; margin revolute or attached to the stipe; hymenium surface undulate-rugose, greyish white to light grey when fresh, yellow brown, orange brown or dark brown when dry; receptacle surface yellow brown, light brown or dark brown when dry, glabrous; stipe sulcate, buff, yellow brown to light brown when dry, $1.5\text{--}3.5 \times 0.2\text{--}0.8$ cm when dry. Ectal excipulum of *textura angularis*, cells hyaline to yellow brown, outer cells $17\text{--}57 \times 8\text{--}25 \mu\text{m}$. Medullary excipulum of *textura intricata*, hyphae hyaline. Asci subcylindrical, tapering at base, eight-spored, $240\text{--}333 \times 14.5\text{--}24 \mu\text{m}$. Paraphyses filiform to clavate, septate, hyaline to yellow brown, 8–13 μm wide at apex and 4–4.5 μm below. Ascospores ellipsoidal, hyaline, smooth, uniguttulate, $16\text{--}20 \times 10.5\text{--}13 \mu\text{m}$, $Q = 1.5$.

Additional specimen examined: China, Hebei Province, Zhangjiakou City, Xiaowutai Mountain National Nature Reserve, Xitai, $39^{\circ}54'49''$ N, $114^{\circ}58'4''$ E, on soil, 29 August 1990, Hua-An Wen and Bin Li 273, HMAS 61920.

Notes: This species is a sister of *H. liui* (Figure 1). Their molecular and morphological distinctions were indicated in the notes of the latter.

Helvella varia X.C. Wang & W.Y. Zhuang, sp. nov. Figures 2J–L, 3A, 4B,C and 5(1–4)

Fungal Names: FN571331

Etymology: The specific epithet refers to the varied color of the apothecia of this species.

Typification: China, Guangdong Province, Shaoguan City, Ruyuan Yao Autonomous County, Nanling National Nature Reserve, Xiaohuangshan, 24°53'47" N, 113°1'8" E, Alt. 1350 m, on the ground of broad-leaved forest, 15 June 2014, Tie-Zheng Wei 3914, HMAS 270932, holotype.

Apothecia saddle-shaped or irregularly lobed, stipitate, 0.3–2.3 cm diam. and 0.8–6 cm high when dry; margin revolute or attached to the stipe; hymenium surface undulate-rugose, white to blackish when fresh, yellow brown to black when dry; receptacle surface buff to dark brown when dry, glabrous; stipe surface sulcate, buff to light brown when dry, 0.5–4.5 × 0.15–0.65 cm when dry. Ectal excipulum of textura angularis, cells hyaline to light brown, outer cells 14.5–46.5 × 9–21.5 μm. Medullary excipulum of textura intricata, hyphae hyaline. Asci subcylindrical, tapering at base, eight-spored, 195–305 × 13.5–22.5 μm. Paraphyses filiform, septate, hyaline to yellow brown, 4.5–8 μm wide at apex and 2.5–5 μm below. Ascospores ellipsoidal, hyaline, smooth, uniguttulate, 14.5–20 × 9.5–14.5 μm, Q = 1.25–1.6.

Additional specimens examined: China, Guangdong Province, Shaoguan City, Ruyuan Yao Autonomous County, Nanling National Nature Reserve, Xiaohuangshan, 24°53'47" N, 113°1'8" E, Alt. 1350 m, on the ground of broad-leaved forest, 15 June 2014, Tie-Zheng Wei 3917, HMAS 270958. Guizhou Province, Bijie City, Nayong County, Zuojiuga Yi and Miao Ethnic Town, 26°49'52" N, 105°3'21" E, on the ground of forest, 27 June 2018, Xing-Liang Wu 345, HMAS 290929. Yunnan Province, Kunming City, Anning City, Wenquan Town, Qiumuyuan, 24°59'7" N, 102°26'58" E, 20 July 1973, Qi-Ming Ma et al. 411, HMAS 186052; Honghe Hani and Yi Autonomous Prefecture, Pingbian Miao Autonomous County, Dawei Mountain National Nature Reserve, Shuiweicheng, 22°56'30" N, 103°41'44" E, Alt. 2100 m, 18 July 2005, Tie-Zheng Wei et al. 730, HMAS 131945. Zhejiang Province, Lishui City, Jingning She Autonomous County, Wangdongyang Nature Reserve, 27°42'32" N, 119°36'59" E, 4 June 2015, Mao-Qiang He ZRL20150069, HMAS 290930; *ibid.*, Yujikeng, 27°41'16" N, 119°34'11" E, 7 September 2019, Xin-Yu Zhu and Jia-Xin Li ZRL20191640, HMAS 290931.

Notes: This species was closely related to *H. vulgata* in all phylogenetic trees (Figures 1 and S1–S4). It differs from the latter in 5 bp for Hsp90, 90 bp for ITS (73 bp in ITS1 and 17 bp in ITS2), 2 bp for LSU, and 3 bp for TEF. Morphological distinctions between them were hardly found (Table 3).

Helvella vitrea X.C. Wang & W.Y. Zhuang, sp. nov. Figures 3L and 5(30)

Fungal Names: FN571332

Etymology: The specific epithet refers to the semitransparent apothecia of this species.

Typification: China, Jiangsu Province, Nanjing City, Xuanwu District, Zijin Mountain, 32°4'17" N, 118°50'57" E, on soil, 29 May 2021, Zi-Han Zhang ZhangZH02, HMAS 290932, holotype.

Apothecia lobed, stipitate, 1–3.2 cm diam. And 1.8–4 cm high when dry; margin revolute or attached to the stipe; hymenium surface undulate-rugose, reddish brown to dark brown when dry; receptacle surface the same color with hymenium when dry; stipe surface sulcate, buff to yellow brown when dry, 1.6–3 × 0.25–1.8 cm when dry. Ectal excipulum not seen. Medullary excipulum of textura intricata, hyphae hyaline. Asci subcylindrical, tapering at base, eight-spored, 293–360 × 16–21 μm. Paraphyses filiform, septate, hyaline, 5–8 μm wide at apex and 2.5–4.5 μm below. Ascospores broad ellipsoidal, hyaline, smooth, uniguttulate, 14.5–18.5 × 12–14 μm, Q = 1.25.

Notes: The fungus formed a distinct lineage and was closely related to *H. huangii*, *H. parva*, *H. fulva*, *H. lobata*, *H. phlebophora*, and *H. phlebophoropsis* (Figure 1). Divergences in the molecular data were distinct enough to separate them at species level. It has much wider ascospores than related fungi (Table 3).

Helvella vulgata X.C. Wang & W.Y. Zhuang, sp. nov. Figures 3G and 5(14–15)

Fungal Names: FN571333

Etymology: The specific epithet refers to its common gross morphology shared with other *Helvella* species of this clade.

Typification: China, Hubei Province, Shennongjia Forestry District, Motianling, 31°30'55" N, 110°35'1" E, on the ground of broad-leaved forest, 26 August 1984, Jin-Xiu Tian 193, HMAS 53683, holotype.

Apothecia saddle-shaped, stipitate, 3 cm high when fresh, 0.4–1.1 cm diam. and 0.75–2.4 cm high when dry; margin revolute or attached to the stipe; hymenium surface undulate-rugose, yellow brown, orange brown, reddish brown, dark brown to black when dry; receptacle surface buff to yellow brown when dry, glabrous; stipe surface sulcate, buff, yellow brown to light brown when dry, 0.6–2 × 0.15–0.4 cm when dry. Ectal excipulum of textura angularis, cells hyaline to yellow brown, outer cells 17–37 × 6.5–17 µm. Medullary excipulum of textura intricata, hyphae hyaline. Asci subcylindrical, tapering at base, eight-spored, 240–306.5 × 12–17 µm. Paraphyses filiform, septate, hyaline to yellow brown, 4–6.5 µm wide at apex and 2.5–4 µm below. Ascospores ellipsoidal, hyaline, smooth, uniguttulate, 15–20 × 10.5–12 µm, Q = 1.55–1.6.

Additional specimens examined: China, Jilin Province, Changbai Mountain National Nature Reserve, on soil, 2 August 2008, Tai-Hui Li, HMIGD 25964; Yanbian Korean Autonomous Prefecture, Dunhua City, Dashitou Town, Alt. 670 m, on rotten wood in forest of *Quercus mongolica*, 15 September 1987, Jin-Zhong Cao 769, HMAS 85589.

Notes: This species was a sister of *H. varia* (Figure 1). Molecular differences were shown in the notes of the latter.

Helvella yunnanensis X.C. Wang & W.Y. Zhuang, sp. nov. Figures 2T,U and 5(29)

Fungal Names: FN571334

Etymology: The specific epithet refers to the type's locality.

Typification: China, Yunnan Province, Kunming City, Panlong District, Yeya Lake, 25°7'22" N, 102°51'36" E, on soil, 25 September 2017, Huan-Di Zheng et al. 11785, HMAS 290933, holotype.

Apothecia saddle-shaped or lobed, stipitate, 1–2 cm diam. and 4–4.5 cm high when fresh, 0.4–0.9 cm diam. and 2.1–2.7 cm high when dry; margin revolute or attached to the stipe; hymenium surface undulate-rugose, light brown to dark brown when fresh, dark brown to black when dry; receptacle surface whitish or light brown when dry, glabrous; stipe surface sulcate, yellow brown to light brown when dry, 2–2.2 × 0.1–0.4 cm when dry. Ectal excipulum of textura angularis, cells hyaline, outer cells 16–36 × 6.5–16 µm. Medullary excipulum of textura intricata, hyphae hyaline. Asci subcylindrical, tapering at base, eight-spored, 280–320 × 13–20 µm. Paraphyses filiform, septate, hyaline to yellow brown, 5–8 µm wide at apex and 2.5–3 µm below. Ascospores ellipsoidal, hyaline, smooth, uniguttulate, 16–20 × 10.5–13 µm, Q = 1.5.

Additional specimen examined: China, Yunnan Province, Kunming City, Panlong District, Yeya Lake, 25°7'22" N, 102°51'36" E, on soil, 25 September 2017, Huan-Di Zheng et al. 11789, HMAS 290934.

Notes: This species has close relationships with *H. jizushanica* and *H. magna* (Figure 1), and molecular differences among them were discussed in the notes of the latter two fungi.

3.2.2. New Chinese Records

Helvella palustris Peck, Ann. Rep. N.Y. St. Mus. Nat. Hist. 33: 31, 1883.

Specimen examined: China, Jilin Province, Yanbian Korean Autonomous Prefecture, Antu County, Changbai Mountain National Nature Reserve, Alt. 1500 m, on rotten wood, 25 August 1960, Yu-Chuan Yang et al. 986, HMAS 30755.

Notes: *Helvella palustris* was originally described from New York, USA [4], and also reported from Norway, Finland, and Japan [20]. The Chinese collection is identical to the European material in the sequence of Hsp90.

Helvella terricola Skrede & T. Schumach., Fungal Syst. Evol. 6: 91, 2020.

Specimen examined: China, Xinjiang Uygur Autonomous Region, Aksu Prefecture, Wensu County, Tuomuer Peak National Nature Reserve, Tailan River Valley, Alt. 2600 m, on the ground of forest, 24 July 1977, Hua-An Wen and Xiao-Lan Mao 158, HMAS 38355.

Notes: *Helvella terricola* was known only from Spain [22]. The Chinese collection extends its distribution to Asia. The Chinese collection is identical with the holotype in the sequence of Hsp90.



Figure 2. Photographs of fresh apothecia of *Helvella* species. (A–C) *H. austrooccidentalis*: (A) 11223 (holotype); (B) 11220; (C) ZRL20200655. (D–F) *H. magna*: (D,E) 10864; (F) 11790. (G–I) *H. plateata*: (G) 11229; (H) 11595; (I) ZRL20201123. (J–L) *H. varia*: (J) Wu345; (K) ZRL20150069; (L) ZRL20191640.

(M) *H. parva* 11559 (holotype). (N,O) *H. ravidata* 10682 (holotype). (P) *H. jizushanica* 11567 (holotype). (Q,R) *H. lobata* HaiY01 (holotype). (S) *H. fulva* 10867 (holotype). (T,U) *H. yunnanensis*: (T) 11785 (holotype); (U) 11789. Bars: (B,N) = 3 cm; (A) = 2.5 cm; (H,K,L,O,P,S,T,U) = 2 cm; (I) = 1.75 cm; (C,F,G,J) = 1.5 cm; (Q,R) = 1.2 cm; (D,E) = 1 cm; (M) = 0.75 cm.



Figure 3. Photographs of dried apothecia of *Helvella* species. (A) *H. varia* HMAS 270932 (holotype). (B) *H. cystidiata* HMAS 275836. (C) *H. huangii* HMAS 45031 (holotype). (D) *H. borealis* 3568 (holotype). (E) *H. parva* 11559 (holotype). (F) *H. magna* HMAS 60679 (holotype). (G) *H. vulgata* HMAS 53683 (holotype). (H) *H. ravidata* 10682 (holotype). (I) *H. liui* HMAS 85725 (holotype). (J) *H. phlebo-
phoropsis* HMAS 85654 (holotype). (K) *H. plateata* HMAS 270642 (holotype). (L) *H. vitrea* ZhangZH02 (holotype). Bars: (F) = 3 cm; (B,D) = 1.5 cm; (C,H,K,L) = 1.2 cm; (A,E,G) = 1 cm; (I,J) = 0.7 cm.

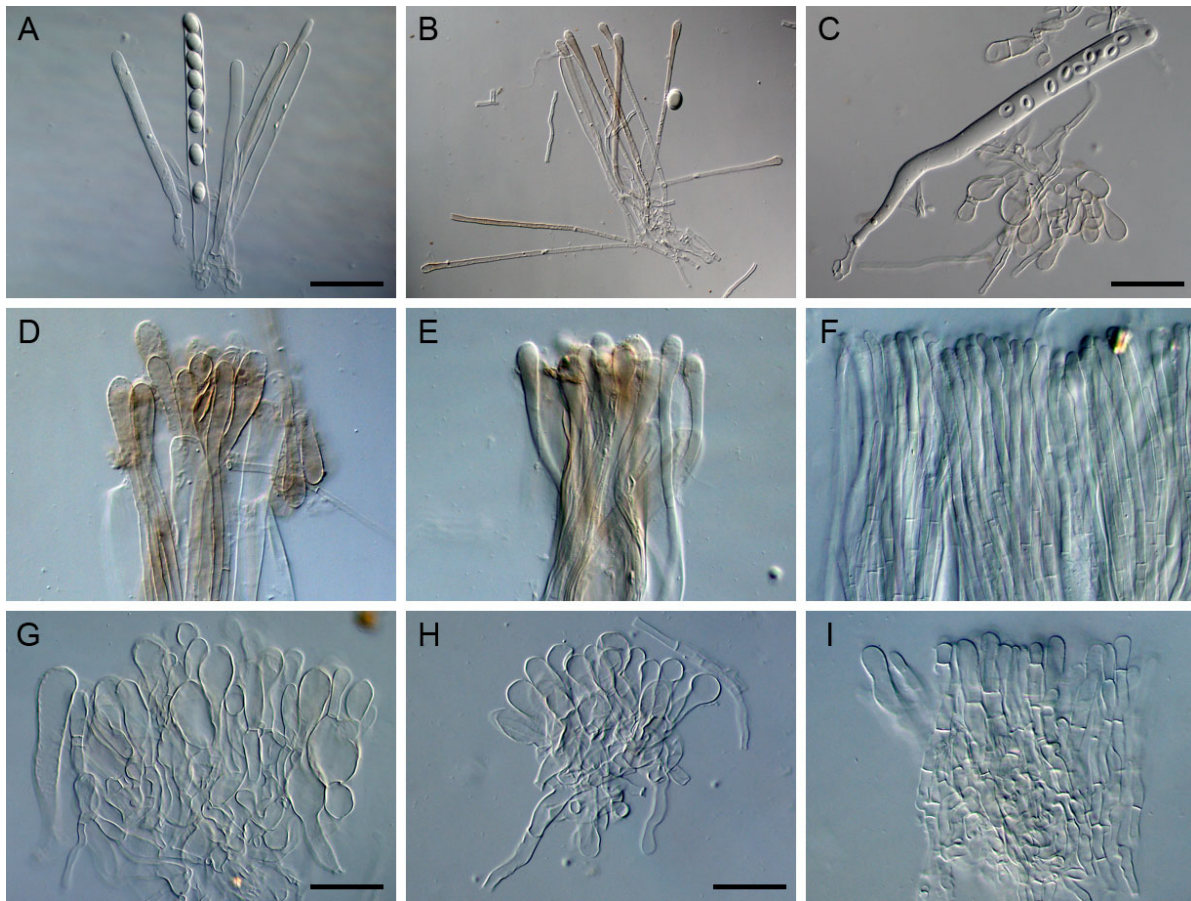


Figure 4. Microscopic characteristics of *Helvella* species. (A–C) Asci and paraphyses [(A) *H. parva* 11559 (holotype); (B–C) *H. varia* HMAS 131945]. (D–F) Paraphyses [(D) *H. austrooccidentalis* 11223 (holotype); (E) *H. magna* HMAS 60679 (holotype); (F) *H. liui* HMAS 85725 (holotype)]. (G–I) Outer cells of ectal excipulum [(G) *H. magna* 10861; (H) *H. fulva* 10867 (holotype); (I) *H. liui* HMAS 85725 (holotype)]. Bars: (A) = 60 μm , applied to (B); (C) = 45 μm ; (G) = 40 μm ; (H) = 30 μm , applied to (D–F) and (I).

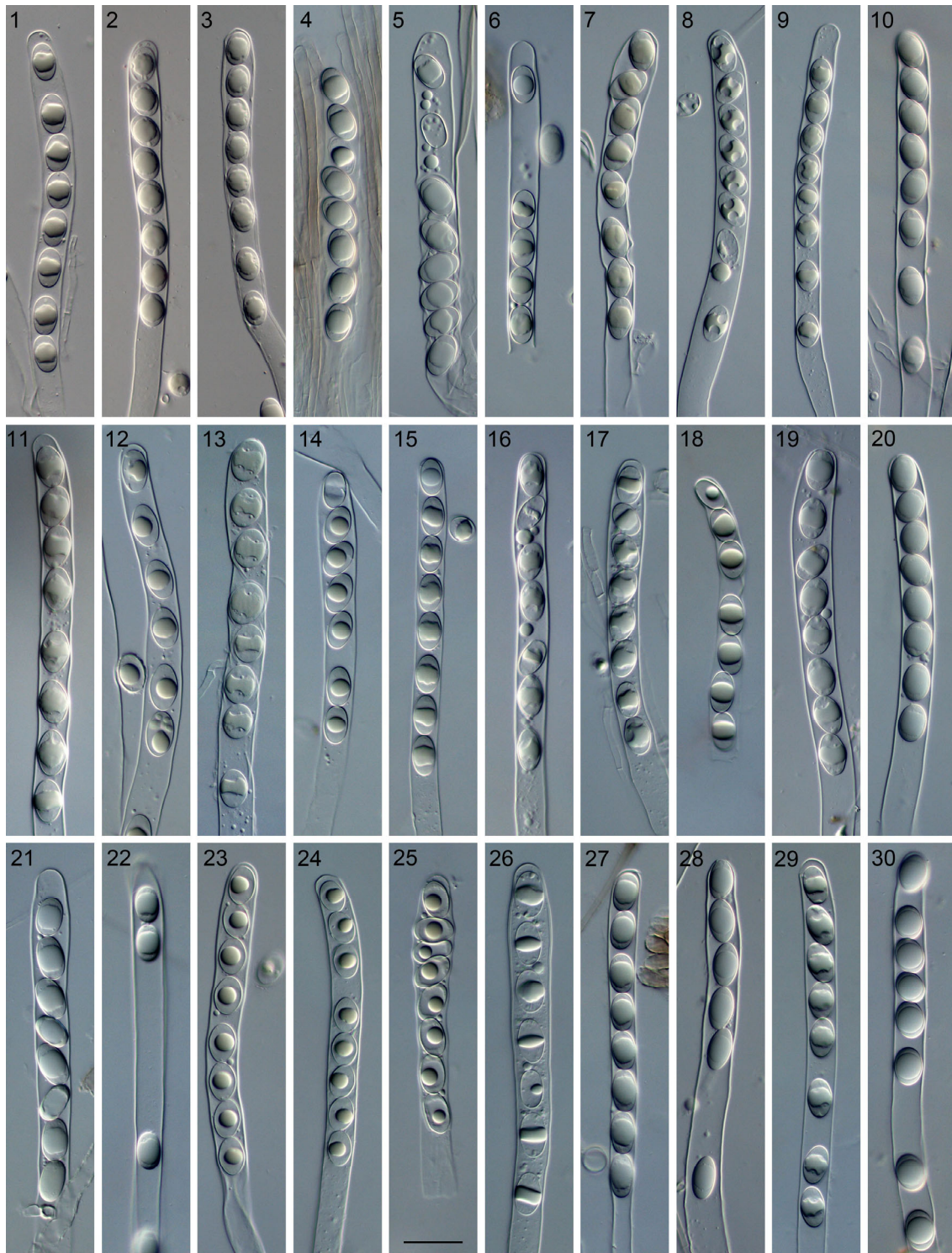


Figure 5. Ascospores in asci of *Helvella* species. From left to right in the top row: (1) *Helvella varia* HMAS 131945; (2) *H. varia* HMAS 270932 (holotype); (3) *H. varia* Wu 345; (4) *H. varia* ZRL20150069; (5) *H. cystidiata* HMAS 275836; (6) *H. cystidiata* HMJAU 150; (7) *H. huangii* HMAS 45031 (holotype); (8) *H. huangii* CFSZ 2652; (9) *H. borealis* 3568 (holotype); (10) *H. parva* 11559 (holotype); from left to right in the middle row: (11) *H. magna* 10861; (12) *H. magna* HMAS 60679 (holotype); (13) *H. magna* HMAS 70345; (14) *H. vulgata* HMAS 53683 (holotype); (15) *H. vulgata* HMIGD 25964; (16) *H. jizushanica* 11567 (holotype); (17) *H. ravida* 10682 (holotype); (18) *H. ravida* HMAS 61920; (19) *H. fulva* 10867

(holotype); (20) *H. lobata* HaiY01 (holotype); from left to right in the bottom row: (21) *H. austrooccidentalis* 11223 (holotype); (22) *H. austrooccidentalis* ZRL20200655; (23) *H. liui* HMAS 85725 (holotype); (24) *H. phlebophoropsis* HMAS 85654 (holotype); (25) *H. phlebophoropsis* HMAS 30757; (26) *H. plateata* HMAS 270642 (holotype); (27) *H. plateata* 11595; (28) *H. plateata* ZRL20201123; (29) *H. yunnanensis* 11785 (holotype); (30) *H. vitrea* ZhangZH02 (holotype). Bar = 30 µm, applied to all the figures.

4. Discussion

A total of 101 specimens from four Chinese fungaria (HMAS, HMIGD, HMJAU, and CFSZ) and recent collections from 10 provinces (Beijing, Fujian, Guizhou, Jiangsu, Jilin, Shanxi, Sichuan, Tibet, Yunnan, and Zhejiang) were molecularly and morphologically examined in this study. Four loci were investigated, and 311 sequences were newly generated, including 101 for Hsp90, 82 for ITS, 69 for LSU, and 59 for TEF. A four-locus phylogeny of *Helvella lacunosa* clade was reconstructed, and 46 lineages were revealed in the tree. All these species occur in the Northern Hemisphere, and 25 of them are discovered in China. Nine species were previously known: *H. atra*, *H. cystidiata*, *H. lacunosa*, *H. palustris*, *H. philonotis*, *H. phlebophora*, *H. rugosa*, *H. sublactea*, and *H. terricola*, while 16 species were determined as new to science and described and illustrated. Two new Chinese records, *H. palustris* and *H. terricola*, were also noted.

Helvella rugosa appears to be the most common species (17 specimens) of this clade in China with the widest distribution in the northeast, south, and southwest of the country (Table 1). The collections of the fungus formed a monophyletic clade in the phylogenies of ITS, LSU, and TEF. However, they were shown as polyphyletic in the Hsp90 tree and divided into four small groups (Figure S1). Although different intra-specific clustering of the examined collections existed in the phylogenies (Figures S1–4), according to Genealogical Concordance Phylogenetic Species Recognition (GCPSR) [51], all of them should belong to the same species. Specimens from the same locality tended to cluster together (Figure 1), which might give the hint that they may be undergoing speciation. This might involve some underlying mechanism, e.g., incomplete lineage sorting.

Intra-specific variations in macro- and micro-morphology have been observed. For example, one specimen (Wu345) of *H. varia* has whitish apothecia when fresh (Figure 2J), while the others (ZRL20150069 and ZRL20191640) are brown to nearly black (Figure 2K,L), which might be influenced by fruitbody age, the ecological niches of a collection, as well as the degree of exposure to light. The collections of *H. magna* also exhibited apothecial color variations (Figure 2D–F). Additionally, apothecial size is also variable within individual species: some collections (HMAS 60679, HMAS 61724, and HMAS 66121, all from Gansu Province) of *H. magna* possess large apothecia (up to 5–6 cm high when dry) and inflated stipes (up to 1.7–2.4 cm diam. when dry, Figure 3F), whereas the others have smaller apothecia (usually less than 2 cm high when dry) and thinner stipes (no more than 0.5 cm diam. when dry); nutrition or texture of the substrates might end up with size changes of apothecia. Microscopically, different lengths of asci were found in *H. austrooccidentalis*, *H. magna*, and *H. varia* (Table 3); the width of the paraphysis apices among collections varied in *H. austrooccidentalis*, *H. cystidiata*, *H. magna*, and *H. plateata*; the color of paraphyses varied in *H. varia* and *H. vulgata*; and variations of the shape of ascospores can be seen in *H. magna* and *H. varia* (Figure 5 and Table 3). These noticeable morphological differences make identifications solely based on morphology unreliable.

Our understanding of the *Helvella lacunosa* clade in China is significantly renewed through this work. *Helvella pseudolacunosa* was proved to be a later synonym of *H. lacunosa* (Figures S2 and S3). Additionally, the previous records of *H. fusca*, *H. helvellula*, *H. lactea*, and *H. sulcata* in China were based on misidentifications and should be excluded from Chinese fungus flora. The unexpectedly high biodiversity of the lacunosa clade suggests that species diversity of macrofungi in Pezizales may have been underestimated. Further large-scale investigations are desperately needed to examine unexplored pezizalean fungi.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/jof9070697/s1>, Figure S1: Maximum-likelihood phylogenetic tree of *Helvella lacunosa* clade inferred from combined Hsp90 dataset. Bootstrap values $\geq 70\%$ (left) are indicated at nodes. Asterisk denotes 100% bootstrap; Figure S2: Maximum-likelihood phylogenetic tree of *Helvella lacunosa* clade inferred from combined ITS dataset. Bootstrap values $\geq 70\%$ (left) are indicated at nodes. Asterisk denotes 100% bootstrap; Figure S3: Maximum-likelihood phylogenetic tree of *Helvella lacunosa* clade inferred from combined LSU dataset. Bootstrap values $\geq 70\%$ (left) are indicated at nodes. Asterisk denotes 100% bootstrap; Figure S4: Maximum-likelihood phylogenetic tree of *Helvella lacunosa* clade inferred from combined TEF1 dataset. Bootstrap values $\geq 70\%$ (left) are indicated at nodes. Asterisk denotes 100% bootstrap.

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