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Morpho-molecular characterization reveals a novel macrofungus, *Helvella griseofuscostipitata* (Helvellaceae, Pezizales), from southwest China

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Abstract

Helvella is the most specious and morphologically prominent genus in Helvellaceae (Pezizales, Pezizomycetes). In our investigations of macroscopic ascomycetes in southwestern China, a novel species *H. griseofuscostipitata* is discovered on the ground covered with fallen pine-needles in a forest farm. *Helvella* species are characterized by white, cream, grey to black, saddle- or cup-shaped, or irregularly lobed apothecia attached to distinct terete stipes with or without longitudinal ribs, ellipsoid or subfusoid ascospores with a large central oil drop. The key morphology of our species consistent with the generic concept of *Helvella*. However, it can be differentiated from its phylogenetically close relatives (*H. orentitomentosa*, *H. suborentitomentosa*, and *H. kunmingensis*) by having mostly bi- to tri-lobate mature apothecia, yellowish gray to brownish gray fresh hymenia, subpubescent stipes (gray to dark brownish gray), an ectal excipulum with both *textura globulosa* and *textura angularis* cells, and finely verrucose younger ascospores. The placement of *H. griseofuscostipitata* as a distinct species, is confirmed based on macro- and micro- morphological characterization and multi-locus phylogeny of a concatenated ITS-LSU-*hsp*90 sequence dataset in Helvellaceae, with maximum likelihood and Bayesian inference analyses. The detailed morphological illustrations, comprehensive morphological description including the phylogenetic relationships of other *Helvella* species also provided.

Key words: 1 new species, *Ascomycota*, macrofungi, morphology, phylogeny

Introduction

Fungi, one of the largest eukaryotic kingdoms, are widely distributed across the biosphere on Earth. In a recent assessment, Niskanen *et al.* (2023) proposed a best estimate of the global fungal number to be approximately 2.5 million, within a range of 1.5 to 3.2 million. *Ascomycota* is the most diverse fungal phylum, comprising over 92,700 extant species (Bánki *et al.* 2022, Wanasinghe *et al.* 2022). It represents the majority of microscopic species as well as macroscopic species such as cup or disc fungi and truffles.

Helvellaceae (Pezizales, Pezizomycetes) is an important family of macrofungal ascomycetes, notable for producing macroscopic, epigeous or hypogeous fruiting bodies. This family was established by Fries (1822) and *Helvella* L. was designated as the type genus. Currently, the family comprises six genera viz., *Balsamia* Vittad., *Dissingia* K. Hansen, X.H. Wang & T. Schumach., *Helvella*, *Midotis* Fr., *Pindara* Velen., and *Underwoodia* Peck (Hansen *et al.* 2019, Yu *et al.* 2023, Hyde *et al.* 2024).

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Helvella is the most specious and morphologically prominent genus in Helvellaceae, comprising over 150 species (Hyde *et al.* 2024, Park *et al.* 2025, Index Fungorum 2026). Generally, these species are referred to as elfin saddles or false morels (Akata & Kaya 2012, Talie *et al.* 2021, Yu *et al.* 2023, Choudhary *et al.* 2024, Park *et al.* 2025). *Helvella* was established by Linnaeus (1753) and it was typified by *H. crispa* (Scop.) Fr. 1822 (Fries 1822). The key morphology of this genus is having white, cream, grey to black, saddle- or cup-shaped, or irregularly folded (lobed) apothecia attached to distinct terete stipes with or without longitudinal ribs, ellipsoid or subfusoid ascospores (in the *H. macropus* complex), and ascospores with a large central oil drop (Skrede *et al.* 2017, Lu *et al.* 2023, Mao *et al.* 2023, Wang *et al.* 2023, Li *et al.* 2025, Park *et al.* 2025, Ullah *et al.* 2025). Initially, *Helvella* was identified based on the species that only exhibited stipitate-capitate (saddle-shaped) apothecia, and subsequent studies revealed that the genus consists of stipitate-cupulate apothecia within *Helvella sensu lato* (Nannfeldt 1937, Dissing 1966, Løken *et al.* 2020). In historical taxonomic studies of *Helvella*, species delineations have been based solely on morphological characterization as in other fungal studies (Wang *et al.* 2023). Both macro- and micro- morphological characteristics such as the shape and color of ascomata (capitate or cupulate apothecia), color of the hymenium and stipe including micro-structures and pigmentations of ectal excipulum tissues, presence of pubescence on the receptacle surface, development of asci, as well as the shape, size and ornamentation of ascospores, and the nature of paraphyses have been employed for species delimitation (Landeros *et al.* 2012, Li *et al.* 2025, Park *et al.* 2025). However, some *Helvella* species share similar morphological characteristics (cryptic species) and are reported to have distant phylogenetic placements due to convergent evolution (Mao et al 2023, Park *et al.* 2025). Therefore, in the recent decade, taxonomic studies of *Helvella* species have increasingly integrated morphology, multi-gene phylogeny and ecological data to determine their taxonomic placements with high accuracy (Zhao *et al.* 2015, Skrede *et al.* 2017, Hansen *et al.* 2019, Bao *et al.* 2023, Mao *et al.* 2023, Wang *et al.* 2023, Yu *et al.* 2023, Li *et al.* 2025, Park *et al.* 2025).

Helvella species have a wide distribution on the grounds of both deciduous and coniferous forests and mossy and grassy terrains in terrestrial ecosystems in northern and the southern hemispheres (Dissing 1979, Landeros *et al.* 2012, Skrede *et al.* 2017, Bao *et al.* 2023, Mao *et al.* 2023, Choudhary *et al.* 2024, Li *et al.* 2025, Park *et al.* 2025). Ecologically, some *Helvella* species have been reported to form ectomycorrhizal relationships (ECM) such as *H. aff. cupuliformis*, *H. crispa, H. cf. crispa*, *H. dovrensis* T. Schumach., *H. lacunosa* Afzel., *Helvella cf. lacunosa H. macropus* (Pers.) P. Karst., *H. reflexa* A. Cumino, and *H. zhongtiaoensis* J.Z. Cao & B. Liu with the roots of Pinaceae (conifers) and Fagaceae (broad-leaved trees) host plants (Tedersoo *et al.* 2006, Hwang *et al.* 2015, Cristina *et al.* 2018, Mao *et al.* 2023, Wei *et al.* 2024, Park *et al.* 2025). Additionally, *H. aestivalis* (R. Heim & L. Rémy) Dissing & Raitv. and two other *Helvella* spp. have been reported to form ECM relationships with *Dryas* sp. and *Salix* sp. hosts, respectively (Weidemann, 1998, Wei *et al.* 2024). Furthermore, some species such as *H. bachu* Q. Zhao, Zhu L. Yang & K.D. Hyde*, H. taiyuanensis* B. Liu, Du & J.Z. Cao and *H. lacunosa* have been reported with dietary and medicinal value (Landeros *et al.* 2021, Mao *et al.* 2023, Wang *et al.* 2023, Wei *et al.* 2024, Li *et al.* 2025).

Helvella species have been studied across different countries in the world including China, Denmark, Finland, France, Hungary, Japan, Korea, India, Pakistan, Norway, Russia, Spain, Sweden, Thailand, Turkey, and the USA (Talie *et al.* 2021, Skrede *et al.* 2017, 2023, Wang *et al.* 2019, 2023, Park *et al.* 2025, Terman *et al.* 2025, Ullah *et al.* 2025). Among them, the biogeography of China provides the most suitable microhabitats and substrates to facilitate rich colonization of different *Helvella* species (Zhao *et al*. 2015, Mao *et al*. 2023, Wang *et al*. 2023). The historical studies of saddle fungi in China were reported by Teng (1963) and Tai (1979). Recently, Li *et al.* (2025) updated that, currently 96 phylogenetically confirmed *Helvella* species are reported from different Chinese habitats. Although numerous taxonomic studies have been conducted continuously on Chinese *Helvella* species (Wang *et al.* 2019, 2023, Xu *et al.* 2022, Bao *et al.* 2023, Lu *et al.* 2023, Mao *et al.* 2023, Li *et al.* 2025), many forest regions remain underexplored for their hidden diversity.

The southwestern region of China exhibits a diverse ecological and geographical heterogeneity, characterized by a complex topography, wide elevation gradients, climate variation, and vegetation. The landscapes range from subtropical, lowland plains to temperate or alpine high-altitude plateaus surpassing 4,000 m a.s.l. (above sea level) (Habib *et al.* 2025). The vegetation types range from tropical evergreen forests to alpine meadows (Habib *et al.* 2025). In our fungal investigation in Yunnan forest ecosystems dominated by coniferous trees, we discovered *Helvella griseofuscostipitata sp. nov.* The species boundary was delineated based on comprehensive macro- and micro-morphological characteristics, multi-locus (ITS, LSU, and *hsp*90) phylogenetic analyses using both maximum likelihood (ML) and Bayesian inference analysis (BI), as well as considering fungal habitats.

Materials and Methods

Fungal specimens were collected from a ground of a forest habitat covered with fallen pine needles, Yunnan Province, China. The photographs of the fresh fungal specimens were taken in the field using a Nikon D7100 digital camera and field notes were prepared based on the macro- morphological characters. Samples were wrapped in aluminum foil and brought into the laboratory. Specimens were dried in an electric food dehydrator at 40°C and the dried specimens were then sealed and preserved in a paper envelope for depositing in the Herbarium of Southwest Forestry University (SWFC), Kunming, Yunnan Province, P.R. China. Macro-morphological characters were observed in the laboratory according to the methods described by Dong *et al.* 2024 and Yang *et al.* 2025. Colors were followed by the details in Kornerup & Wanscher (1978). Hand-sectioned structures of the specimens were prepared using a Phenix compound stereomicroscope for examining micromorphological characteristics. Micro- structures were photographed using a light microscope, Nikon Eclipse E100, fitted with a MIchrome 20 (20MP) color microscope camera by preparing 5% KOH and water-mounted clean glass slides. Some sections were stained with 2% phloxine B dye and cotton blue (CB) for clear visualization and Melzer's reagent for understanding amyloid reactions of micromorphological structures. The following abbreviations were used in the descriptions: L = mean spore length; W = mean spore width; L/W = ratios between the measured L and W; n = number of structures (fruiting bodies and spores) measured. The measurements of photomicrographic structures were made using Mosaic version 3.0.7.0 software. Images were edited with Adobe Photoshop CS6 Extended version 13.0.1 software (Adobe Systems, San Jose, California, USA).

DNA extraction, PCR amplification and sequencing

DNA extraction, PCR, gel electrophoresis, and sequencing procedures were followed, as detailed in Dissanayake *et al.* (2020). Genomic DNA was extracted from the dried apothecia directly using EZNA HP Fungal DNA Kit (Omega Biotechnologies Co., Ltd., Kunming, China) following the guidelines provided by the manufacturer. Polymerase chain reactions (PCRs) were performed to amplify internal transcribed spacer (ITS), large subunit (LSU), and heat shock protein 90 (*hsp*90). The thermal cycle programs of PCR for each locus are presented in Table 1. PCR products were stored at 4°C for regular use and the original DNA samples were stored at −20°C for long-term preservation. The PCR products were verified by staining with ethidium bromide on 1% agarose electrophoresis gels. Product purification and sequencing were outsourced from the laboratory in Qingke Co., China. Newly generated sequences were submitted to NCBI GenBank (www.ncbi.nlm.nih.gov/genbank). The Index Fungorum identity number was registered as detailed in the Index Fungorum (2026).

TABLE 1. Genes/loci, primers, and PCR thermal cycle programs used in this study.

Genes/loci	PCR primers (forward/ reverse)	PCR conditions Reference(s)	Reference(s)
ITS	ITS5/ITS4	95 °C; 3 min (94 °C; 40 s, 58 °C; 40 s, 72 °C; 1 min) × 35 thermal cycles, 72 °C; 10 min	White *et al.* (1990)
LSU	LR0R/LR7	98 °C; 5 min (98 °C; 30 s, 52 °C; 30 s, 72 °C; 45 s) × 34 thermal cycles, 72 °C; 7 min	Vilgalys & Hester (1990)
*hsp*90	H_hspf/ H_hspr	94 °C; 4 min (94 °C; 30 s, 58 °C; 45 s, 72 °C; 1 min) × 35 thermal cycles, 72 °C; 10 min	Skrede *et al.* (2017)

TABLE 2. Taxa used in the phylogenetic analyses of this study and their GenBank accession numbers.

Species name	Voucher	ITS	LSU	*hsp*90
Balsamia guozigouensis	HMAS 97107	NR_160638	NG_066428	_
B. luyashanensis	BJTC FAN764	NR_160637	NG_066427	_
Choiromyces meandriformis	SOMF30859	OQ398590	_	_
C. venosus	AH38915	JF300146	JF300157	_
C. venosus	RH691	HM485330	FJ809794	_
Dissingia confusa	FV2016060901	ON622916	ON622510	_

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TABLE 2. (Continued)

Species name	Voucher	ITS	LSU	*hsp*90
D. oblongispora	HSA 137	OR355181	OR355355	OR366160
Helvella acetabuloides	CFSZ2044	OR355015	OR355185	MK652219
H. acetabuloides	BJTC FM1264	OR355166	OR355337	OR366140
H. acetabulum	H410	_		KY784506
H. acetabulum	O-253212	_	KY773055	_
H. acetabulum	O-64925	_	KY772985	KY784267
H. albopatella	BJTC FM2610-A	OR355082	OR355252	OR366079
H. albopatella	BJTC FM2610-B	OR355176	OR355350	OR366151
H. alborava	BJTC C316-A	OR355106	OR355276	OR366098
H. alborava	BJTC C316-B	OR355173	OR355347	OR366148
H. alpestris	O-253221	_	KY772909	KY784191
H. alpestris	O-253220		KY772908	KY784190
H. alpicola	TROM-F-610062	_	MN655848	MN692345
H. alpicola	O-185924	_	KY773020	KY784304
H. alpina	O-253228	_	KY773054	KY784343
H. alpina	KH.12.69(S)	_	MK100261	MK179405
H. arctoalpina	O-72616 (H293)	_	_	KY784406
H. arctoalpina	O-253229	_	KY773128	KY784461
H. atra	KH.10.97(S)	KC122809	KC122771	MK179402
H. atra	HMAS 290900	OQ600286	OQ586677	OQ597592
H. atra	HMAS 290901	OQ600287	OQ586678	OQ597593
H. atroides	KA24-1294	PP545280	PP545109	PP782874
H. atroides	KA24-1295	PP545284	PP545114	PP782879
H. atroides	HKAS 90544	OQ866043	OQ866058	_
H. atroides	MFLU 23-0102	_	NG229117	OQ863541
H. austrooccidentalis	HMAS 290902	OQ600290	OQ586680	OQ597597
H. austrooccidentalis	HMAS 290903	OQ600291	OQ586681	OQ597598
H. bachu	HKAS 88105	NR_155171	NG_059662	OR220557
H. bachu	BJTC FM382	OR355062	OR355232	OR366059
H. bicolor	O-255759	MN656168	MN655851	MN692352
H. bicolor	C F-45334	_	NG_068799	KY784402
H. borealis	HMAS 290905	OQ600293	OQ586683	OQ597600
H. brunneogaleriformis	BJTC FM272	OR355064	OR355234	OR366061
H. brunneogaleriformis	BJTC FM911	OR355065	OR355235	OR366062
H. caespitosa	HSA 379-A	OR355091	OR355261	OR366087
H. caespitosa	HSA 379-B	OR355092	OR355262	OR366088
H. calycina	O-253255	MN656158	KY772915	KY784198
H. calycina	HMAS 279704	OR355013	MK592100	_
H. capucina	O 253256	_	NG_060703	KY784331
H. capucinoides	BJTC FM1094	OR355037	OR355207	OR366040
H. capucinoides	BJTC FM242	OR355040	OR355210	OR366041
H. capucinoides	HMJAU 33777	OR355043	OR355213	OR366043
H. carnosa	O 68100	_	NG_060699	KY784279
H. carnosa	BJTC FM1032	OR355021	OR355191	OR366035

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TABLE 2. (Continued)

Species name	Voucher	ITS	LSU	*hsp*90
H. carnosa	BJTC FM274	OR355022	OR355192	OR366036
H. cf. compressa	AFTOL-ID 66	_	AY544655	_
H. compressa	FH(H112)	_	KY772968	KY784250
H. convexa	H761	OQ641537	_	OQ633414
H. corbierei	HSA 138	OR355071	OR355241	OR366068
H. corbierei	HSA 181	OR355072	OR355242	OR366069
H. corium	O-255756	MN656185	MN655873	MN692370
H. corium	O-255757	MN656165	MN655870	MN692363
H. costifera	BJTC FM1742	OR355129	OR355300	OR366118
H. costifera	HMAS 187120	OR355179	MK592102	_
H. cremeoinvoluta	BJTC FM941-A	OR355153	OR355324	OR366131
H. cremeoinvoluta	BJTC FM941-B	OR355154	OR355325	OR366132
H. crispa	H408	_	_	KY784504
H. crispa	KH.09.186(S)	_	MK100266	MK179400
H. crispa	O-18774	_	KY772986	KY784268
H. crispoides	HKAS 90585	KX507002	OR355183	OR366032
H. crispoides	HKAS 90583	KX507001	OR355184	OR366033
H. cystidiata	HMJAU 52	OQ600295	OQ586684	OQ597602
H. cystidiata	HMJAU 150	OQ600296	OQ586685	OQ597603
H. dalgeri	O-F-256528	_	_	MN598202
H. dalgeri	O-F-256527	_	_	MN598125
H. danica	BJTC L235	OR355047	OR355217	OR366045
H. danica	BJTC ZH1249	OR355049	OR355219	OR366046
H. deflexa	HSA 240-A1	OR355069	OR355239	OR366066
H. deflexa	HSA 240-A2	OR355070	OR355240	OR366067
H. densipila	KA24-1268	PP545228	PP545046	PP782814
H. densipila	KA24-1269	_	PP545048	PP782816
H. dryadophila	O-72617	_	_	KY784412
H. dryadophila	C-F-52701	_	KY773140	KY784477
H. elastica	C-F-51672	_	_	KY784433
H. elastica	HKAS:83158	KU739800	KU739827	_
H. elastica	HKAS:83157	KU739799	KU739826	_
H. elastica	O-253311	_	KY772950	KY784230
H. ephippioides	KA24-1281	PP545266	PP545091	PP782857
H. ephippioides	HMJAU 44584	OR355107	OR355277	OR366099
H. fallax	C-F-84621	_	KY773117	KY784442
H. fibrosa	O-291352	_	KY773069	KY784358
H. fibrosa	C-F-92109	_	KY773136	KY784469
H. fibrosa	DM1064	MT640262	MT640262	_
H. fistulosa	KA24-1284	PP545226	PP545044	PP782812
H. fistulosa	KA24-1285	PP545227	PP545045	PP782813
H. fistulosa	O 291887	_	NG_060704	KY784359
H. flavopus	KA24-1291	PP545246	PP545069	PP782838
H. flavopus	Juk15068	PP545134	PP544940	_

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TABLE 2. (Continued)

Species name	**Voucher**	**ITS**	**LSU**	***hsp*90**
H. flavopus	KA16-0688	PP545149	PP544956	_
H. flavostipitata	HSA 387-B	OR355036	OR355206	OR366039
H. flavostipitata	HSA 387-A	OR355035	OR355205	_
H. floriforma	HKAS 90224	NR_171723	NG_059685	_
H. fulva	HMAS 290906	OQ600297	OQ586686	OQ597604
H. fusca	C-F-92122	_	_	KY784415
H. fuscolacunosa	TRH-12623	_	_	MN598179
H. fuscolacunosa	TRH-12618	_	_	MN598173
H. galeriformis	HSA 232	OR355066	OR355236	OR366063
H. galeriformis	HSA 240-B	OR355067	OR355237	OR366064
H. griseoalba	C-F-92112	_	_	KY784416
H. griseobrunnea	KA24-1321	PP545278	PP545106	PP782871
H. griseobrunnea	KA24-1322	PP545288	PP545118	PP782882
H. griseofuscostipitata	SWFC 00019347	PX608658	PX517622	PX573143
H. griseofuscostipitata	SWFC 00019323	PX608656	PX517620	PX573141
H. griseofuscostipitata	SWFC 00019332	PX608657	PX517621	PX573142
H. guttata	HKAS 57439	KX506975	KX506930	_
H. guttata	HKAS 87759	_	OQ866049	OQ863531
H. guttata	HKAS 67836	_	OQ866045	OQ863527
H. helvellula	C-F-92128	_	_	KY784418
H. helvellula	C-F-45507	_	KY773090	KY784393
H. hispanica	5064	PP719470	PP738544	_
H. hispanica	O-F-256536	_	MN644504	MN598112
H. huangii	HMAS 290907	OQ600298	OQ586687	OQ597605
H. huangii	HMAS 45031	OQ600299	OQ586688	OQ597606
H. hyperborea	C-F-45306	_	_	KY784569
H. hyperborea	C-F-54473	_	_	KY784486
H. hypocrateriformis	C-F-45379	_		KY784411
H. hypocrateriformis	C-F-57126	_	_	KY784390
H. involuta	BJTC FM2940	OR355157	OR355328	_
H. involuta	HKAS 74281	NR_155166	KR493492	_
H. japonica	H093	OQ645455	KY772961	KY784243
H. jizushanica	HMAS 290908	OQ600301	OQ586690	OQ597609
H. jizushanica	HMAS 59718	OQ600302	OQ586691	OQ597610
H. kunmingensis	HKAS 145326	PQ821435	PQ821421	PQ845411
H. kunmingensis	HKAS 145327	PQ821436	PQ821422	PQ845412
H. lacunosa	BJTC FM1162	OR355108	OR355278	OR366100
H. lacunosa	BJTC FM546	OR355110	OR355280	OR366101
H. lacunosa	BJTC FM813	OR355112	OR355282	OR366102
H. levis	C-F-55188	_	NG_068800	KY784403
H. levis	C-F-40830	_	KY773148	KY784490
H. liquii	KA24-1299	PP545233	PP545053	PP782821
H. liquii	KA24-1303	PP545272	PP545098	PP782864
H. liquii	HKAS 90563	KX506994	KX506949	OR291044

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TABLE 2. (Continued)

Species name	Voucher	ITS	LSU	*hsp*90
H. liui	HMAS 85725	OQ600310	_	OQ597622
H. lobata	KA24-1310	PP545232	PP545052	PP782820
H. lobata	KA24-1311	PP545252	PP545075	PP782844
H. lobata	HMAS 290910	OQ600311	OQ586698	OQ597623
H. macropus	KA24-1315	PP545238	PP545060	PP782828
H. macropus	KA24-1316	_	PP545085	PP782852
H. macropus	H412	_	_	KY784507
H. macropus	O-291425	_	KY773067	KY784356
H. macrosperma	O-253328	MN656159	KY772921	KY784205
H. macrosperma	TROM-F-610001	MN656176	MN655842	MN692319
H. macrospora	KA24-1318	PP545290	PP545120	PP782884
H. macrospora	KA24-1319	PP545291	PP545121	PP782885
H. macrospora	KA24-1320	_	PP545122	PP782886
H. maculata	OSC 72027	EU834201	_	_
H. maculata	HC-PNNT-207	KT875010	_	_
H. magna	HMAS 60679	OQ600315	OQ586702	OQ597627
H. magna	HMAS 290911	OQ600312	OQ586699	OQ597624
H. monachella	C-F-92121	_	_	KY784383
H. monachella	C-F-92120	_	KY773084	KY784384
H. multiformis	BJTC FM1130	OR355100	OR355270	OR366092
H. multiformis	BJTC FM1131	OR355101	OR355271	OR366093
H. nannfeldtii	O-253338	_	KY772919	KY784203
H. nannfeldtii	O-253333	_	KY773048	KY784337
H. neofistulosa	BJTC ZH1213	OR355059	OR355229	OR366056
H. neofistulosa	BJTC ZH1251	OR355060	OR355230	OR366057
H. neopallescens	O-F-256551	_	_	MN598113
H. neopallescens	IS_y-p-24	OR142390	_	PQ072280
H. nigra	O-253345	_	KY772947	KY784227
H. nigra	HMAS262949	OQ600321	OQ586707	OQ597636
H. nigrorava	BJTC ZH67	OR355105	OR355275	OR366097
H. nordlandica	BJTC FM346-A	OR355081	OR355251	OR366078
H. orentitomentosa	MFLU 23-0099	_	NG229116	OQ863538
H. orentitomentosa	HKAS 90543	OQ866042	OQ866057	_
H. orienticrispa	KA24-1323	PP545270	PP545096	PP782862
H. orienticrispa	BJTC BP066	OR355158	OR355329	OR366136
H. orienticrispa	BJTC FM418	OR355160	OR355331	OR366137
H. oroarctica	H1983	MN656177	OQ626671	OQ633408
H. pakistanica	M.jabba01-1	PQ410250	_	_
H. pakistanica	M.jabba01-2	PQ410251	_	_
H. palustris	O-253359	_	KY772933	KY784214
H. palustris	O-253358	_	KY772914	KY784196
H. palustris	HMAS 30755	_	_	OQ597638
H. panormitana	O-253363	_	KY772948	KY784228
H. paraphysitorquata	MA Fungi:24512	_	NG_064430	_

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TABLE 2. (Continued)

Species name	Voucher	ITS	LSU	*hsp*90
H. paraphysitorquata	C-F-45305	_	KY773085	KY784386
H. parva	HMAS 290914	OQ600323	OQ586710	OQ597639
H. parviflava	KA24-1336	PP545261	PP545084	PP782851
H. parviflava	KA24-1338	PP545282	PP545112	PP782877
H. pezizoides	O-253366	_	KY772945	KY784225
H. pezizoides	O-253367	_	KY772949	KY784229
H. philonotis	HMAS 290915	OQ600324	OQ586711	OQ597640
H. philonotis	HMAS 264754	OQ600327	OQ586712	OQ597644
H. philonotis	O-255760	MN656182	MN655853	MN692353
H. phlebophora	HMAS 268001	OQ600328	OQ586713	OQ597645
H. phlebophora	C F-45405	_	NG_068797	KY784388
H. plateata	HMAS 290916	OQ600330	OQ586714	OQ597648
H. plateata	HMAS 270642	OQ600331	OQ586715	OQ597649
H. plateata	HMAS 290917	OQ600332	OQ586716	OQ597650
H. pseudoalpina	TROM-F-610048	MN656173	MN655866	MN692355
H. pseudoatra	HKAS 74023	NR190916	KX506946	OR291045
H. pseudoatra	HKAS 54996	KX506992	KX506947	_
H. pseudoelastica	BJTC C351-A	OR355170	OR355341	OR366143
H. pseudoelastica	BJTC C351-B	OR355174	OR355348	OR366149
H. pseudofallax	HSA 356	OR355083	OR355253	OR366080
H. pseudofallax	BJTC ZH1283	OR355084	OR355254	OR366081
H. pseudolobata	KA24-1324	PP545231	PP545050	PP782818
H. pseudolobata	KA24-1325	PP545235	PP545057	PP782825
H. pseudopezizoides	BJTC FM1045-A	OR355089	OR355259	OR366085
H. pseudopezizoides	BJTC FM1045-B	OR355090	OR355260	OR366086
H. pseudoreflexa	HKAS 74311	NR_138384	_	_
H. pseudoreflexa	BJTC C549	OR355137	OR355308	OR366124
H. pseudoreflexa	BJTC FM1409	OR355139	OR355310	OR366126
H. pubescens	BJTC BP020	OR355093	OR355263	OR366089
H. pubescens	FH H121	_	NG_064429	KY784257
H. pubescens	BJTC FM259	OR355097	OR355267	OR366091
H. pulla	O-69282	MN656161	KY772998	KY784282
H. queletiana	C-F-45303	_	KY773151	KY784499
H. ravida	HMAS 290919	OQ600334	OQ586718	OQ597652
H. ravida	HMAS 61920	OQ600335	OQ586719	OQ597653
H. rivularis	O-255764	MN656175	MN655850	MN692371
H. rivularis	C F-59447	_	NG_068798	KY784391
H. rugosa	KA24-1326	PP545237	PP545059	PP782827
H. rugosa	KA24-1327	PP545239	PP545062	PP782831
H. rugosa	HMAS 290920	OQ600336	OQ586720	OQ597654
H. scyphoides	BJTC FM1158	OR355073	OR355243	OR366070
H. scyphoides	BJTC FM899	OR355074	OR355244	OR366071
H. scyphoides	HSA 166	OR355075	OR355245	OR366072
H. scyphoides	O 65348	_	NG_060698	KY784273

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TABLE 2. (Continued)

Species name	Voucher	ITS	LSU	*hsp*90
H. semiobruta	C-F-45507	_	_	KY784392
H. semiobruta	C-F-45467	_	KY773102	KY784417
H. sichuanensis	10706	OR355014	MK592107	_
H. sinocrispa	BJTC FM96-A	OR355155	OR355326	_
H. sinocrispa	BJTC FM96-B	OR355156	OR355327	_
H. sinohyperborea	BJTC FM105	OR355132	OR355303	OR366121
H. sinohyperborea	BJTC FM165	OR355133	OR355304	OR366122
H. solitaria	BJTC FM417	OR355131	OR355302	OR366120
H. stevensii	C-F-92117	_	_	KY784491
H. stevensii	C-F-45350	_	_	KY784408
H. subglabra	C-F-65405	_	_	KY784394
H. subglabra	HKAS 133801	PV706665	PV731342	_
H. subglabroides	KA24-1332	PP545264	PP545089	PP782855
H. subglabroides	BJTC C614	OR355086	OR355256	OR366083
H. subglabroides	BJTC FM2686	OR355088	OR355258	OR366084
H. sublactea	KA24-1335	PP545230	PP545049	PP782817
H. sublactea	HKAS 69753	_	_	OR366154
H. sublactea	BJTC FM347	OR355123	OR355294	OR366112
H. sublicia	C-F-39823	_	KY773155	KY784512
H. sublicia	KH.11.84	_	MK100273	MK179403
H. sublicia	O-70080	_	KY772997	KY784281
H. suborentitomentosa	KA24-1339	PP545248	PP545071	PP782840
H. suborentitomentosa	KA24-1340	PP545251	PP545074	PP782843
H. subtinta	BJTC FM1307	OR355130	OR355301	OR366119
H. sulcatoides	BJTC FM1416	OR355119	OR355290	OR366108
H. sulcatoides	BJTC FM263	OR355120	OR355291	OR366109
H. taiyuanensis	HMAS 277500	MK592152	MK592105	MK652216
H. taiyuanensis	119250	MK592151	MK592104	MK652215
H. taiyuanensis	BJTC FM192	OR355167	OR355338	OR366141
H. terrestris	H284	_	KY773094	KY784398
H. terricola	O-F-256562	_	_	MN598197
H. terricola	HMAS 38355	OQ600354	_	OQ597679
H. tianshanensis	BJTC FM175	OR355125	OR355296	OR366114
H. tianshanensis	HSA 179	OR355126	OR355297	OR366115
H. tianshanensis	HSA 185	OR355127	OR355298	OR366116
H. tinta	HKAS 82560	KX239842	KX239772	OR366031
H. varia	KA24-1342		PP545102	PP782867
H. varia	HMAS 270932	OQ600357	OQ586737	OQ597682
H. varia	HMAS 290929	OQ600359	OQ586738	OQ597684
H. vespertina	H102	_	KY772963	KY784245
H. vespertina	H116	_	KY772971	KY784254
H. vitrea	HMAS 290932	OQ600362	OQ586741	OQ597687
H. vulgata	HMAS 53683	OQ600363	OQ586742	OQ597688
H. vulgata	HMIGD 25964	OQ600365	OQ586743	OQ597690

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TABLE 2. (Continued)

Species name	**Voucher**	**ITS**	**LSU**	***hsp*90**
H. xiaohuipan	BJTC FM367	OR355078	OR355248	OR366075
H. xiaohuipan	BJTC FM2317	OR355079	OR355249	OR366076
H. yongpingensis	HKAS 145324	PQ821433	PQ821419	PQ845409
H. yongpingensis	HKAS 145325	PQ821434	PQ821420	PQ845410
H. yunnanensis	HMAS 290933	OQ600366	OQ586744	OQ597691
H. yunnanensis	HMAS 290934	OQ600367	OQ586745	OQ597692
H. zhongtiaoensis	HKAS 74335	JX462578	KR493484	OR366156
H. zhongtiaoensis	HKAS 74343	JX462583	KR493489	OR366157
Midotis lingua	Sch 84.51 (C-F-57385)	_	MK100276	KY784396
M. subalpina	HKAS:78940	KX034102	KT581119	_
M. subalpina	HKAS:45750	KX034101	KT581118	_
Pindara terrestris	ARON 2666	AF046219	_	_
Tuber aereum	ACAM-Tub245	PP425915	PP425961	_
Underwoodia beatonii	JT28380	JQ925655	JQ925716	_
U. columnaris	Kanouse1951	_	U42685	_
U. columnaris	FLAS-F-58861	_	MK430973	_

Notes: Sequences of the newly generated taxon are in blue, and type collections are in bold. "_" demarcated sequences that are not available in the GenBank.

Molecular data and phylogenetic analyses

Newly generated sequence chromatograms were subjected to quality checking using the BioEdit v 7.0.9.0 program (Hall 1999). DNASTAR Lasergene SeqMan v. 7.0.1 (44.1) software was used for assembling both forward and reverse sequences. Preliminary conclusions for the phylogenetic analysis were made with contig sequences to identify high similarity indexes through BLAST searches in NCBI (National Center for Biotechnology Information; https://blast.ncbi.nlm.nih.gov/) and NGDC (The National Genomics Data Center; https://ngdc.cncb.ac.cn/). Sequences for final phylogenetic analyses were downloaded from GenBank (Table 2) following the updated research studies in October 2025. Each gene matrix was aligned with MAFFT version 7 (Katoh *et al.* 2019) with L-INS-i iterative refinement method for ITS (sequences with one conserved domain and long gaps) and default auto parameters for LSU and *hsp*90 and manually adjusted for improvement where necessary using the BioEdit. Two separate final phylogenetic analyses were performed: Maximum Likelihood (ML) and Bayesian Inference (BI). A concatenated sequence dataset of ITS, LSU, and *hsp*90 regions was assembled to identify the taxonomic placements of *Helvella* species, including our newly collected species.

Maximum likelihood (ML) was executed through the IQ-Tree web server (http://iqtree.cibiv.univie.ac.at/) with bootstrap support obtained from 1,000 pseudo replicates (Nguyen *et al.* 2014, Chernomor *et al.* 2016). Bayesian Inference (BI) analysis was performed with MrBayes version 3.2.6 (Ronquist *et al.* 2012). MrModeltest version 2.3 (Nylander 2004) was run under the Akaike Information Criterion implemented in PAUP version 4.0b10 (Swofford 2003) to estimate the best evolutionary model and GTR+I+G was identified as the best-fit model for ITS and LSU, while GTR+G was identified for *hsp*90. Six simultaneous Markov chains were run for 1,000,000 generations, and trees were sampled every 1,000th generation, ending the run automatically when the standard deviation of split frequencies dropped below 0.01. Phylogenetic trees were visualized with FigTree version 1.4.0 (Rambaut 2012) and modified in Microsoft PowerPoint (2023).

Results

Phylogenetic analysis

The combined ITS, LSU, and *hsp*90 alignment was used to construct the final phylogenetic analysis (Figure 1) of maximum likelihood (ML) and Bayesian inference (BI).

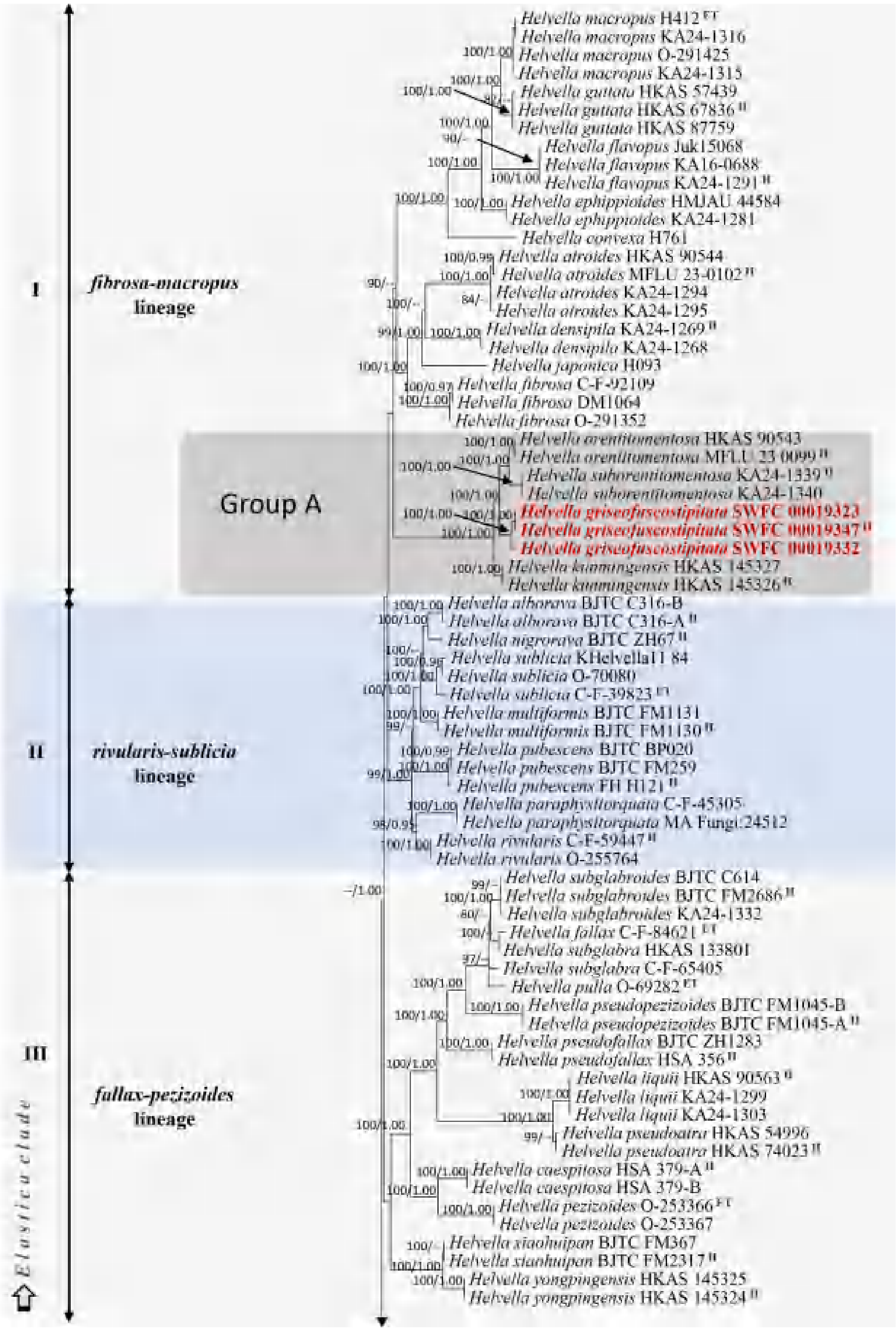

FIGURE 1. Phylogram generated from maximum likelihood analysis based on combined ITS, LSU, and *hsp*90 sequenced data. Two-hundred and eighty-six specimens were included in the combined sequence analyses, which comprised 3004 characters with gaps (ITS = 1783, LSU = 930, *hsp*90 = 285). Single gene analyses were also performed, and topology and clade stability were compared from the combined gene analyses. *Choiromyces meandriformis* Vittad. (SOMF30859), *Choiromyces venosus* (Fr.) Th. Fr. (AH38915*,* RH691) and *Tuber aereum* Polemis, Daskalopoulos & Zervakis (ACAM Tub245) were used as the outgroup taxa. The final ML optimization likelihood is -43015.172. The matrix included 1947 distinct alignment patterns including undetermined characters. Bootstrap support values for ML (first set) equal to or greater than 75% and BYPP equal to or greater than 0.95 are given above or below the nodes. The specimens from the current study are in red-bold and the holotype, epitype and neotype collections are indicated with $^{H, ET, NT}$. The scale bar represents the expected number of nucleotide substitutions per site.

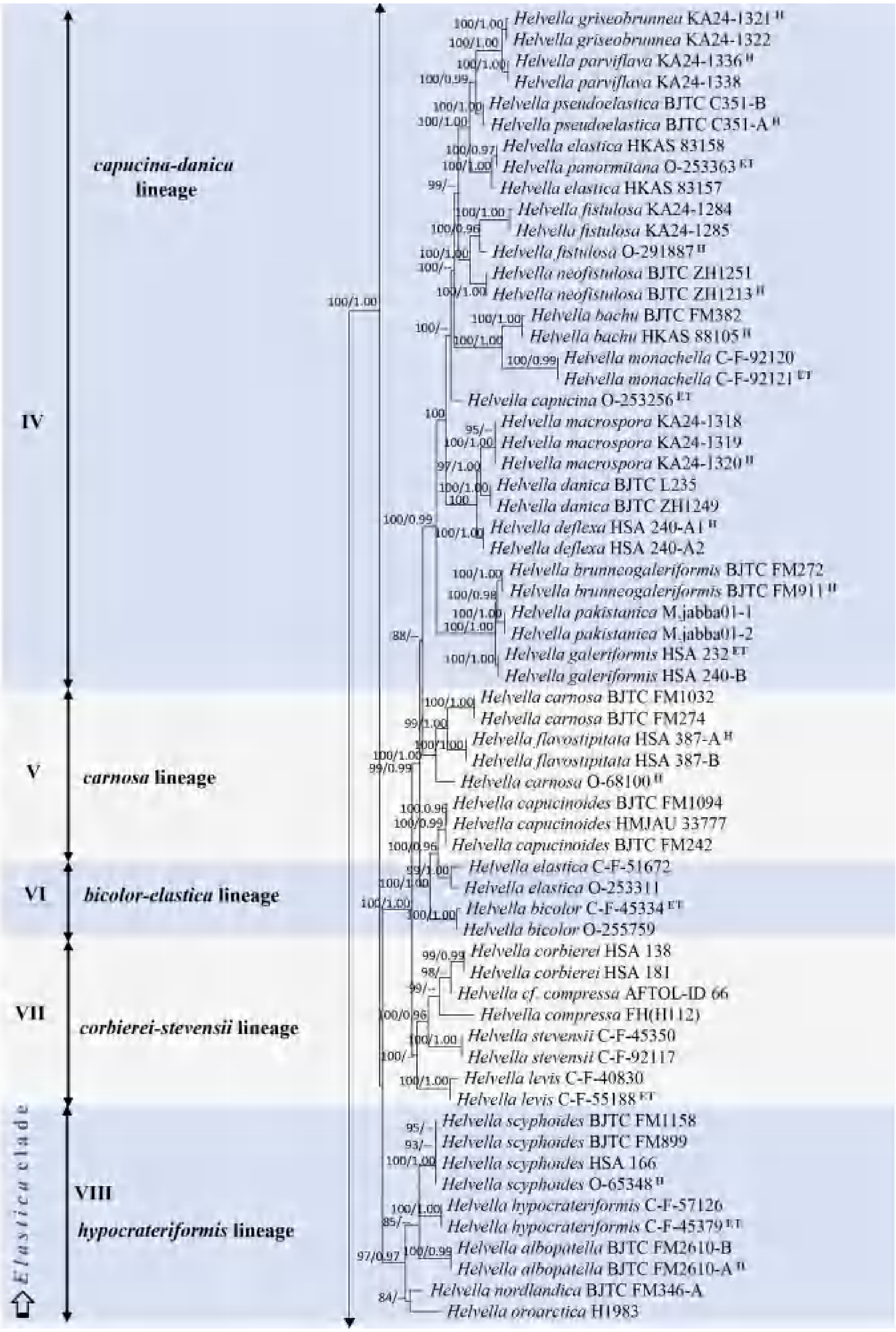

FIGURE 1. (Continue)

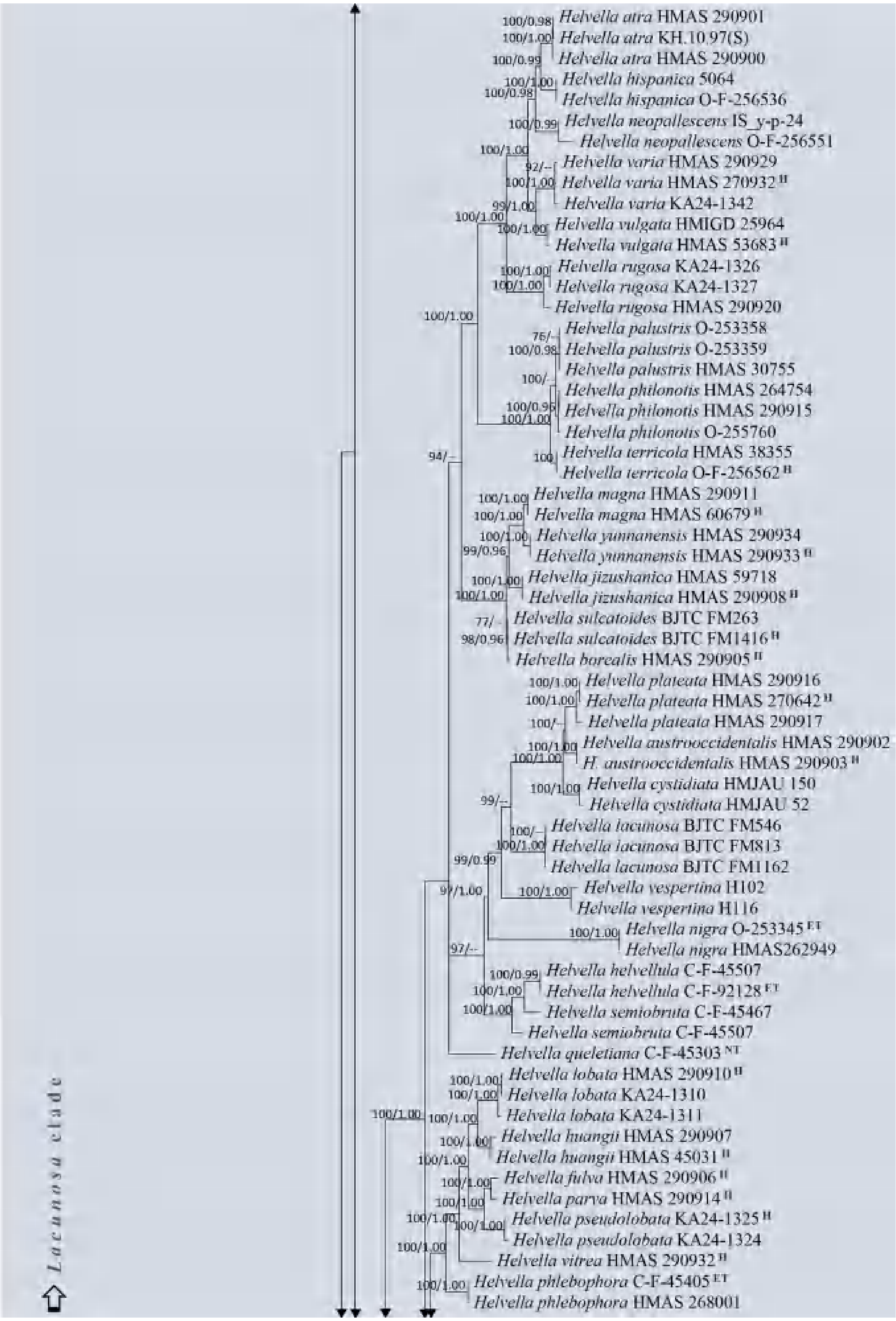

FIGURE 1. (Continue)

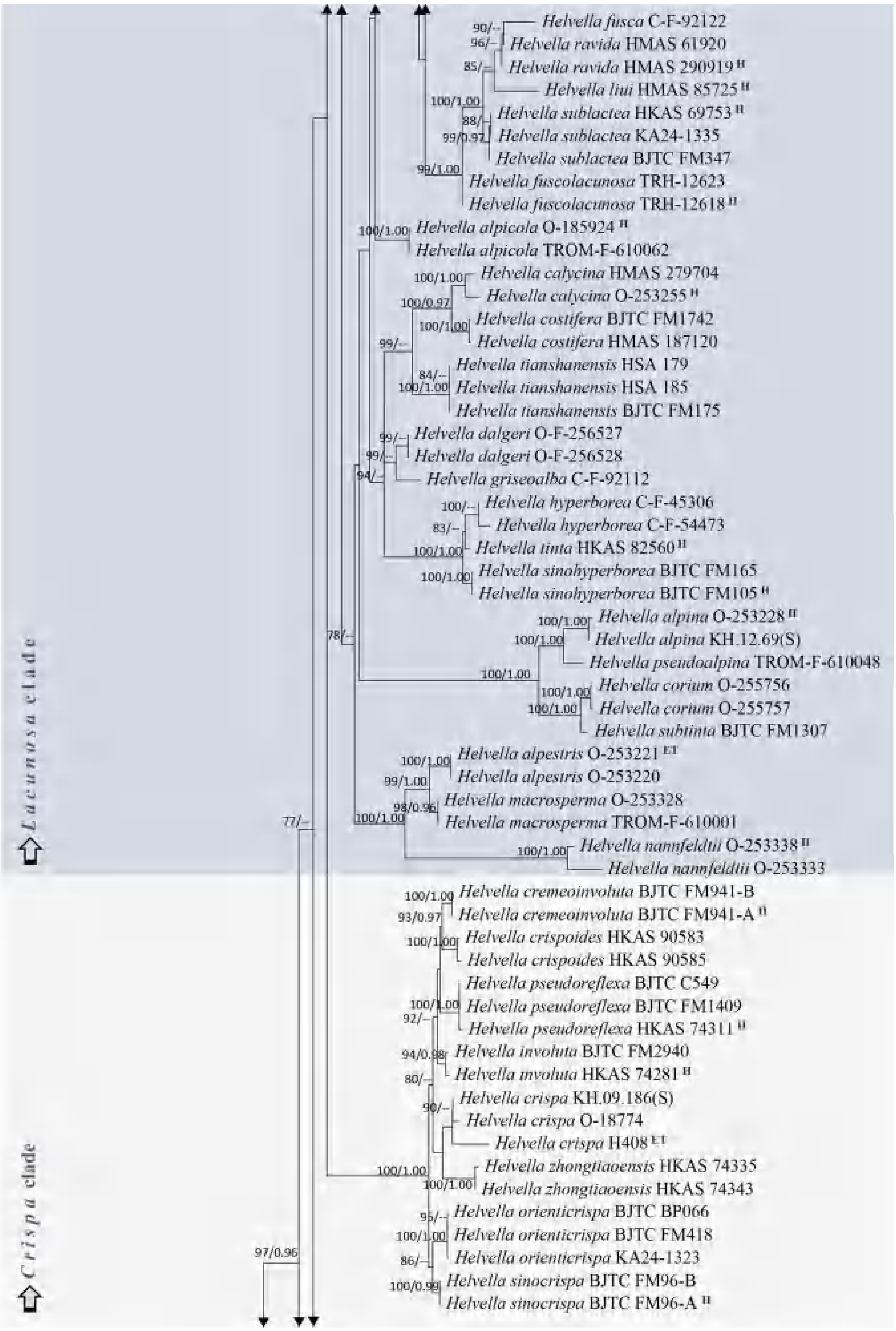

FIGURE 1. (Continue)

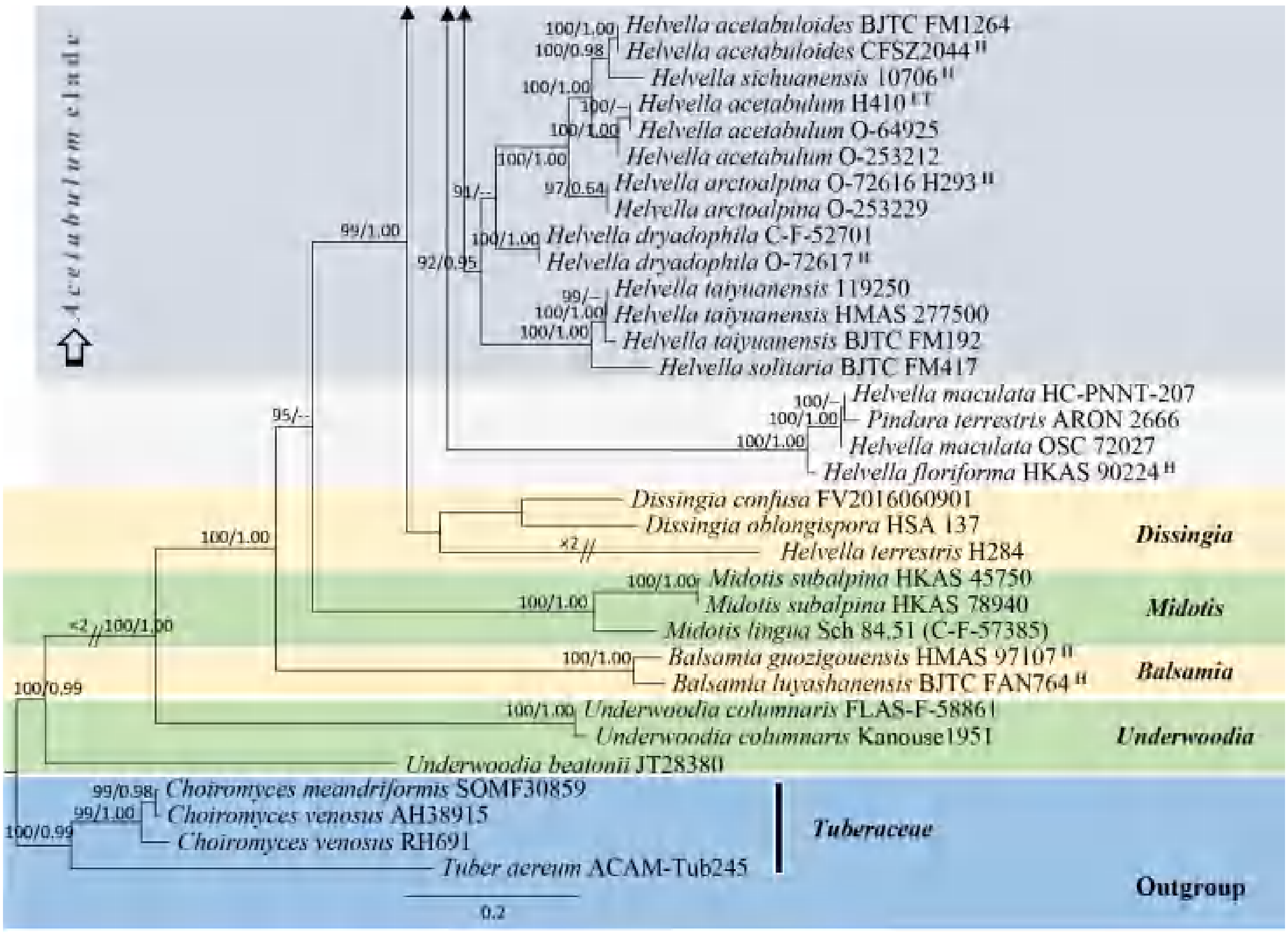

FIGURE 1. (Continue)

Taxonomy

Helvella griseofuscostipitata Wijes., C.L. Zhao, *sp. nov.* (Figure 2)
Index Fungorum number: IF904694

Etymology: *griseofuscostipitata* (Lat.) = the gray to brown stipe; referring to the gray to brownish gray stipe.

Diagnosis: *Helvella griseofuscostipitata* is distinguished by its bi- to tri-lobate mature apothecia, yellowish gray to brownish gray fresh hymenia, subpubescent, gray to dark brownish gray stipes with longitudinal shallow grooves, ectal excipulum with both *textura globulosa* and *textura angularis* cells, and finely verrucose younger ascospores.

Fruiting bodies 3–5.5 cm high (n = 5), epigeous, distributed solitary or aggregated and scattered on the ground. *Apothecia* 1–3 cm diam., 0.5–1 cm high (only cap), slightly cupulate when young, becoming discoid or irregularly lobed with age (mainly bi- to tri-lobate), stipitate, margin slightly undulate, free from stipe, sometimes split with age and folded upward from the stipe; *hymenium* even, yellowish gray to brownish gray when fresh, becoming grayish (chocolate) brown when drying; receptacle surface finely subpubescent, gray to dark brownish gray, concolorous with stipe. *Stipe* 2.5–5 cm long, 0.2–0.3 cm diam. (at apex), 0.2–0.4 cm diam. (at middle), 0.3–0.5 cm diam. (at base), terete, solid, with longitudinal shallow grooves, gray to dark brownish gray, whitish creamy near the base, outermost layer densely subpubescent, with white basal mycelia.

Ectal excipulum 200–275 µm broad, composed of several layers of densely packed, hyaline to pale brown cells of *textura globulosa* to *textura angularis*, outermost layers composed of short cylindrical to cylindric-clavate cells, with catenuliform hyphal fascicles, hyphal fascicles becoming blue evenly in CB, terminal cells 20–30 × 10–15 µm, J−. *Medullary excipulum* 190–300 µm broad, mostly hyaline to pale brown, composed of 5–7.5 µm wide, septate hyphae, J−. *Stipitipellis* 200–300 µm wide, hyaline to pale brown, outermost layers composed of short cylindrical cells, with catenuliform hyphal fascicles, only hyphal fascicles become blue evenly in CB, terminal cells 17–33 × 10–15 µm,

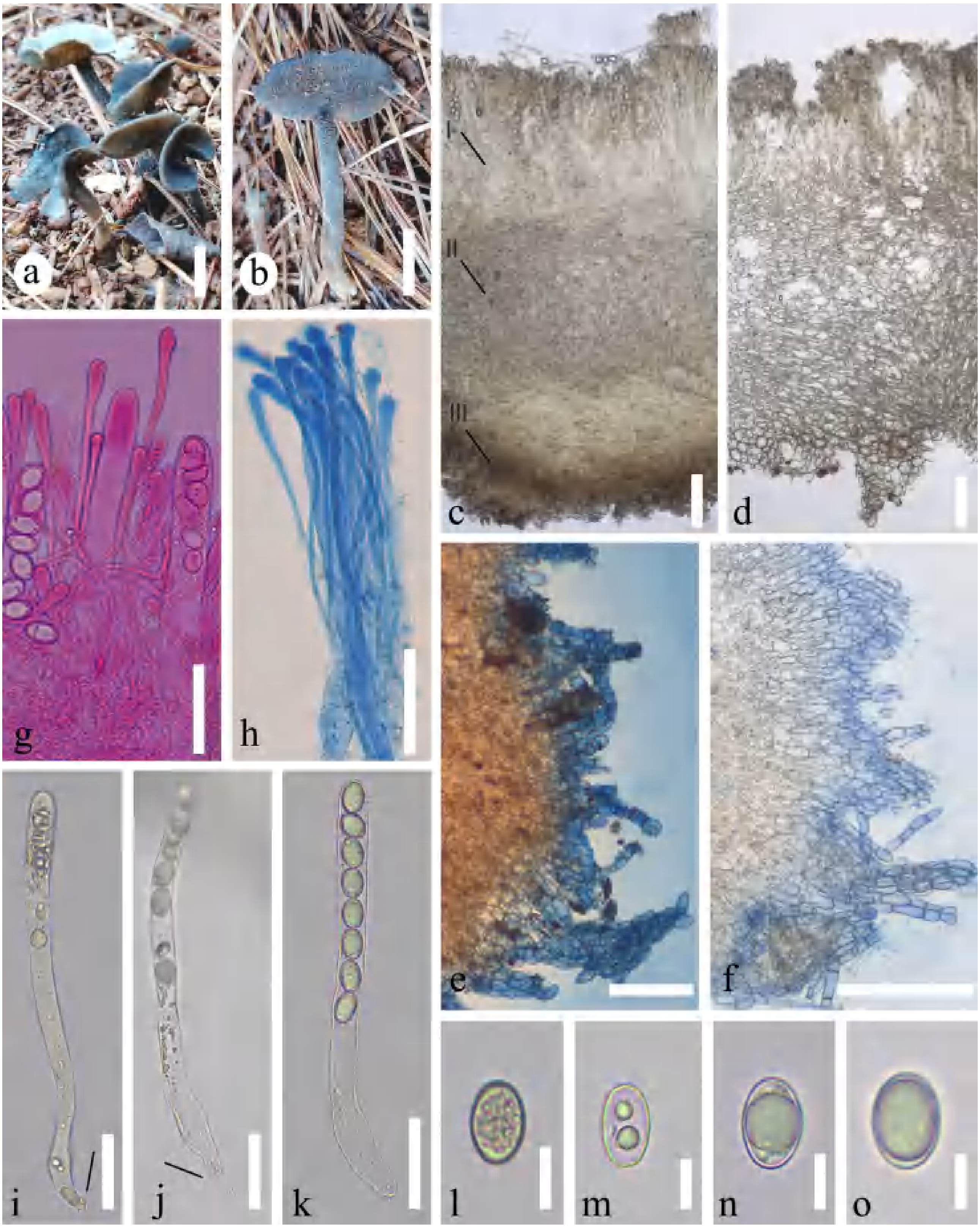

FIGURE 2. Morphological characteristics of *Helvella griseofuscostipitata sp. nov.* CLZhao 19347 (SWFC 00019347, holotype). a Fruit bodies on the natural ground. b Lower surface view of a fruit body. c-d Longitudinal sections of apothecium (arrangement of I. hymenium II. Medullary excipulum III. Ectal excipulum). e Ectal excipulum (stained with CB). f Stipitipellis (stained with CB). g Paraphyses (stained with 2% phloxine B dye). h Paraphyses (stained with CB). i-k Asci (arrowed pleurorhynchous base). l-o Ascospores. Scale bars: a–b = 1 cm, c–f = 100 µm, g–k = 50 µm, l–o = 10 µm.

J^-. *Paraphyses* 3–4.5 µm diam., filiform, septate, sparsely branched, slightly longer than asci, with 8–10 µm wide enlarged apex, hyaline, becoming blue in CB, J^-. *Asci* 200–250 × 12–19 µm, cylindrical to subcylindrical, rounded at the apex, pleurorhynchous, 8-spored, uniseriate, J^-. *Ascospores* (14–)15−17(–18.6) × (9–)10–12.5 µm ($\bar{x}$ = 16.70 × 11.25; L/W = 1.4–1.5; n = 60/3/2 in H_2O), broadly ellipsoid, thin-walled, hyaline, verrucose when young, dominant oil droplet at the middle and smooth with age.

Material examined: CHINA. Yunnan Province, Zhaotong City, Qiaojia County, Mashu State-owned Forest Farm, on the ground, 900 m a.s.l., 18 Jul. 2020, Chang-Lin Zhao (leg.), CLZhao 19347 (SWFC 00019347, holotype), *ibid.*, CLZhao 19323 (SWFC 00019323), CLZhao 19332 (SWFC 00019332) (isotypes).

Habitat: on the ground covered with fallen pine-needles.

Notes: In the multi-locus phylogenetic analysis of the combined ITS-LSU-*hsp*90 sequence dataset of the taxa in Helvellaceae, our new collections (CLZhao 19347, CLZhao 19323, CLZhao 19332) were grouped within *Helvella* (Group A, Fig. 1) in the *fibrosa-macropus* lineage of the *Elastica* clade. In the preliminary phylogenetic analysis, BLAST searches of ITS regions of our collections showed 98.10% similarity to unidentified *Helvella* sp. (HKAS 87779) and 97.62% similarity with *Helvella* sp. (HKAS 90564), with a 94% query cover. Given the unpublished status and the lower query cover, these sequences were excluded from the final phylogenetic reconstruction, same as most recent published study (Park *et al.* 2025).

The key morphology of our collections consistent with the generic concept of *Helvella* (Skrede *et al.* 2017, Mao *et al.* 2023, Li *et al.* 2025, Park *et al.* 2025, Ullah *et al.* 2025). Morphologically, our new collection shares some similar morphologies with its phylogenetically closely related species viz., *H. orentitomentosa* Q. Zhao (MFLU 23-0099; holotype), *H. suborentitomentosa* S.Y. Park & Hwa Y. Lee (KA24-1339; holotype), and *H. kunmingensis* T.S. Li & Q. Zhao (HKAS 145326; holotype) (Fig. 2, Supplementary Table 1).

However, the considerable macro- and micro- morphological differences have observed among ours and these phylogenetically close collections (Fig. 1, Group A). *Helvella griseofuscostipitata* differs to *H. orentitomentosa* by having yellowish gray to brownish gray hymenium that becoming grayish (chocolate) brown at maturity (vs. gray and becoming grayish when dried); subpubescent, slightly longer (2.5–5 cm) and wider stipe (0.2–0.5 cm) with longitudinal shallow grooves (vs. tomentose, 4–6 cm long, and 0.4–0.7 cm thick); hyaline to pale brown, septate hyphae in the medullary excipulum (vs. hyaline hyphae); and hyaline to pale brown cells of *textura globulosa* to *textura angularis* cells in the ectal excipulum (Yu *et al.* 2023). Also, *H. griseofuscostipitata* differs to *H. suborentitomentosa* by having larger apothecia (0.5–1 cm high, 1–3 cm diam. vs. 0.3–0.6 cm high, 0.4–1.4 cm diam); subpubescent, longer stipe (2.5–5 cm vs. 0.8–2 cm); hyaline to pale brown cells of *textura globulosa* to *textura angularis* in the ectal excipulum; and paraphyses with wider (8–10 µm vs. 4.5–7. 2 µm) enlarged apex (Park *et al.* 2025). Further, our collection exhibits finely subpubescent, gray to dark brownish gray receptacle surface; longer stipes (2.5–5 cm long vs. 1.5–3 cm long); broader ectal excipulum (200–275 µm vs. 100–210 µm) with *textura globulosa* to *textura angularis* cells (vs. *textura angularis* cells); broader stipitipellis (200–300 µm vs. 170–210 µm); hyaline, slightly wider enlarged apex of paraphyses (8–10 µm vs. 4–7 µm) and shorter asci (200–250 × 12–19 µm vs. 250–320 × 11–14 µm) compared to *Helvella kunmingensis* (Li *et al.* 2025). Basically, our collections differentiate by having mainly bi- to tri-lobate mature apothecia, yellowish gray to brownish gray fresh hymenia, subpubescent, gray to dark brownish gray stipes with longitudinal shallow grooves, ectal excipulum with both *textura globulosa* and *textura angularis* cells, and finely verrucose younger ascospores (Supplementary Table 1). Thus, based on morphology and multi-gene phylogeny we introduced our collection as a new species, *Helvella griseofuscostipitata*.

Discussion

The historical taxonomy solely based on the macro- and micro- morphological characteristics under morphological species concept, in species level identification of *Helvella* species (Skrede *et al.* 2017). However, the current high species diversity of this genus makes it challenging. Therefore, polyphasic taxonomic approach integrated with morphology, phylogeny and ecology (substrates/habitats) are highly recommended in *Helvella* taxonomy. Based on our phylogenetic reconstruction of concatenated Helvellaceae sequence dataset of ITS-LSU-*hsp*90, the phylogenetic tree clearly visualized four distinct clades viz. *Acetabulum*, *Crispa*, *Elastica*, and *Lacunosa* as similar to the previous studies (Li *et al.* 2025, Park *et al.* 2025). Phylogenetically, our new species grouped within the *Elastica* clade, a species-rich group including eight lineages (Fig. 1) viz., *fibrosa-macropus*, *rivularis-sublicia*, *fallax-pezizoides*, *capucina-danica*, *carnosa*, *bicolor-elastica*, *corbierei-stevensii*, and *hypocrateriformis*. The *Elastica* clade consists of the species generally exhibit cup or saddle-shaped apothecia, thin and solid, terete stipes without ribs, sometimes with slight grooves, mostly with ellipsoid ascospores and sometimes with fusiform to subfusiform (that seems to be unique in *macropus* lineage) ascospores (Skrede *et al.* 2017, Yu *et al.* 2023, Park *et al.* 2025). In this clade, our new species *H. griseofuscostipitata* was grouped within *fibrosa-macropus* lineage which is currently consists of 13 species.

Even if DNA-based molecular phylogeny is currently demanding, still morphological characterization of *Helvella* species is important, as their morphology provides more informative characters in species identification. In the phylogenetic context, using a single molecular marker for species identification is debatable. Based on the data in GenBank (2026), ITS nrDNA region is highly fragmented when sequence aligning within *Helvella* species. Therefore, only ITS based phylogenetic analyses are not suitable for *Helvella* species identification. Following the previous taxonomic studies with multi-locus phylogeny including both protein-coding and non-coding genes (Skrede *et al.* 2017, Bao *et al.* 2023, Mao *et al.* 2023, Yu *et al.* 2023, Li *et al.* 2025, Park *et al.* 2025), we have conducted three loci phylogeny of ITS-nrLSU-*hsp*90 molecular markers.

Studies on global distribution of *Helvella* have been geographically uneven, with most investigations concentrated in Europe, followed by East Asia (mainly in China), Southeast Asia, and North America (Yu *et al.* 2023, Park *et al.* 2025). This seems due to different reflections in sampling effort rather than focusing on the true patterns of *Helvella* species richness. Therefore, increasing taxon sampling in poorly studied regions is required. Several *Helvella* species are known for their ectomycorrhizal associations with coniferous and broad-leaved trees. Therefore, forest habitats with such vegetations in underexplored tropical and subtropical regions are especially suitable for future surveys. These efforts will expand our understanding of biogeography and conservation planning for studying ecology of *Helvella* across underexplored localities.

Acknowledgements

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SUPPLEMENTARY TABLE 1. Synopsis of morphological characters phylogenetically closely related species to our new collection.

Species	***H. orentitomentosa* (MFLU 23-0099)**	***H. suborentitomentosa* (KA24-1339)**	***H. kunmingensis* (HKAS 145326)**	***H. griseofuscostipitata* (SWFC 00019347)**
Apothecia (high, broad)	5 cm, 1–3 cm, cupulate to lightly cupulate when young, irregularly lobed to discoid when mature	0.3–0.6 cm (cap), 0.4–1.4 cm, stipitate-cupulate, regular cupulate to saucer-shaped	2.5–4.5 cm, 1–3 cm, shallowly cupulate to cupulate when young, irregularly lobed to discoid when mature	3–5.5 cm high (cap + stipe), 1–3 cm, slightly cupulate when young, becoming discoid, bi- to tri-lobate or irregularly lobed with age
Hymenium	gray, becoming grayish when dried	beige to grayish brown	greyish black, becoming brown when dried	yellowish gray to brownish gray, becoming grayish brown when dried
Receptacle surface	tomentose, gray, becoming grayish when dried	pubescent, concolorous with hymenium	densely pubescent, grey to dark grey when fresh, becoming brown when dried	finely subpubescent, gray to dark brownish gray, concolourous with stipe
Stipe (high, broad)	4–6 cm, 0.4–0.7 cm, terete, tomentose, concolorous with receptacle surface, paler to yellowish white near the base	0.8–2 cm, 0.1–0.3 cm, yellowish white to beige, pubescent	1.5–3 cm, 0.3–0.5 cm, terete, densely pubescent, white to greyish white, becoming greyish brown when dried, white at the base	2.5–5 cm, 0.2–0.5 cm, terete, with longitudinal shallow grooves, gray to dark brownish gray, whitish creamy near the base, densely subpubescent
Excipulum; Medullary excipulum:	180–300 µm broad, hyaline, 7–10 µm broad hyphae, J–	*textura intricate* cells, hyaline to pale brown, hyphae 2.6–5.4 µm	190–290 µm thick, hyaline, *textura intricate* cells (4–8 µm diam.), J–	190–300 µm broad, hyaline to pale brown, 5–7.5 µm wide, septate hyphae, J–
Ectal excipulum:	70– 200 µm broad, outermost cells catenuliform in long fascicled tufts, hyaline, cylindrical to subclavate, end cells 20–55 × 12–30 µm, J–	*textura angularis* cells, hyaline to pale brown, outermost cells 12.7–36 × 8.9–16.6 µm, drum-shaped	100–210 µm thick, hyaline to pale brown cells of *textura angularis*, terminal cells 20–33 × 10–18 µm, J–	200–275 µm wide, hyaline to pale brown cells of *textura globulosa* to *textura angularis*, outermost layers with short cylindrical to cylindric-clavate cells, with catenuliform hyphal fascicles, terminal cells 20–30 × 10–15 µm, J–
Stipitipellis (width)	200–320 µm, hyaline, terminal cells 18–31 × 8–15 µm, clavate, J–	N/A	170–210 µm, hyaline cells of *textura angularis*, terminal cells 20–33 × 11–16 µm, J–	200–300 µm, hyaline to pale brown, outermost layers with short cylindrical cells, terminal cells 17–33 × 10–15 µm, J–

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SUPPLEMENTARY TABLE 1. (Continued)

Species	***H. orentitomentosa* (MFLU 23-0099)**	***H. suborentitomentosa* (KA24-1339)**	***H. kunmingensis* (HKAS 145326)**	***H. griseofuscostipitata* (SWFC 00019347)**
Paraphyses	3–4.5 µm broad, filiform, apex obviously enlarged, 8–11.5 µm broad	2.8–4.2 µm broad, filiform, septate, clavate, 4.5–7.6 µm broad at the apex	4–5 µm broad, filiform, apex slightly enlarged, 4–7 µm broad, brown	3–4.5 µm broad, filiform, septate, sparsely branched, 8–10 µm wide at the enlarged apex
Asci	210–250 × 16–18 µm, pleurorhynchous, 8-spored, subcylindrical to clavate	211.3–292.4 × 12.3–16.9 µm, pleurorhynchous, 8-spored, subcylindrical	250–320 × 11–14 µm, pleurorhynchous, 8-spored, subcylindrical to clavate	200–250 × 12–19 µm, pleurorhynchous, 8-spored, cylindrical to subcylindrical
Ascospores	(15–) 16–19 (-20) × 11–13 (-14) µm, ellipsoid, smooth-walled	(14.6–)17–17.6(–19.8) × (10.4-)11.3–11.7(-12.5) µm, broadly ellipsoid, hyaline, smooth, uni-guttulate	(16–) 17–21 (–21.5) × 10–12.5 (–13) µm, ellipsoid, smooth-walled, with one large oil drop in central when mature	(14–)15−17(–18.6) × (9–)10–12.5 µm, broadly ellipsoid, thin-walled, verrucose when young, with a dominant oil droplet at the middle when mature
Habitat/Locality	In a conifer forest dominated by *Pinus kesiyi*, in Thailand	On leaf litter or moss-covered ground in deciduous or coniferous forests in South Korea	On the ground in the *Quercus* forest, in Yunnan, China	On the ground covered with fallen pine-needles in Yunnan, China
Reference(s)	Yu *et al.* (2023)	Park *et al.* (2025)	Li *et al.* (2025)	This study

N/A—Data not available.