

Two new species and a new record of *Helvella* (Helvellaceae, Pezizales) from South Korea


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Abstract

In this study, we conducted morphological examinations and multi-locus phylogenetic analyses using ITS2, nrLSU, and *hsp90* markers on seven *Helvella* specimens collected in Korea in 2024. Our analyses confirmed the presence of six phylogenetic species, viz. including two novel species *H. griseomacropus* and *H. koreana* and one new record for Korea, *H. pseudoelastica*. The two new species formed independent clades within the *Macropus* and *Solitaria* lineages, respectively, and were clearly distinguishable from related taxa based on both morphological characteristics and molecular data. Notably, *H. koreana* formed a sister clade to *H. taiyuanensis*, but its distinct morphology and phylogenetic placement support its recognition as a new species. In addition, we secured a specimen of *H. acetabulum*, previously reported in Korea only in literature, but without any voucher specimens; its presence is now confirmed with our collection.

Key words: Acetabulum clade, Asia, Elastica clade, Ascomycota, Molecular phylogeny

Introduction

Members of the genus *Helvella* (Ascomycota, Pezizales, Helvellaceae) are widely distributed in temperate and boreal regions of the Northern Hemisphere and typically occur solitarily or gregariously on soil or moss in broadleaf forests (Skrede *et al.* 2017). Depending on the species, they are either saprotrophic or ectomycorrhizal in association with trees, thus contributing to various ecological functions in forest ecosystems (Hwang *et al.* 2015). Additionally, several *Helvella* species are traded commercially in certain regions for their edible and medicinal properties (Zhao *et al.* 2016, Landeros *et al.* 2021). Given these characteristics, *Helvella* species are regarded as fungal resources with both ecological and economic value, although their economic use is limited to certain regions.

Members of *Helvella* produce apothecia in various forms, including cupulate, saddle-shaped, and irregular morphologies. Most *Helvella* species bear terete or ribbed and furrowed stipes, except for a few sessile species that lack distinct stipes (Skrede *et al.* 2017). These macroscopic features distinguish *Helvella* from other macrofungal genera, but they are often insufficient for species delimitation within the genus. Historically, species identification has been based on macroscopic characters and microscopic structures, such as spores, paraphyses, medullary excipulum, and ectal excipulum. Numerous infrageneric classification systems have been proposed based on these traits (Dissing 1966, Weber 1972, Abbott & Currah 1997, Landeros *et al.* 2012, 2015).

Skrede *et al.* (2017) performed a multi-locus phylogenetic analysis using four genetic markers (nrLSU, *tef1-α*, *rpb2*, and *hsp90*) on 432 specimens collected from multiple continents (mostly from Europe). Their results indicated that *Helvella* species are highly endemic to continents, suggesting a geographically restricted distribution.

Recent taxonomic studies of *Helvella* in Asia have been actively conducted, supporting the evidence of strong regional endemism within the genus. Furthermore, these studies have revealed that the species diversity of Asian *Helvella* is much higher than previously recognized (Li *et al.* 2023, Mao *et al.* 2023, Wang *et al.* 2023, Yu *et al.* 2023, Park *et al.* 2025, Ullah *et al.* 2025).

In particular, Mao *et al.* (2023) conducted a phylogenetic study using Chinese specimens and global sequences and confirmed the presence of 4 clades and 24 lineages within *Helvella*. Their analyses revealed at least 93 phylogenetic species in China, including 53 previously reported Chinese species, 5 new records for China, 18 newly described species, and 17 putatively new species requiring further study. In Korea, 202 *Helvella* specimens collected from 1986 to 2023 were analyzed, and the results were integrated with representative sequences from all clades and lineages identified by Mao *et al.* (2023) (Park *et al.* 2025). Their results showed that only 3 of the 13 previously reported Korean species were phylogenetically confirmed, while 7 species were newly described and 8 were newly recorded from Korea. Furthermore, they identified 17 putatively distinct phylogenetic species that require further study and concluded that at least 35 phylogenetic species are present in Korea.

In this study, we analyzed seven *Helvella* specimens collected in Korea during a 2024 field survey. Morphological and multilocus phylogenetic analyses confirmed that three phylogenetic species were present in each of the *Acetabulum* and *Elastica* clades. In the *Acetabulum* clade, this study confirmed the presence of *H. acetabulum*, previously reported only in literature, in Korea, and *H. koreana* was proposed as a new species. In the *Elastica* clade, *H. pseudoelastica* was proposed as a new record from Korea, and *H. griseomacropus* was proposed as a new species.

Materials and methods

Fungal materials

A total of ten *Helvella* specimens were analyzed in this study. Seven specimens were newly collected between May and August 2024, and three additional specimens collected in 2023 (KA24-1347, KA24-1348, and KA24-1349). The specimens were collected from temperate broadleaf and mixed forests, mostly on soil or mossy ground under *Quercus* and *Pinus* trees. All specimens were photographed in the field using a digital camera (Olympus OM-D E-M1 Mark III, Tokyo, Japan), and metadata, such as GPS coordinates, habitat description, collection date, and collector information, were recorded (Rathnayaka *et al.* 2025). After the specimens were taken to the laboratory in plastic collection boxes, each specimen was assigned a field collection number (KH), dried at 40 °C for 72 h, and subsequently deposited in the Korea National Arboretum with accession numbers (KA).

Morphology descriptions

Morphological examinations were conducted on the ten specimens described above. Macroscopic and microscopic characteristics of the ascomata were examined following the methods of Landeros *et al.* (2015) and Skrede *et al.* (2017), including the shape and color of the apothecia, hymenium, and stipe, and microscopic features such as ascospores, asci, paraphyses, and excipular tissues. For microscopic observations, dried specimens were rehydrated by alternately soaking them in 70% ethanol and distilled water, and tissue structures were examined under a light microscope. Thirty ascospores per specimen were measured, along with 20 measurements each for other microscopic structures. Tissue sections were stained with cotton blue for microscopic observation. The overall observation protocols and format for reporting measurements followed the guidelines of Park *et al.* (2025).

DNA extraction, PCR amplification and sequencing

DNA extraction, PCR amplification, and sequencing were newly performed for the seven specimens collected in 2024, while the three specimens collected in 2023 were included using the sequence data and accession numbers reported in Park *et al.* (2025). Protocols for DNA extraction, PCR, and sequencing followed the procedures described by Park *et al.* (2025). Three commonly used genetic barcode markers for *Helvella* were employed: the internal transcribed spacer (ITS), nrLSU, and *hsp90*. The nrLSU region was amplified using the primer pair H_LSUf1/H_LSUr2 (Landeros *et al.* 2015), and the *hsp90* region was amplified using the primer pair H_hspf/H_hspr (Skrede *et al.* 2017). For the ITS region, initial amplification was attempted using the ITS1/ITS4 primer pair (White *et al.* 1990). Samples that failed to amplify with this combination were re-tested using the ITS5/ITS4 primer pair (White *et al.* 1990). For samples that did not yield amplification with either pair (KA25-0479, KA25-0480, KA25-0482, and KA25-0483), partial ITS2 sequences were successfully amplified using the ITS3/ITS4 primer pair (White *et al.* 1990). The amplified PCR

products were sequenced using the Sanger method by Cosmogenetech (Daejeon, Korea). As a result, a total of eight ITS, ten nrLSU, and ten *hsp90* sequences were analyzed from the ten specimens examined in this study. All sequences were submitted to GenBank and accession numbers were obtained (Table 1).

TABLE 1. Korean *Helvella* species and sequences analyzed in this study. Species names in bold indicate sequences obtained from the ten specimens that were examined for both morphological and molecular phylogenetic analyses. A hyphen (–) represents data not available.

Species name	Type	Sample ID	Voucher No.	Accession no.			Country
				ITS	LSU	<i>hsp90</i>	
<i>Dissingia oblongispora</i>			HSA 137	OR355181	OR355355	OR366160	China
<i>Dissingia oblongispora</i>			HSA 169	OR355182	OR355356	OR366161	China
<i>Helvella acetabuloides</i>	holotype		CFSZ2044	OR355015	OR355185	MK652219	China
<i>Helvella acetabuloides</i>			BJTC FM1264	OR355166	OR355337	OR366140	China
<i>H. acetabulum</i>		H134	O-64925	-	KY772985	KY784267	Norway
<i>H. acetabulum</i>		H225	O-253212	-	KY773055	KY784344	Norway
<i>H. acetabulum</i>	epitype	H410	C-F Fungi Exs. Suec. 1354	-	-	KY784506	Sweden
<i>H. acetabulum</i>		KH089	KA25-0481	PV830655	PV830661	PV853822	Korea
<i>H. alborava</i>	holotype		BJTC C316-A	OR355106	OR355276	OR366098	China
<i>H. alborava</i>			BJTC C316-B	OR355173	OR355347	OR366148	China
<i>H. arctoalpina</i>			N127	OQ065745	PP396828	-	Turkey
<i>H. arctoalpina</i>			VANF127-2	PQ512823	PQ507477	-	Turkey
<i>H. arctoalpina</i>			VANF127-3	PQ512824	PQ507478	-	Turkey
<i>H. atroides</i>			MFLU23-0101	-	OQ866058	OQ863540	Thailand
<i>H. atroides</i>	holotype		MFLU23-0102	-	OQ866059	OQ863541	Thailand
<i>H. atroides</i>			MFLU23-0103	-	OQ866060	OQ863542	Thailand
<i>H. elastica</i>		H066	O-253311	-	KY772950	KY784230	Sweden
<i>H. fistulosa</i>			MFLU23-0096	-	OQ866053	OQ863535	Thailand
<i>H. fistulosa</i>			MFLU23-0097	-	OQ866054	OQ863536	Thailand
<i>H. fistulosa</i>			MFLU23-0098	-	OQ866055	OQ863537	Thailand
<i>H. griseomacropus</i> sp. nov.		H41	KA16-0551	PP545146	PP544953	-	Korea
<i>H. griseomacropus</i> sp. nov.		H59	KA20-0060	PP545162	PP544970	-	Korea
<i>H. griseomacropus</i> sp. nov.		H72	KA21-1232	PP545173	PP544981	-	Korea
<i>H. griseomacropus</i> sp. nov.		KH027	KA24-1348	PP545244	PP545067	PP782836	Korea
<i>H. griseomacropus</i> sp. nov.		KH028	KA24-1349	PP545245	PP545068	PP782837	Korea
<i>H. griseomacropus</i> sp. nov.	holotype	KH099	KA25-0485	-	PV830665	PV853826	Korea
<i>H. griseomacropus</i> sp. nov.		N39	NIBRFG0000511082	PP545198	PP545015	-	Korea
<i>H. griseomacropus</i> sp. nov.		N40	NIBRFG0000511110	PP545199	PP545016	-	Korea
<i>H. griseomacropus</i> sp. nov.		N48	NIBRFG0000513941	PP545205	PP545022	-	Korea
<i>H. koreana</i> sp. nov.	holotype	KH087	KA25-0479	PV830653	PV830659	PV853820	Korea
<i>H. koreana</i> sp. nov.		KH088	KA25-0480	PV830654	PV830660	PV853821	Korea
<i>H. macropus</i>		H238	O-291425	-	KY773067	KY784356	Norway

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TABLE 1. (Continued)

Species name	Type	Sample ID	Voucher No.	Accession no.			Country
				ITS	LSU	hsp90	
<i>H. macropus</i>		H239	O-291391	-	KY773068	-	Norway
<i>H. macropus</i>	epitype	H412	C-F Fungi Exs. Suec. 3266	-	-	KY784507	Sweden
<i>H. neofistulosa</i>	holotype		BJTC ZH1213	OR355059	OR355229	OR366056	China
<i>H. neofistulosa</i>			BJTC ZH1251	OR355060	OR355230	OR366057	China
<i>H. nigrorava</i>	holotype		BJTC ZH67	OR355105	OR355275	OR366097	China
<i>H. orentitomentosa</i>	holotype		MFLU23-0099	-	OQ866056	OQ863538	Thailand
<i>H. orentitomentosa</i>			MFLU23-0100	-	OQ866057	OQ863539	Thailand
<i>H. pakistanica</i>	holotype		M.jabba01	PQ410250	-	-	Pakistan
<i>H. pakistanica</i>			M.jabba02	PQ410251	-	-	Pakistan
<i>H. pseudoelastica</i>		KH056	KA24-1347	-	PP545094	PP782860	Korea
<i>H. pseudoelastica</i>		KH090	KA25-0482	PV830656	PV830662	PV853823	Korea
<i>H. pseudoelastica</i>	holotype		BJTC C351-A	OR355170	OR355341	OR366143	China
<i>H. pseudoelastica</i>			BJTC C351-B	OR355174	OR355348	OR366149	China
<i>H. rivularis</i>		H1978	O-255764	MN656175	MN655850	MN692371	Norway
<i>H. rivularis</i>	holotype	H276	C-F-59447	-	-	KY784391	Norway
<i>H. rivularis</i>			VANF714	PP359562	PP396830	-	Turkey
<i>H. rivularis</i>			VANF714-2	PQ512821	PQ507475	-	Turkey
<i>H. rivularis</i>			VANF714-3	PQ512822	PQ507476	-	Turkey
<i>H. rugosa</i>			MFLU23-0093	-	OQ866050	OQ863532	Thailand
<i>H. rugosa</i>			MFLU23-0094	-	OQ866051	OQ863533	Thailand
<i>H. rugosa</i>			MFLU23-0095	-	OQ866052	OQ863534	Thailand
<i>H. solitaria</i>		H090	O-253371	-	KY772959	KY784241	France
<i>H. solitaria</i>		H215	O-253379	-	KY773047	KY784336	Norway
<i>H. solitaria</i>			BJTC FM417	OR355131	OR355302	OR366120	China
<i>H. sp. K18</i>		KH092	KA25-0483	PV830657	PV830663	PV853824	Korea
<i>H. sp. K7</i>		KH096	KA25-0484	PV830658	PV830664	PV853825	Korea
<i>H. sp. K7</i>		S07	SFC20150813-12	PP545213	PP545030	-	Korea
<i>H. sublactea</i>			VANF141	PP359561	PP396829	-	Turkey
<i>H. sublactea</i>			VANF141-2	PQ512819	PQ507473	-	Turkey
<i>H. sublactea</i>			VANF141-3	PQ512820	PQ507474	-	Turkey
<i>H. sublicia</i>		H148	O-70080	-	KY772997	KY784281	Norway
<i>H. sublicia</i>			KH.11.84(S)	-	MK100273	MK179403	Sweden
<i>H. submacropus</i>	holotype		HKAS 70217	KX506977	KX506932	OR220563	China
<i>H. submacropus</i>			HKAS 78944	-	KX506934	OR220561	China
<i>H. submacropus</i>			HKAS 78930	KX506978	KX506933	OR220562	China
<i>H. submacropus</i>			HKAS 57739	KX506980	KX506935	OR220560	China
<i>H. submacropus</i>			HKAS 90593	KX506982	KX506937	OR220559	China
<i>H. taiyuanensis</i>			HMAS 277500	MK592152	MK592105	MK652216	China
<i>H. taiyuanensis</i>			119250	MK592151	MK592104	MK652215	China
<i>H. taiyuanensis</i>			BJTC FM192	OR355167	OR355338	OR366141	China
<i>H. taiyuanensis</i>			BJTC FM861	OR355168	OR355339	OR366142	China
<i>H. ulvinenii</i>			HKAS 90321	-	KU167483	OR366155	China

Phylogenetic analyses

The newly obtained sequences from this study were first checked for quality, assembled, and compared using the BLASTn search engine to identify the most similar publicly available sequences. The top matches corresponded to sequences previously published by Skrede *et al.* (2017), Mao *et al.* (2023), Li *et al.* (2023), and Park *et al.* (2025), and these sequences were used as references in subsequent phylogenetic analyses.

Sequence alignment and editing were conducted using Geneious Prime 2023.2 (<https://www.geneious.com>). Alignments were performed using MAFFT v7.490 (Katoh *et al.* 2002, Katoh & Standley 2013), followed by manual trimming to remove ambiguous or low-confidence regions. For ITS sequences, the trimmed region was adjusted to match the ITS3/ITS4 amplification range. Each locus (ITS2, nrLSU, and *hsp90*) was aligned separately, and both single-locus and concatenated datasets were prepared for phylogenetic analyses.

Phylogenetic trees were inferred using the maximum likelihood (ML) analysis was conducted using IQ-TREE v2.3.6 (Nguyen *et al.* 2015). The best-fit substitution models for each dataset were determined based on the Bayesian Information Criterion using ModelFinder (Kalyaanamoorthy *et al.* 2017). The optimal partitioning scheme was selected using the integrated PartitionFinder2 algorithm (Lanfear *et al.* 2017) implemented in IQ-TREE. TPM2u+F+G4 for the ITS2 region, TN+F+I+R2 for LSU, and K2P+G4 for *hsp90*. For the concatenated dataset, TPM2u+F+G4 was applied to ITS (1–238 bp) and TN+F+I+R2 was applied to LSU (239–888 bp) and K2P+G4 was applied to *hsp90* (889–1105 bp). Ultrafast bootstrap (Hoang *et al.* 2018) with 1,000 replicates was used to assess branch support and generate the consensus tree. Bayesian inference (BI) analyses were performed using MrBayes v3.2.7 (Ronquist *et al.* 2012) on both the concatenated ITS–nrLSU–*hsp90* dataset and individual single-locus datasets. The GTR + G substitution model was applied, with all model parameters unlinked across partitions. Two independent runs, each consisting of four Markov chain Monte Carlo (MCMC) chains, were executed for 2,000,000 generations, sampling every 1,000 generations. Convergence was assessed by monitoring the average standard deviation of split frequencies (< 0.01) and confirming that potential scale reduction factors (PSRF) approached 1.0. The first 25 % of sampled trees were discarded as burn-in, and the remaining trees were used to construct a 50 % majority-rule consensus tree with posterior probability (PP) values. Clades with ultrafast bootstrap (UFBoot) support values ≥ 95 % and Bayesian posterior probability (PP) values > 0.95 were considered strongly supported. The resulting trees were visualized using iTOL v6 (Letunic & Bork 2024).

Results

Phylogenetic analyses

A total of 171 sequences representing 26 species were included in the phylogenetic analysis (Fig. 1). The aligned length of each locus was as follows: ITS2, 238 bp (47 sequences); nrLSU, 650 bp (69 sequences); and *hsp90*, 217 bp (55 sequences). The final concatenated alignment consisted of 74 sequences with a total length of 1,105 bp. The concatenated dataset comprised 285 distinct alignment patterns, 262 parsimony-informative sites, and 13 singleton sites. The optimal log-likelihood of the dataset was –4492.908, and the proportion of undetermined characters or gaps was 18.36%. Detailed phylogenetic information for each single-locus dataset is provided in Supplementary Table 1 (Table S1). The ML and BI analyses yielded similar topologies; therefore, only the ML tree is presented, with UFB and PP support values indicated on branches (UFB/PP).

Three major clades were recognized in the phylogenetic analyses, and the ten specimens analyzed in this study were placed within the *Acetabulum* and *Elastica* clades. In the *Acetabulum* lineage, KA25-0481 formed a monophyletic group with *H. acetabulum* (UFB=96, PP=0.90). In the *Solitaria* lineage, KA25-0483 clustered with *H. taiyuanensis* (UFB=88, PP=0.99), whereas KA25-0479 and KA25-0480 formed a well-supported independent branch (UFB=100, PP=1), representing *H. koreana*.

The remaining six specimens were placed within three distinct lineages of the *Elastica* clade. In the *Capucina*–*Danica* lineage, KA25-0482 formed a monophyletic group with *H. pseudoelastica* (UFB=96, PP=0.95). In the *Rivularis*–*Sublicia* lineage, KA25-0484 formed a well-supported monophyletic branch with *H. alborava* (UFB=99, PP=1). In the *Macropus* lineage, KA25-0485 formed a robust independent branch along with *H. sp.* K17 specimens (UFB=100, PP=1), which represent *H. griseomacropus*.

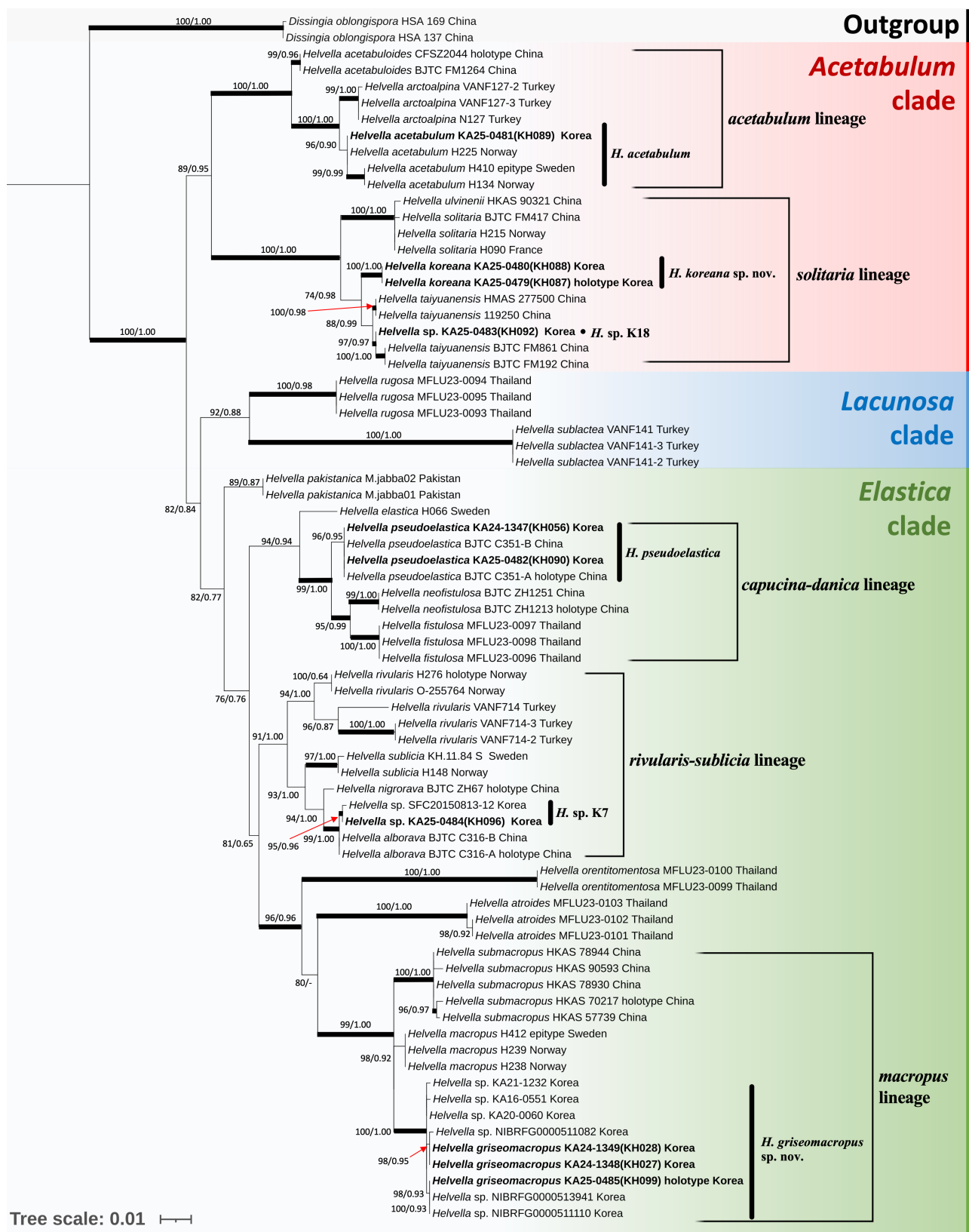


FIGURE 1. Phylogenetic tree of Korean *Helvella* species constructed using maximum likelihood (ML) and Bayesian inference (BI) analyses based on concatenated ITS, nrLSU, and *hsp90* sequences. Numbers on branches indicate ML ultrafast bootstrap (UFB) and Bayesian posterior probability (PP) support values (UFB/PP). Bold branches indicate strongly supported clades with UFB ≥ 95% and PP > 0.95. Species names in bold represent specimens examined in this study.

Taxonomy

Helvella griseomacropus S.Y. Park & H. Lee, *sp. nov.* (Fig. 2)

MycoBank: MB#859720

Etymology: The name *griseomacropus* is derived from *griseo*-, meaning gray, and *macropus*, referring to its resemblance to *Helvella macropus*.

Diagnosis: Very similar to *Helvella submacropus*, but differs by the presence of a distinct subhymenium layer and longer ascospores.

Type: SOUTH KOREA, Chungcheongbuk-do, Yeongdong-gun, Sangchon-myeon, Mulhan-ri, San 50-1, elev. 551 m, 7 August 2024, S.Y. Park, KH099 (KA25-0485, **holotype**).

Apothecia stipitate-cupulate. **Cap** 0.5–2.0 cm high, 1.2–4.0 cm broad, cup-shaped to discoid, occasionally laterally compressed, margin even to reflexed, free from stipe. **Hymenium** pale gray or brownish gray when fresh, becoming brownish when dried, surface smooth. **Receptacle surface** concolorous with hymenium, inconspicuously pubescent. **Stipe** 2.3–9.0 cm high, 0.2–0.5 cm broad, pale grey to grey, tapering upwards, sometimes brownish tint at the base, pubescent, terete, sometimes with one or more longitudinal grooves.

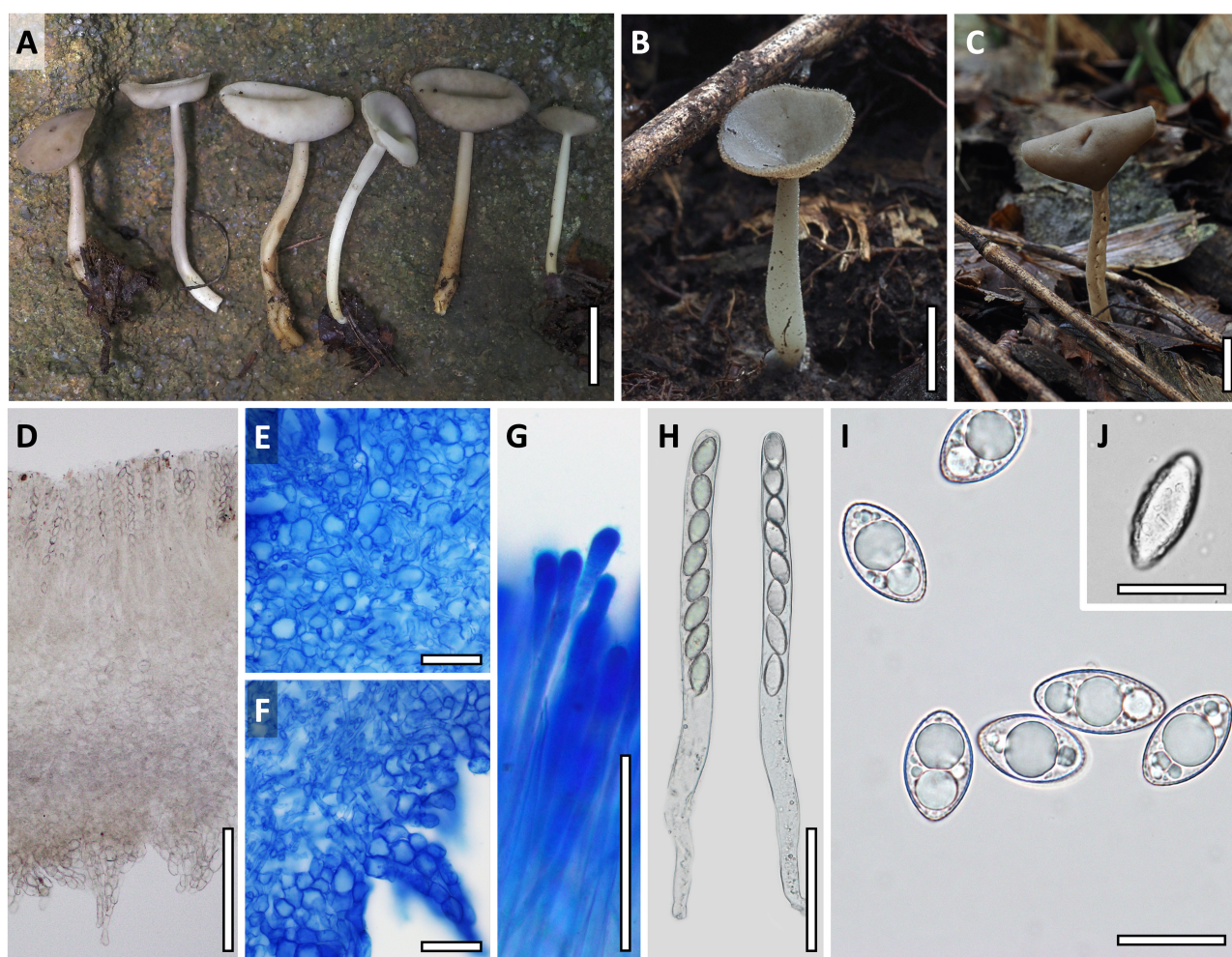


FIGURE 2. Morphological characteristics of *Helvella griseomacropus* *sp. nov.* **A–C** Fruit bodies; **A**: KA25-0485 (KH099), **B**: KA24-1348 (KH027), **C**: KA24-1349 (KH028). **D** Vertical section of apothecium of KA25-0485 in water. **E** Subhymenium of KA25-0485 in cotton blue. **F** Medullary and ectal excipulum of KA25-0485 in cotton blue. **G** Paraphyses of KA25-0485 in cotton blue. **H** Asci of KA24-1349 in water. **I** Ascospores of KA25-0485 in water. **J** Warted spore of KA24-1349 in water. Scale bars: **A–C** = 1 cm; **D** = 200 μ m; **E–H** = 50 μ m; **I–J** = 20 μ m.

Ectal excipulum 60–100 μ m broad, of textura globulosa-angularis, 17.4–35.3 \times 14–25.6 μ m. **Outermost cells** 80–210 μ m broad, drum-shaped, 13.2–41.1 \times 7.9–18.9 μ m. **Medullary excipulum** 150–240 μ m broad, of textura intricata, hyphae 3–5.8 μ m. **Subhymenium** 30–170 μ m broad, of textura globulosa-intricata. **Asci** (204.6–) 239.8–242.4 (–310) \times (13–) 14.9–15.1 (–18.6) μ m, pleurohynchous, subcylindrical, eight-spored. **Ascospores** [90/3/3 in H₂O]

(20.8–) 23.3–24.3 (–26.7) \times (10.3–) 11.3–11.7 (–12.5) μm , ellipsoid to broadly ellipsoid, subfusoid, smooth, hyaline, [Q (1.85–) 2.03–2.13 (–2.36), Q_{av} 2.08 \pm 0.15]. **Paraphyses** 3–4.3 μm , filiform, septate, hyaline. **Apex of paraphyses** 5.4–9.9 μm

Habitat and known distribution: Solitary or scattered on the ground in broad-leaved forest.

Additional specimen examined: SOUTH KOREA, Jeju, Jeju-si, 1100-ro 2073, elev. 1,055 m, 9 July 2023, S.Y. Park, KH027 (KA24-1348), SOUTH KOREA, Jeju, Jeju-si, 1100-ro 2073, elev. 1,055 m, 9 July 2023, S.Y. Park, KH028 (KA24-1349)

Notes: In the phylogenetic analysis, sequences of *Helvella griseomacropus* formed an independent branch with strong support within the *Macropus* lineage. *Helvella macropus* and *Helvella submacropus* were represented as the most closely related taxa. One of the distinct traits of *H. griseomacropus* is its grey-colored ascomata, which distinguishes it from *H. macropus*, whose ascomata are yellowish-brown to pale greyish-brown (Dissing 1966). *H. submacropus* is very similar to *H. griseomacropus* in many traits, including color, size, and microscopic features; however, several notable differences were observed. The color of *H. griseomacropus* is paler than that of *H. submacropus*, and its apothecia are more plane to discoid in shape (Fig. 2B), rather than shallowly cupulate as in *H. submacropus* (Li *et al.* 2023). Microscopically, *H. griseomacropus* has a distinct subhymenial layer composed of textura globulosa-intricata. In addition, the ascospores of *H. griseomacropus* are longer (20.8–26.7 \times 10.3–12.5 μm vs. 17–23 \times 10–13 μm), and the average Q value (length/width ratio) is markedly higher than in *H. submacropus* (2.08 \pm 0.15 vs. 1.73 \pm 0.12).

Helvella koreana S.Y. Park & H. Lee, *sp. nov.* (Fig. 3)

Mycobank: MB#859722

Etymology: The specific epithet *koreana* refers to the type locality, Korea.

Diagnosis: Similar to *Helvella solitaria*, which has compressed cup-shaped to cup-shaped apothecia at maturity, but the apothecia of *Helvella koreana* remain persistently compressed cup-shaped throughout development.

Type: SOUTH KOREA, Gyeonggi-do, Paju-si, Jori-eup, Samneung-ro 89, elev. 28 m, 13 May 2024, S.Y. Park & H.P. Choi, KH087 (KA25-0479, **holotype**).

Apothecia stipitate-cupulate. **Cap** 1.0–3.5 cm high, 1.3–3.6 cm broad, laterally compressed cup-shaped, margin deflexed to even, free from stipe. **Hymenium** grayish brown to dark brown. surface smooth. **Receptacle surface** concolorous with the hymenium, covered with whitish tufts. blunt ribs nearly absent or covering approximately one-third of the receptacle surface. **Stipe** 1.0–5.2 cm high, 0.3–1.3 cm broad, cream to white at the base, gradually becoming dark brown toward the apex and concolorous with the receptacle surface, tapering upwards, glabrous but covered with tufts at the apex, ribbed and furrowed, ribs blunt, exhibiting both single- and double-edged forms, with anastomosis present.

Ectal excipulum 70–110 μm broad, of textura angularis, 10.4–28.4 \times 6.3–21.6 μm . **Outermost cells** 40–100 μm broad, club-shaped, 9.4–25.1 \times 6.2–13.1 μm . **Medullary excipulum** 360–490 μm broad, of textura intricata, hyphae 2.4–5 μm . **Asci** (266.1–) 310.4–313.2 (–356.1) \times (13.8–) 16.2–16.4 (–20.7) μm , pleurohynchous, subcylindrical, eight-spored. **Ascospores** [60/2/2 in H_2O] (17.8–) 19.6–20 (–22.1) \times (13–) 14.6–15 (–16) μm , ellipsoid to broadly ellipsoid, smooth, hyaline, [Q (1.15–) 1.32–1.36 (–1.55), Q_{av} 1.34 \pm 0.08]. **Paraphyses** 2.2–4.9 μm , clavate, septate, yellowish-brown. **Apex of paraphyses** 4.3–8.5 μm .

Habitat and known distribution: Scattered on moss or soil in broad-leaved or mixed forests.

Additional specimen examined: SOUTH KOREA, Gyeonggi-do, Paju-si, Jori-eup, Samneung-ro 89, elev. 28 m, 13 May 2024, S.Y. Park & H.P. Choi, KH088 (KA25-0480).

Notes: *Helvella koreana* belongs to the *Solitaria* lineage and forms a sister relationship with *Helvella taiyuanensis* in the phylogenetic tree. However, morphologically it shows a closer resemblance to *Helvella solitaria*. The apothecia of *H. koreana* remain laterally compressed cup-shaped throughout development, whereas those of *H. taiyuanensis* are irregular to saddle-shaped, and *H. solitaria* develops from a compressed form when young to a regular cup shape at maturity.

Ascospore dimensions of *H. koreana* (17.8–22.1 \times 13–16 μm) are comparable to those of *H. solitaria* (19–24 \times 12–15 μm) (Dissing 1966), but larger than those of *H. taiyuanensis* (15–18.9 \times 11.3–13.4 μm) (Liu 1985). The stipe of *H. koreana* is cream to white and glabrous, becoming concolorous with the receptacle surface toward the apex and bearing scattered tufts. In contrast, *H. solitaria* has a whitish to grayish-white stipe, and *H. taiyuanensis* is white to cream, both showing uniform coloration from base to apex, with *H. taiyuanensis* bearing a single rounded longitudinal ridge (Wang *et al.* 2019).

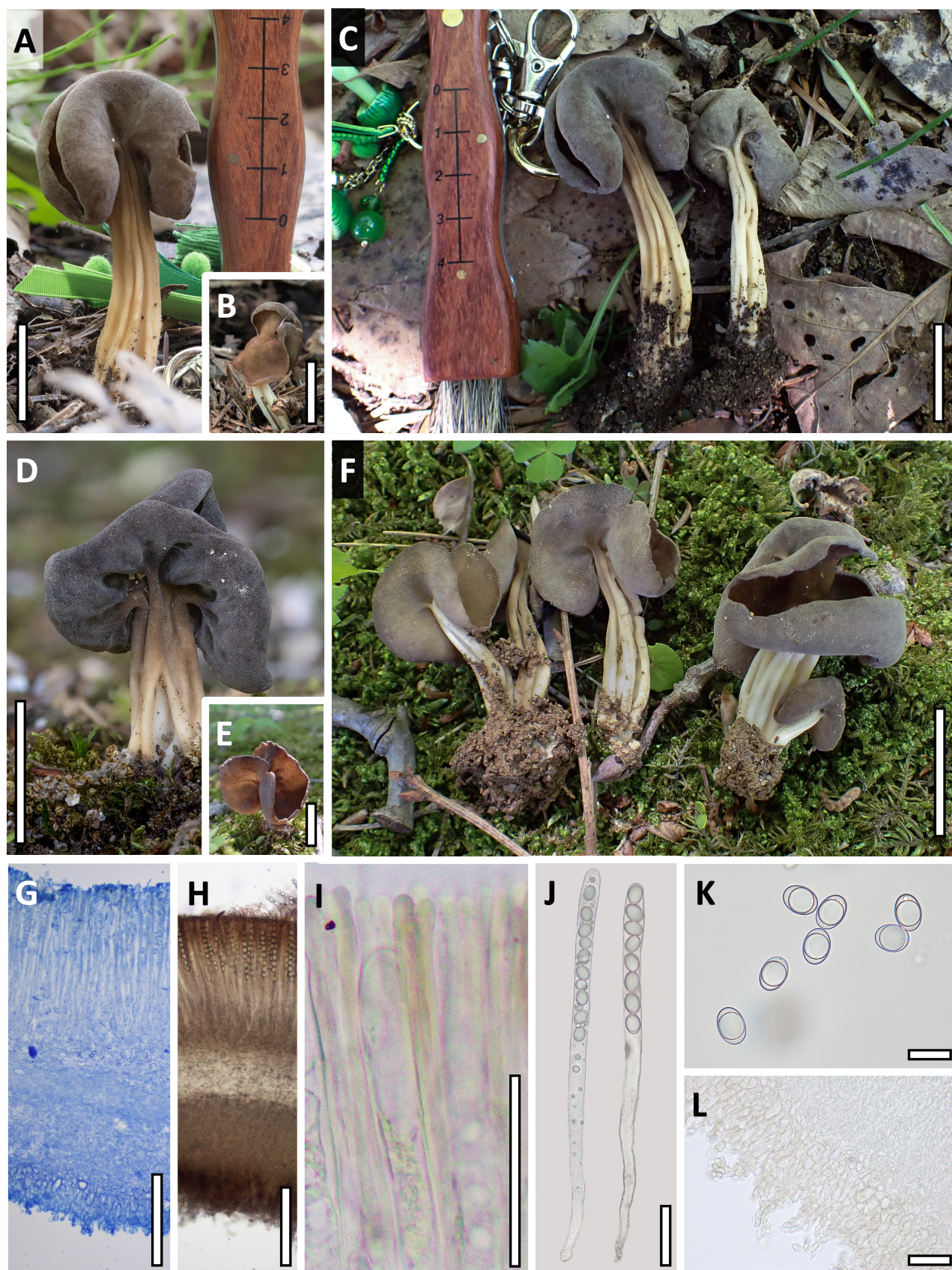


FIGURE 3. Morphological characteristics of *Helvella koreana* sp. nov. A–F Fruit bodies; A–C: KA25-0479 (KH087), D–F: KA25-0480 (KH088). G Vertical section of apothecium of KA25-0479 in cotton blue. H Vertical section of apothecium of KA25-0480 in water. I Paraphyses of KA25-0480 in water. J Asci of KA25-0479 in water. K Ascospores of KA25-0479 in water. L Medullary and ectal excipulum of KA25-0480 in water. Scale bars: A–C = 2 cm; D–F = 1 cm; G–H = 200 µm; I–J = 50 µm; K = 20 µm; L = 50 µm.

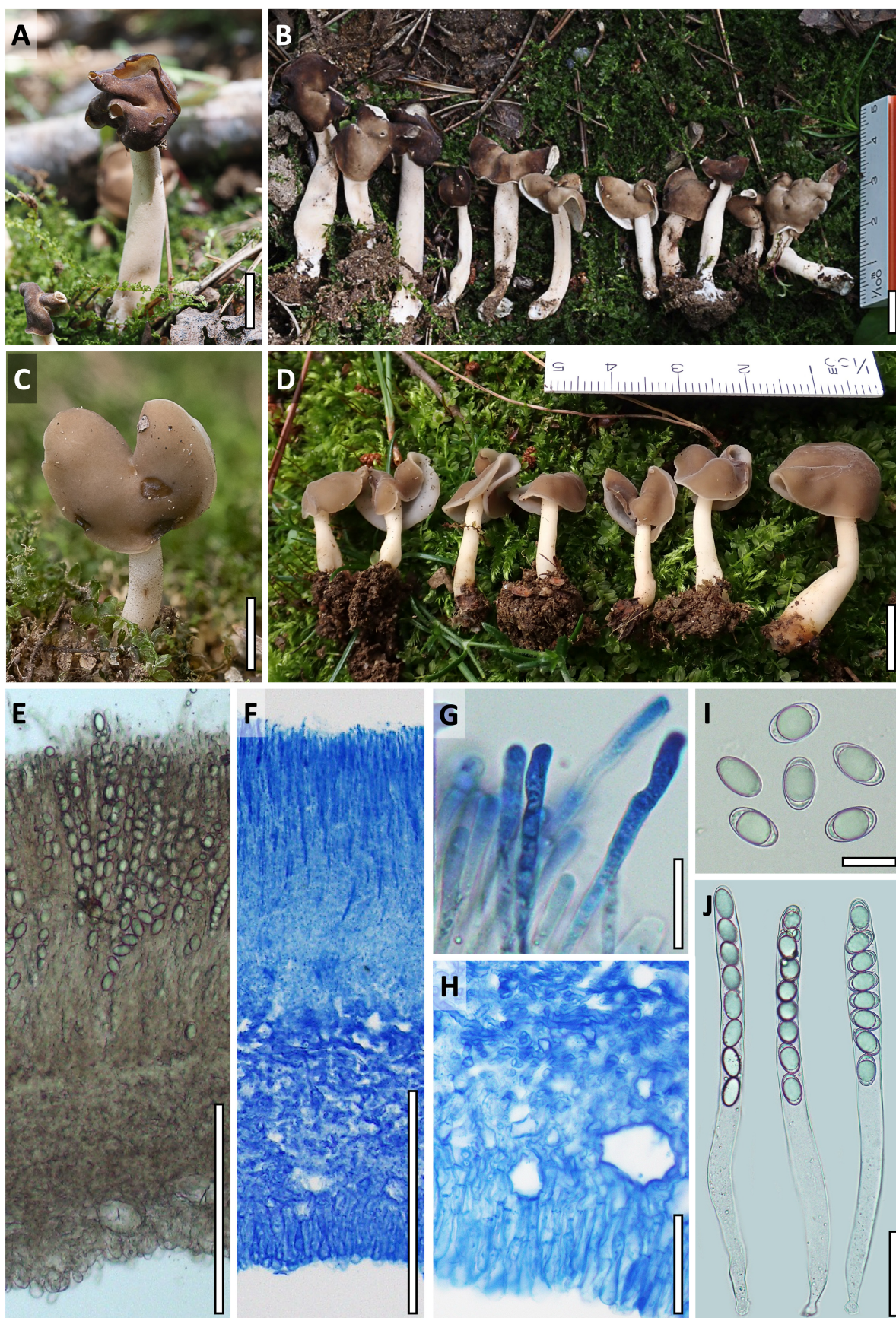


FIGURE 4. Morphological characteristics of *Helvella pseudoelastica*. **A–D** Fruit bodies; **A–B**: KA24-1347 (KH056), **C–D**: KA25-0482 (KH090). **E** Vertical section of apothecium of KA24-1347 in water. **F** Vertical section of apothecium of KA25-0482 in cotton blue. **G** Paraphyses of KA24-1347 in cotton blue. **H** Medullary and ectal excipulum in cotton blue. **I** Ascospores of KA24-1347 in water. **J** Asci of KA24-1347 in water. Scale bars: **A–D** = 1 cm; **E–F** = 200 μ m; **G** = 20 μ m; **H** = 50 μ m; **I** = 20 μ m; **J** = 50 μ m.

Apothecia stipitate-capitate. **Cap** 0.6–1.6 cm high, 0.6–2.0 cm broad, saddle-shaped, bilobate, occasionally irregularly lobed, margin deflexed to even. **Hymenium** beige to brown, glabrous, smooth, becoming brown when dry. **Receptacle surface** grayish white to white. **Stipe** 1–3 cm high, 0.3–0.6 cm broad, white to yellowish white, terete.

Ectal excipulum 40–80 µm broad, of textura angularis, 21–42 × 14.2–24.5 µm, occasionally with large globose cells in the inner layer. **Outermost cells** 20.2–44 × 10.4–17.7 µm, elongate club-shaped. **Medullary excipulum** 130–180 µm broad, of interwoven textura intricata, hyphae 3–4.7 µm. **Asci** (256.6–) 268.6–274.8 (–297.1) × (14.1–) 16.9–17.7 (–22.1) µm, pleurohynchous, subcylindrical, eight-spored. **Ascospores** [30/1/1 in H₂O] (17.4–) 19.4–20.8 (–22.9) × (12.2–) 12.6–13.2 (–14.4) µm, ellipsoid to broadly ellipsoid, smooth, hyaline, [Q (1.3–) 1.51–1.61 (–1.79), Qav 1.56 ± 0.12]. **Paraphyses** 2.6–4.7 µm, filiform, septate, pale brown. **Apex of paraphyses** 6.2–7.6 µm.

Habitat and known distribution: Solitary on mossy ground in mixed forests.

Specimen examined: SOUTH KOREA, Gangwon-do, Taebaek-si, Hwangji-dong 25-2, elev. 688 m, 22 July 2023, S.Y. Park, KH056 (KA24-1347). SOUTH KOREA, Gangwon-do, Taebaek-si, Hwangji-dong 25-2, elev. 688 m, 23 July 2024, S.Y. Park, KH090 (KA25-0482).

Notes: Specimen KA24-1347 was collected in 2023, and KA25-0482 was collected from the same locality in 2024. The collection site was a well-lit mixed forest park located in a high-altitude area, where the specimens were found scattered on moss under trees. Both specimens shared common morphological characteristics, including small, compressed apothecia (Fig. 4A–D) and the occasional presence of large, globose cells in the ectal excipulum (Fig. 4E, H).

Notably, KA25-0482 exhibited no development of asci in any of the apothecia, even in mature specimens, and no developing asci were observed.

Discussions

Helvella griseomacropus formed an independent branch within the *Macropus* lineage, which is defined by the shared derived traits of stipitate-cupulate apothecia and subfusoid ascospores (Mao *et al.* 2023), distinguishing it from other members of the *Elastica* clade. Our morphological observations confirmed that *H. griseomacropus* shares synapomorphic traits. Although it resembles *Helvella macropus* and *Helvella submacropus* but it differs in several aspects (Table 2). *H. macropus* is characterized by a yellowish-brown to pale grayish-brown hymenium (Dissing 1966), whereas *H. griseomacropus* exhibits a gray to pale grayish coloration with little to no brown hue. *H. submacropus* is very similar to *H. griseomacropus*, but the latter has an overall paler ascocarp and less conspicuous pubescence on the stipe and receptacle surfaces (Li *et al.* 2023).

Helvella koreana formed an independent branch within the *Solitaria* lineage, as a sister group to *H. taiyuanensis*. Despite its close phylogenetic relationship to *H. taiyuanensis* and *H. solitaria*, it shows morphological differences (Table 3). For instance, *H. solitaria* develops cup-shaped apothecia that become laterally compressed over time (Dissing 1966), whereas *H. koreana* exhibits laterally compressed cup-shaped apothecia throughout its developmental stage. *H. koreana* also differs from *H. taiyuanensis* in several morphological aspects: the hymenium of *H. koreana* is grayish brown to dark brown, and the receptacle surface is sometimes covered by ribs extending up to one-third of its area, whereas in *H. taiyuanensis*, ribs do not extend onto the receptacle surface (Liu 1985). In addition, *H. koreana* consistently produces slightly larger ascospores (17.8–22.1 × 13–16 µm) than *H. taiyuanensis* (15–18.9 × 11.3–13.4 µm).

Helvella pseudoelastica was suggested to occur in South Korea by Mao *et al.* (2023), based on the Korean specimen KA12-1701, whose ITS sequence (KR673633) was identical to that of *H. pseudoelastica*, although it had been previously identified as *Helvella cf. elastica* by Kim *et al.* (2015). In this study, KA24-1347 and KA25-0482 formed a strongly supported monophyletic group with *H. pseudoelastica*, supporting the hypothesis that *H. pseudoelastica* may occur in South Korea (Fig. 1). However, these specimens exhibited several morphological differences from the original description of the species. According to the original description of *H. pseudoelastica* by Mao *et al.* (2023), the hymenium is grayish white and turns yellowish when dried, whereas the Korean specimens displayed a beige to brown hymenium that became brown upon drying. Particularly, stipe coloration showed a marked difference: the original description noted distinct pinkish tints at the stipe base as a characteristic feature of the species, which were not

observed in the Korean specimens (Fig. 4A–D). Such morphological discrepancies are comparable to those reported for *H. fistulosa* (Skrede *et al.* 2017, Yu *et al.* 2023, Park *et al.* 2025). In the original description of *H. fistulosa*, the stipe occasionally exhibited a reddish-brown color upon drying (Skrede *et al.* 2017). A subsequent report from Thailand described the stipe as white to cream, which becomes yellowish when dried (Yu *et al.* 2023). In Korea, *H. fistulosa* is generally observed with white to cream-colored stipes, but some specimens exhibit a distinctly reddish tint at the base (Park *et al.* 2025). This degree of phenotypic variation suggests that these traits may vary depending on the environmental conditions or locality.

TABLE 2. Morphological comparison among *Helvella griseomacropus*, *H. macropus*, and *H. submacropus*.

	<i>Helvella griseomacropus</i>	<i>Helvella submacropus</i>	<i>Helvella macropus</i>
Apothecia	0.5–2.0 cm high, 1.2–4.0 cm broad, cup-shaped to discoid, occasionally laterally compressed	0.5–1.5 cm high, 1–3 cm broad, shallowly cupulate to cupulate	2.0-3.0 cm broad, deep, regular cupulate
Hymenium	pale gray or brownish gray when fresh, becoming brownish when dried	greyish to pale grey when fresh, yellowish when dried	yellowish-brown to pale greyish-brown
Receptacle surface	concolorous with hymenium, inconspicuously pubescent	greyish when fresh, becoming yellowish when dried, villose to densely pubescent	concolorous with hymenium or grey, villose
Stipe	2.3–9.0 cm high, 0.2–0.5 cm broad, pale grey to grey, tapering upwards, sometimes brownish tint at the base, pubescent, sometimes with one or more longitudinal grooves	4–7 cm long, 0.2–0.6 cm broad, light brown or grey brown at upper and middle parts, and pale yellow to yellow brown at base, villose to densely pubescent, slightly sulcate near the base	2.5-4.0 cm high, 0.3-0.5 cm broad, concolorous with outside, but often gradually becoming whitish below, thickened near the base and often compressed above, villose
Subhymenium	<i>Textura globulosa-intricata</i>	—	very variable in thickness
Medullary excipulum	<i>Textura intricata</i> , hyphae 3–5.8 μm	<i>Textura intricata</i> , hyphae 3–6 μm	<i>Textura intricata</i> , hyphae 3–5 μm
Ectal excipulum	<i>Textura globulosa-angularis</i> , innermost cells 17.4–35.3 × 14–25.6 μm	<i>Textura angularis</i> , innermost cells 17–35 × 8–13 μm	<i>Textura angularis</i> , innermost cells 10–30 μm broad
Asci	204.6–310 × 13–18.6 μm	230–270 × 15–20 μm	13-18 μm broad
Ascospores	20.8–26.7 × 10.3–12.5 μm	17–23 × 10–13 μm	19–24 × 12–15 μm
Q value	2.08 ± 0.15	1.73 ± 0.12	—
Paraphyses	3-4.3 μm broad, apex 5.4-9.9 μm	4–5 μm broad, apex 8-11 μm	5–7 μm broad
Habitat	Solitary or scattered on the ground in broad-leaved forest	Scattered or gregarious on the ground, under <i>Quercus</i> sp. and <i>Pinus</i> sp. forest.	on calcareous soil, often gregarious.
References	This study	Li <i>et al.</i> 2023	Dissing 1966

Given that *H. pseudoelastica* belongs to the same clade (*Capucina-Danica* lineage) as *H. fistulosa*, it is plausible that this species also exhibits phenotypic plasticity. Indeed, the original description acknowledged the possibility that the presence or absence of such color traits may not be diagnostic, emphasizing the need to examine additional

specimens to confirm their taxonomic significance (Mao *et al.* 2023). Despite the variation in macroscopic features, the microscopic traits of the Korean specimens were consistent with those described in the original description (Mao *et al.* 2023).

Helvella acetabulum was previously reported in South Korea based on morphological identification (Kim *et al.* 2004). However, Park *et al.* (2025) found no matching specimens among 202 collections made between 1986 and 2023. In this study, the specimen KA24-0481, collected in 2024, formed a monophyletic group with *H. acetabulum* and exhibited identical morphological features (Harmaja 1977). Therefore, this study confirmed that this species exists not only in the literature but also in South Korea (Fig. 5A–C).

In the phylogenetic analysis, KA25-0484 formed a strongly supported clade (UFB=99, PP=1) with *H. alborava*, including *H. sp.* K7 (SFC20150813-12), whereas KA25-0483 showed relatively weak support (UFB=88, PP=0.99) as a clade with *H. taiyuanensis*. These specimens were not formally described due to the limited material, each represented by a single ascoma (Fig. 5D–F).

In conclusion, this study suggests that *H. griseomacropus* and *H. koreana* are new species within the genus *Helvella*, and confirms the presence of *H. acetabulum* in Korea. Increasing the species richness of *Helvella* species could serve as a valuable resource for promoting the development and utilization of the genus.

TABLE 3. Morphological comparison among *Helvella koreana*, *H. taiyuanensis*, and *H. solitaria*.

	<i>Helvella koreana</i>	<i>Helvella taiyuanensis</i>	<i>Helvella solitaria</i>
Apothecia	1.0–3.5 cm high, 1.3–3.6 cm broad, laterally compressed cup-shaped throughout development	3.5–5 cm broad, irregular or saddle-shaped, with margin always free	1–4 cm, initially compressed, becoming regular cup-shaped at maturity
Hymenium	Grayish brown to dark brown	Dark brown to blackish	Greyish-brown, dark brownish when dried
Receptacle surface	Concolorous with hymenium, covered with whitish tufts; blunt ribs nearly absent or covering approx. one-third of surface	Gray to dark gray-brown, smooth, sparsely pubescent	upper surface concolorous with hymenium, lower part pale grayish-brown to whitish, pubescent, blunt absent
Stipe	1.0–5.2 cm high, 0.3–1.3 cm broad, cream to white at base, dark brown toward apex, concolorous with receptacle; tapering upwards, glabrous, but pubescent near apex; ribs blunt, single/double-edged with anastomosis	2–3 high, 0.8–1.5 cm broad, white to cream, yellowish brown when dry, solid, with a single rounded longitudinal ridge	1–2.5 cm high, whitish to grayish-white, with 2-5 regular blunt ribs
Medullary excipulum	<i>Textura intricata</i> , hyphae 2.4–5 µm	<i>Textura intricata</i> , hyphae 3–11 µm	<i>Textura intricata</i> , hyphae 3–5 µm
Ectal excipulum	<i>Textura angularis</i> , innermost cells 10.4–28.4 × 6.3–21.6 µm	—	<i>Textura angularis</i> , innermost cells 30–45 × 6–21 µm
Asci	266.1–356.1 × 13.8–20.7 µm	13-15 µm broad	13-15 µm broad
Ascospores	17.8–22.1 × 13–16 µm	15–18.9 × 11.3–13.4 µm	19–24 × 12–15 µm
Paraphyses	2.2–4.9 µm broad, apex 4.3–8.5 µm	3.5–4 µm broad, apex 7 µm	5–7 µm broad
Habitat	On moss or soil in broad-leaved or mixed forests	On the ground in forest	on calcareous soil, often gregarious.
References	This study	Liu 1985	Dissing 1966



FIGURE 5. Fruiting bodies of *Helvella* species not covered in this study. **A–C** Fruit body of *H. acetabulum* (KA25-0481, KH089). **D** Fruit body of *H. cf. alborava* (KA25-0484, KH096). **E–F** Fruit body of *H. cf. taiyuanensis* (KA25-0483, KH092). Scale bars: A = 1 cm; B = 2 cm; C–F = 1 cm.

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