



A synopsis of the saddle fungi (*Helvella*: Ascomycota) in Europe – species delimitation, taxonomy and typification

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Key words

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Abstract *Helvella* is a widespread, speciose genus of large apothecial ascomycetes (*Pezizomycetes*: *Pezizales*) that are found in terrestrial biomes of the Northern and Southern Hemispheres. This study represents a beginning on assessing species limits and applying correct names for *Helvella* species based on type material and specimens in the university herbaria (fungaria) of Copenhagen (C), Harvard (FH) and Oslo (O). We use morphology and phylogenetic evidence from four loci – heat shock protein 90 (*hsp*), translation elongation factor alpha (*tef*), RNA polymerase II (*rpb2*) and the nuclear large subunit ribosomal DNA (LSU) – to assess species boundaries in an expanded sample of *Helvella* specimens from Europe. We combine the morphological and phylogenetic information from 55 *Helvella* species from Europe with a small sample of *Helvella* species from other regions of the world. Little intraspecific variation was detected within the species using these molecular markers; *hsp* and *rpb2* markers provided useful barcodes for species delimitation in this genus, while LSU provided more variable resolution among the pertinent species. We discuss typification issues and identify molecular characteristics for 55 European *Helvella* species, designate neo- and epitypes for 30 species, and describe seven *Helvella* species new to science, i.e., *H. alpicola*, *H. alpina*, *H. carnosa*, *H. danica*, *H. nannfeldtii*, *H. pubescens* and *H. scyphoides*.

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INTRODUCTION

Helvella is a widespread, speciose genus of apothecial ascomycetes (*Pezizomycetes*: *Pezizales*) whose members are found in terrestrial biomes of the Northern and Southern Hemispheres. The genus contains many of the larger and charismatic species of the order *Pezizales* and comprises a range of elaborate apothecia, from cupulate to saddle-shaped, and convex to campanulate, including species with folded and lobed caps seated on a simple, ribbed or furrowed stipe.

Although easily separated from other macrofungi by conspicuous polymorphic apothecia, it is surprisingly difficult to distinguish between *Helvella* species. Historically, the shape and colour and outer surface characters have been emphasized in species discrimination, whilst microanatomy of the sterile and fertile structures has added few characters of value in species recognition. Weber (1972), after extensive studies of Michigan collections of *Helvella*, concluded that: “in summary, most morphological and anatomical characters exhibit nearly continuous variation in the genus as a whole. Each species, however, represents only one area on the spectrum of variation for each character, and several species may share a given part of the spectrum for a character. Thus a group of characters must be used to delimit species”.

Linnaeus (1737, 1753) proposed the genus *Elvela* (= *Helvella*, orth. var.) for *Elvela mitra* (= *Helvella crispa* ss. Fries (1822)). Fries (1822) erected the family *Elvellaceae*, which was later referred to as *Helvellaceae* (Corda 1842). Generic delimitation of the morphologically diverse *Helvella* has varied. Fuckel (1870) segregated two new genera, i.e., *Macroscyphus* and *Paxina*, and Boudier (1907a) recognized altogether five genera, i.e., *Leptopodia*, *Cyathipodia*, *Acetabula*, *Macropodia* and *Helvella* s.str., for what was later merged into a broadly defined *Helvella*

(Quélet 1886, Nannfeldt 1932, 1937, Dissing 1966a, b, Weber 1972, 1975, Häffner 1987, Abbott & Currah 1997). In its widest circumscription over the last century, *Helvella* encompassed the monotypic genera *Underwoodia* (Peck 1890, Eckblad 1968, Harmaja 1974), *Wynnella* (Boudier 1885, 1907, Harmaja 1974, Abbott & Currah 1997), *Pindara* (Velenovský 1934, Landvik et al. 1999) and the hypogeous *Helvella astieri* (Korf 1973a).

A number of *Helvella* taxa dating from late 18th (pre-Friesian) and early 19th century taxonomic works, have been variously interpreted over time. Most taxonomists, including Fries himself, applied a broad species concept allowing for a lot of morphological variation among the *Helvella* species that were accepted in their monumental works (Afzelius 1783, Fries 1822, Dissing 1966a, b, Weber 1972, 1975, Abbott & Currah 1997). These works also listed a number of heterotypic synonyms for many *Helvella* species, mostly assessed based on similarities of published descriptions rather than as a result of comparative studies of type specimens. Furthermore, the iconic European *Helvella* species names, e.g., *H. lacunosa*, *H. corium*, *H. elastica* and *H. acetabulum* have been applied to specimens belonging to a number of phylogenetically related or unrelated *Helvella* taxa in regional or local reports on the genus, and misidentifications of *Helvella* spp. in the literature and on the web are common. The more comprehensive 20th and 21st century taxonomic works on the genus *Helvella* in Europe include the works of Dissing (1966a, b, 2000), Harmaja (1977b, 1979), Häffner (1987) and Van Vooren (2010, 2014). Dissing (1966b) recognised 26 species of *Helvella* in Europe, a list which was later expanded to 28 (Dissing 1972) and to 38 in a later survey of the species confined to the restricted area of the Nordic countries (Dissing 2000). Häffner (1987) accepted altogether 41 species from Germany and the rest of the European continent.

The development of molecular systematics and the possibility of employing DNA barcode sequences as a more robust tool to identify specimens of closely related species have recently and

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to some extent been applied to taxonomic studies of *Helvella*. Landvik et al. (1999) used nrDNA sequences to characterise a small subset of *Helvella* species from Norway and emphasized the general limitation of single locus analyses and the unsuitability of ITS to infer phylogeny and discriminate species across the breadth of the genus. Nguyen et al. (2013) used ITS and LSU nrDNA sequences and morphology to discriminate among at least four distinct species of the *H. lacunosa* species complex in western North America, and Landeros et al. (2015) used partial LSU sequences to study infrageneric groups of *Helvella* from Europe and North America. Recently, Ariyawansa et al. (2015) used the ITS, Zhao et al. (2015) ITS and a concatenated multilocus dataset of ITS, LSU, *tef*, *rpb2* and *mcm7*, and Zhao et al. (2017) a dataset of ITS, LSU and *tef* to discriminate and describe new species of the *H. lacunosa*, *H. crispa* and *H. monachella* morphospecies complexes in China. To this array of genes we add *hsp* as an informative additional gene of utility in species identification in *Helvella*.

We use sequence data and a simplified genealogical concordance phylogenetic species recognition (GCPSR) (Avice & Ball 1990, Taylor et al. 2000, Dettman et al. 2003) approach to resolve species-level lineages and phylogenetic species of *Helvella* in Europe. By using this molecular approach in combination with morphological data, we reassess species limits within *Helvella* in Europe. We hypothesize that well-supported terminal clades based on more than one locus and unique singletons linked to geographic separation in our phylograms represent biological species of *Helvella*. Another major objective of this study has been to undertake a nomenclatural revision and propose typifications of *Helvella* spp. in Europe to stabilize name use and bring the nomenclature in accordance with the Code (ICN 2012). This will hopefully form a basis for further studies to critically assess the biogeography and ecology of *Helvella* species worldwide.

MATERIALS AND METHODS

The present morphological and molecular synopsis of *Helvella* species in Europe is based on a selection of *Helvella* specimens from Europe, America, Asia and Oceania stored at the herbaria (fungaria) of Copenhagen (C), Harvard (FH) and Oslo (O). All sequenced specimens used in this study were given a number for easier recognition throughout the study (H001-H1030). The studied material also includes a large collection of *helvellas* made by the senior author in the 1980s and 1990s (Herb. T. Schumacher, now deposited in O). The fungarium collections were supplemented with 28 freshly collected specimens made by the authors in 2009. Colour codes of fresh apothecia are based on Kornerup & Wanscher (1961). We used water and Cotton Blue in lactic acid (CB) to observe microanatomical features of hymenium and receptacle (excipular tissues) of fresh and rehydrated materials. We present an artificial key to 55 species, provide full descriptions of seven new species and 12 emended species concepts, and refer to good discriminating descriptions of the rest of the treated species of *Helvella* in Europe. Macromorphological and microanatomical terminology used in descriptions and key follow Dissing (1966a, b),

Dissing & Lange (1967), Eckblad (1968), Weber (1972, 1975) and Korf (1973b).

We use sequence data from four loci to obtain an initial estimate of the genetic diversity represented by 432 collections of dried and fresh specimens of *Helvella*, each annotated by a 'H' number. In addition to a broad sample of European *Helvella* collections, we included some collections from the American and Asian continents in order to evaluate and better understand the intra- and intercontinental variations and distributions of the pertinent species.

DNA extraction and PCR

DNA was extracted using the E.Z.N.A HP Fungal DNA kit (Omega Bio-Tek, Norcross, GA, USA) protocol for dried samples, except that tissue was not ground, but frozen and thawed two times in the extraction buffer, and subsequently vortexed thoroughly with one tungsten bead. Samples collected by the authors were stored directly in extraction buffer and thus, were not dried before DNA extraction, but extracted using the same protocol as above.

Efforts were made to PCR amplify parts (270–700 bp) of four genetic loci that had been found useful in resolution of lower level relationships in other fungal groups; i.e., the translation elongation factor 1- α (*tef*), the large subunit RNA polymerase II (*rpb2*), the heat shock protein 90 (*hsp*) and the nuclear LSU ribosomal DNA (including D1–D2 domains) (Johannesson et al. 2000, Taskin et al. 2010, O'Donnell et al. 2011, Bonito et al. 2013, Hansen & Olariaga 2015).

A combination of previously published and newly designed primers was used (Table 1). Universal rDNA primers and primer pairs published for *rpb2* and *hsp* failed to produce amplicons from many of the fungarium specimens. Therefore, new primer pairs were designed for *rpb2* and *hsp*, while *Helvella* specific rDNA primers from Landeros et al. (2015) were used to amplify the parts of the nuclear LSU ribosomal DNA. We initially used the *hsp* primer pair from Johannesson et al. (2000) and the *rpb2*-7cf (Liu et al. 1999) and *rpb2*-9f (Taskin et al. 2010) to generate a few sequences that were used to design new internal primers using Primer3 (Koressaar & Remm 2007, Untergrasser et al. 2012) within in Geneious (<http://www.geneious.com>; Kearse et al. 2012). The *Helvella* specific *rpb2* forward primer is only 2 bp different from the *rpb2*-3r primer from Taskin et al. (2010).

We generated amplicons for the four loci using the following PCR protocols: 4 min at 95 °C, followed by 40 (50 for LSU) cycles of 25 s (30 s for LSU and *hsp*) at 95 °C, 30 s at 53 °C (52 °C for LSU, 58 °C for *hsp*) and 60 s at 72 °C, followed by a 10 min extension at 72 °C and a indefinite hold at 10 °C. For all PCR reactions, we used the PuReTaq Ready-To-Go PCR Beads (GEhealthcare, Waukesha, WI) in 25 μ L reactions (12 μ L for *hsp* and *rpb2*). We purified 8 μ L PCR products with 0.2 μ L ExoSAP-IT or ExoSTAR (GEhealthcare) and 1.8 μ L H₂O. Sequencing was performed at the in-house ABI-laboratory, Department of Biosciences, UiO or GATC Biotech (Constance, Germany). All sequences were assembled and edited using Geneious R4-7. All sequences have been deposited in GenBank and accession numbers are given in Table 2.

Table 1 PCR and sequencing primers used in this study. Novel synthesized primers in this study are indicated in *italics*.

Locus ¹	Forward primer sequence (5'-3')	Reverse primer sequence (5'-3')
LSU	H_LSUf1 ² : AGCGGAGGAAAGAAACCAACA	H_LSUr2 ² : TCCCAACAGCTATGCTCCTAC
<i>rpb2</i>	H_rpb2r2: TCCACAATCTGCATCCCGATTCCG	H_rpb2f: CCAGACATGGACAGAAGGTTGAGCT
<i>hsp90</i>	H_hspf: CRGGCATCCGGGTGACGTAAT	H_hspr: AGGGKTTGTCCGACTCCGAGG
<i>tef</i>	EF595F ³ : CGTGACTTCATCAAGAACATG	EF1160R ³ : CCGATCTGTAGACGTCCTG

¹ LSU: 28s large subunit ribosomal RNA, domains D1/D2; *rpb2*: RNA polymerase II; *hsp*: heat shock protein 90; *tef*: translation elongation factor 1- α .

² From Landeros et al. (2015). They added a G at the 3' end of forward primer and TC at the 3' end of the reverse primer, which were not used in the current study.

³ From Kausserud & Schumacher (2001).

Table 2 Geographic origin, ID and type information for *Helvella* specimens included in this study.

Species	Type/Sample ID/Fungaria ¹	Locality	Collection year	GenBank accession numbers ²				
				LSU	<i>tef</i>	<i>hsp</i>	<i>rpb2</i>	
<i>H. acetabulum</i>	epitype , H410, C-F Fungi Exs. Suec. 1354	Sweden, Östergötland	1945	KY773154	–	KY784506	KY772752	
	H126, O-178001	Norway, Møre og Romsdal	2004	KY772978	–	KY784259	KY772509	
	H127, O-178005	Norway, Møre og Romsdal	2004	–	KY772872	KY784260	KY772510	
	H128, O-284420	Norway, Vestfold	2006	KY772979	KY772873	KY784261	KY772511	
	H133, O-286533	Norway, Vestfold	2005	KY772984	KY772875	KY784266	KY772516	
	H134, O-64925	Norway, Østfold	2001	KY772985	KY772876	KY784267	KY772517	
	H225, O-253212	Norway, Oppland	1984	KY773055	KY772894	KY784344	KY772594	
	H226, O-253213	Norway, Oppland	1984	KY773056	–	KY784345	KY772595	
	H261, C-F-21174	Iceland, Nordur-Mulasysla	1983	KY773082	–	KY784376	KY772625	
	H286, O-253214	Norway, Oppland	1983	–	–	KY784399	KY772648	
	H287, O-253215	Norway, Oppland	1982	KY773095	–	KY784400	KY772649	
	H409, C-F Fungi Exs. Suec. 3261	Sweden, Öland	1967	KY773153	–	KY784505	KY772751	
	H427, C-F-45314	Czech Republic, Vändra	1960	KY773159	–	KY784521	KY772764	
	H485, O-253211	Norway, Finnmark	1961	–	–	KY784564	–	
	<i>H. aestivalis</i>	H007, O-253216	Norway, Oppland	2007	KY772905	–	KY784187	–
		H024, O-253217	Norway, Oppland	2009	KY772917	–	KY784200	KY772444
		H185, O-253218	Norway, Oppland	2001	KY773028	–	KY784312	KY772563
		H288, C-F-45329	Kyrgyz Republic, Thien Shan	1967	KY773096	–	KY784401	KY772650
		H355, O-129530	Norway, Oppland	1957	–	–	KY784456	–
<i>H. alpestris</i>	epitype , H014, O-253221	Norway, Oppland	2007	KY772909	KY772826	KY784191	KY772435	
	H013, O-253220	Norway, Oppland	2007	KY772908	KY772825	KY784190	KY772434	
	H031, O-253222	Norway, Oppland	2009	KY772922	KY772840	–	KY772451	
	H036, O-253223	Norway, Oppland	2007	KY772927	KY772842	KY784210	–	
	H042, O-253224	Norway, Oppland	2009	KY772932	KY772847	–	KY772457	
	H246, O-253219	Norway, Oppland	1997	KY773073	–	KY784364	–	
	H460, O ex DAOM574891	Canada, Nunavut	2014	–	–	KY784542	KY772789	
	H483, O-253225	Norway, Oppland	1984	–	–	KY784562	KY772807	
<i>H. alpicola</i>	H231, O-253226	Switzerland, Graubünden	1984	KY773061	–	KY784349	KY772598	
	holotype , H175, O-185924	Norway, Nordland	1988	KY773020	–	KY784304	KY772554	
<i>H. alpina</i>	H336, O-253227	Canada, British Columbia	1994	KY773116	–	KY784439	KY772690	
	H349, C-F-63820	Greenland, Qeqertarsuaq	1977	–	–	KY784450	KY772701	
<i>H. arctoalpina</i>	holotype , H223, O-253228	France, Savoie	1992	KY773054	–	KY784343	KY772593	
	H003, O-253232	Norway, Oppland	2001	–	KY772818	KY784183	–	
	H011, O-253233	Norway, Oppland	2007	–	KY772823	–	–	
	H012, O-253234	Norway, Oppland	2007	KY772907	KY772824	KY784189	–	
	H026, O-253235	Norway, Oppland	2009	–	KY772835	KY784202	KY772446	
	H030, O-253236	Norway, Oppland	2009	–	KY772839	KY784206	KY772450	
	H033, O-253237	Norway, Oppland	2009	KY772924	KY772841	KY784207	KY772453	
	H040, O-253238	Norway, Oppland	2009	KY772931	KY772846	–	KY772456	
	H083, O-253239	Norway, Oppland	1984	KY772955	KY772865	KY784235	KY772482	
	H084, O-253240	Norway, Oppland	1996	KY772956	KY772866	KY784236	KY772483	
	H086, O-253241	Norway, Oppland	1966	–	–	KY784238	KY772485	
	H087, O-253242	Norway, Oppland	1966	–	–	KY784239	KY772486	
	H173, O-69063	Norway, Nordland	2008	–	–	KY784302	KY772552	
	H182, O-253243	Norway, Oppland	2001	–	KY772885	KY784310	–	
	H255, O-253403	Norway, Oppland	1997	KY773077	–	KY784371	KY772620	
	H337, C-F-56723	Canada, Nunavut	1984	–	–	KY784440	KY772691	
	H338, C-F-56722	Canada, Nunavut	1984	–	–	KY784441	KY772692	
	H342, C-F-34334	Iceland, Nordur-Mulasysla	1993	KY773120	–	KY784445	KY772696	
	H354, O-174714	Norway, Oppland	1957	–	–	KY784455	KY772706	
	H356, O-253244	Norway, Oppland	1984	KY773124	–	KY784457	KY772707	
	H359, C-F-50652	Greenland, Ella Isl.	1957	KY773127	–	KY784460	KY772710	
	H360, O-253229	France, Val d'Isère	1992	KY773128	–	KY784461	KY772711	
	H456, O-253230	Norway, Hordaland	2014	–	–	–	KY772785	
	H472, O-253231	Norway, Hordaland	2014	–	–	KY784553	KY772800	
	holotype , H293, O-72616	Norway, Hordaland	1959	–	–	KY784406	KY772655	
	<i>H. atra</i>	epitype , H406, C-F Fungi Exs. Suec. 2066	Sweden, Uppland	1938	–	–	KY784502	KY772748
		H016, O-253251	Norway, Oppland	2007	KY772911	KY772828	KY784193	KY772437
H151, O-281641		Norway, Nordland	2006	KY773000	KY772881	–	KY772534	
H233, O-253245		Georgia, Caucasus	1988	KY773063	–	KY784351	KY772600	
H375, O-253246		Georgia, Caucasus	1988	KY773138	–	KY784474	KY772723	
H462, O-253249		Norway, Nordland	2010	–	–	KY784544	KY772791	
H464, O-253250		Norway, Nordland	2005	–	–	KY784545	KY772792	
H465, O-253252		Norway, Oppland	1981	–	–	KY784546	KY772793	
H467, C-F-45782		Denmark, Zealand	1999	–	–	KY784548	KY772795	
H481, O-291384		Norway, Sør-Trøndelag	2009	–	–	KY784560	KY772805	
H484, O-253247		Norway, Finnmark	1961	–	–	KY784563	–	
H487, O-253248		Norway, Finnmark	1961	–	–	KY784566	KY772809	
<i>H. bicolor</i>		epitype , H289, C-F-45334	Sweden, Gästrikland	1978	KY773097	–	KY784402	KY772651
		H056, O-253253	Norway, Akershus	2009	KY772940	–	KY784220	KY772467
	H057, O-253254	Norway, Akershus	2009	KY772941	–	KY784221	KY772468	
	H129, O-65375	Norway, Hedmark	2002	KY772980	–	KY784262	KY772512	
	H147, O-105346	Norway, Vestfold	2000	KY772996	–	KY784280	KY772530	
<i>H. calycina</i>	epitype , H022, O-253255	Norway, Oppland	2009	KY772915	KY772833	KY784198	KY772442	
	H382, C-F-21122	Denmark, Klim Bjerg	1993	KY773143	–	KY784480	KY772727	
	H384, C-F-41038	Denmark, Klim Bjerg	1999	KY773144	–	KY784482	KY772729	
	H387, C-F-71286	Denmark NE Jutland	1998	KY773147	–	KY784484	KY772732	

Table 2 (cont.)

Species	Type/Sample ID/Fungaria ¹	Locality	Collection year	GenBank accession numbers ²				
				LSU	<i>tef</i>	<i>hsp</i>	<i>rpb2</i>	
<i>H. capucina</i>	epitype , H208, O-253256	France, Savoie	1992	KY773041	–	KY784331	KY772582	
	H009, O-253258	Norway, Oppland	2007	–	–	KY784188	KY772432	
	H034, O-253259	Norway, Oppland	2007	KY772925	–	KY784208	KY772454	
	H035, O-253260	Norway, Oppland	2007	KY772926	–	KY784209	KY772455	
	H046, O-253261	Norway, Oppland	2009	KY772935	KY772849	KY784216	KY772461	
	H082, O-253262	Norway, Oppland	1983	–	–	KY784234	KY772481	
	H089, O-253263	Norway, Oppland	1996	KY772958	–	KY784240	KY772487	
	H201, O-253264	Norway, Oppland	1989	KY773036	–	KY784325	KY772576	
	H202, O-253265	Norway, Oppland	1989	KY773037	–	KY784326	KY772577	
	H203, O-253266	Switzerland, Graubünden	1984	–	–	KY784327	KY772578	
	H211, O-253257	France, Savoie	1992	KY773043	–	KY784333	KY772584	
	H397, C-F-92107	Canada, NW Territory	1971	–	–	KY784494	KY772741	
	H459, O ex DAOM574890	Canada, Nunavut	2014	–	–	KY784541	KY772788	
	H488, C-F-50768	Greenland, Mestervig	1982	–	–	KY784567	KY772810	
	<i>H. capucinoides</i>	H113, FH	USA, Maine	1997	KY772969	–	KY784251	KY772501
		H398, C-F-92116	USA, Michigan	1968	–	–	KY784495	KY772742
	<i>H. carnosa</i>	holotype , H146, O-68100	Norway, Oslo	2006	KY772995	–	KY784279	KY772529
		KH.10.277, S	Sweden, Gotland	2010	KY660042 ³	–	–	KY660044 ³
	<i>H. compressa</i>	H112, FH	USA, California	1998	KY772968	–	KY784250	KY772500
<i>H. confusa</i>	H008, O-253269	Norway, Oppland	2007	KY772906	–	–	KY772431	
	H092, O-253272	Switzerland, Graubünden	1984	KY772960	–	KY784242	KY772489	
	H155, O-71947	Norway, Aust Agder	1998	–	–	–	KY772538	
	H192, O-253270	Norway, Østfold	1987	–	–	–	KY772570	
	H253, O-253271	Norway, Østfold	1981	–	–	–	KY772618	
	H279, C-F-92132	Sweden, Uppland	1965	KY773091	–	–	KY772642	
	H313, C-F-58808	Norway, Nordland	1998	KY773104	–	–	KY772670	
	H320, C-F-92125	Norway, Nordland	1979	KY773107	–	–	KY772676	
	H331, C-F-56845	Switzerland, Graubünden	1979	KY773113	–	KY784435	KY772686	
	H386, C-F-55016	Norway, Nordland	1981	KY773146	–	–	KY772731	
	H437, O-253268	Norway, Buskerud	2014	KY773164	–	KY784529	KY772772	
	H438, C	Denmark, Northern Jutland	1986	KY773165	–	–	KY772773	
	H439, O-129435	Norway, Oppland	1987	KY773166	–	KY784530	KY772774	
	H446, C-F-45513	India, Kupwara	1967	–	–	KY784532	KY772776	
	H449, C-F-56513	USA, Oregon	1991	–	–	–	KY772779	
	<i>H. corbierei</i>	isotype , H477, C-F-70807	Denmark, Northern Jutland	1965	–	–	–	KY772802
		epitype , H392, C-F-57133	Switzerland Graubünden	1982	–	–	KY784489	KY772737
		H178, O-253273	Norway, Oppland	2001	KY773023	–	KY784307	KY772557
		H191, O-253274	Norway, Oppland	2001	–	–	KY784317	KY772569
H232, O-253275		Switzerland, Graubünden	1984	KY773062	–	KY784350	KY772599	
H346, C-F-56503		USA, Oregon	1991	KY773121	–	KY784448	KY772699	
H390, C-F-53800		Norway, Nordland	1972	–	–	KY784487	KY772735	
H391, C-F-57087		Switzerland, Graubünden	1982	–	–	KY784488	KY772736	
<i>H. corium</i>		epitype , H352, C-F-71638	Denmark, Mid Zealand	1984	–	–	KY784453	KY772704
		H242, O-362201	Svalbard, Kongsfjord	1986	KY773071	–	KY784360	KY772609
	H248, O-253277	Norway, Hordaland	1996	KY773075	–	KY784366	KY772614	
	H292, C-F-92111 (holotype of <i>H. arctica</i>)	Sweden, Norrbotten	1928	KY773099	–	KY784405	KY772654	
	H294, C-F-16568	Russia, N Ural Mts	1990	KY773100	–	KY784407	KY772656	
	H324, C-F-55580	Svalbard, Bunsow Land	1985	KY773111	–	KY784429	KY772680	
	H328, C-F-34476	Russia, Ural Mts	1992	–	–	KY784432	KY772683	
	H434, O-253280	Norway, Troms	1989	KY773162	–	KY784527	KY772770	
	H436, O-253281	Svalbard, Kongsfjord	1988	KY773163	–	KY784528	KY772771	
	H451, O-253278	Norway, Hordaland	2014	KY773171	–	KY784535	KY772781	
<i>H. costata</i>	H453, O-253279	Norway, Hordaland	2014	KY773173	–	KY784537	KY772783	
	H100, FH	USA, California	1998	KY772962	–	KY784244	KY772491	
	<i>H. costifera</i>	epitype , H298, C-F Fungi Exs. Suec. 2061	Sweden, Uppland	1948	–	–	KY784409	–
		H131, O-68514	Norway, Akershus	2007	KY772982	KY772874	KY784264	KY772514
		H209, O-253282	Norway, Oppland	1985	KY773042	–	KY784332	KY772583
		H227, O-253285	Norway, Sør-Trøndelag	1984	KY773057	–	KY784346	KY772596
		H247, O-253283	Norway, Oppland	1998	KY773074	KY772900	KY784365	KY772613
		H347, O-253284	Norway, Oppland	1982	KY773122	–	KY784449	KY772700
		H383, C-F-92113	Denmark, Zealand	1984	–	–	KY784481	KY772728
		H385, C-F-53538	Norway, Finnmark	1986	KY773145	–	KY784483	KY772730
H388, C-F-53529		Norway, Finnmark	1986	–	–	KY784485	KY772733	
<i>H. crassitunicata</i>		H222, O-253286	Canada, British Columbia	1994	KY773053	–	KY784342	KY772592
	isoparatype , H299, C-F-92106	USA, Washington	1952	–	–	–	KY772658	
	<i>H. crispa</i>	epitype , H408, C-F Fungi. Exs. Suec. 2062	Sweden, Blekinge	1946	–	–	KY784504	KY772750
		H062, O-253287	Sweden, Hallan	2009	KY772946	–	KY784226	KY772472
H105, FH		England, Surrey	1994	KY772965	–	–	KY772495	
H107, FH		Latvia, Riga	1982	–	–	–	KY772496	
<i>H. danica</i>	H135, O-18774	Norway, Akershus	2004	KY772986	–	KY784268	KY772518	
	H235, O-360158	Norway, Nordland	2005	KY773065	–	KY784353	KY772602	
	H405, C-F Fungi exs. Suec. 3263	Sweden, Öland	1960	–	–	KY784501	KY772747	
	<i>H. danica</i>	H058, O-253288	Norway, Akershus	2009	KY772942	–	KY784222	KY772469
		H111, FH	Russia, St. Petersburg	1982	–	–	–	KY772499
		H177, O-129543	Norway, Finnmark	1983	KY773022	–	KY784306	KY772556
		H396, C-F-64512	Denmark, Zealand	1974	–	–	KY784493	–
	holotype , H263, C-F-85205	Denmark, Jutland	2008	KY773083	–	KY784378	KY772627	

Table 2 (cont.)

Species	Type/Sample ID/Fungaria ¹	Locality	Collection year	GenBank accession numbers ²				
				LSU	<i>tef</i>	<i>hsp</i>	<i>rpb2</i>	
<i>H. dryadophila</i>	H010, O-253306	Norway, Oppland	2007	–	KY772822	–	KY772433	
	H180, O-253307	Norway, Oppland	1997	KY773024	KY772883	KY784309	KY772559	
	H183, O-253308	Norway, Oppland	1996	KY773026	KY772886	KY784311	KY772561	
	H190, O-253309	Norway, Oppland	2005	–	–	–	KY772568	
	H234, O-362204	Svalbard, Kongsfjord	1986	KY773064	–	KY784352	KY772601	
	H321, C-F-55579	Svalbard, Bunsow Land	1985	KY773108	–	KY784426	KY772677	
	H322, C-F-55597	Svalbard, Bunsow Land	1985	KY773109	–	KY784427	KY772678	
	H323, C-F-55578	Svalbard, Bunsow Land	1985	KY773110	–	KY784428	KY772679	
	H335, C-F-56772	Canada, Nunavut, Ellesmere Isl.	1984	KY773115	–	KY784438	KY772689	
	H378, C-F-52701	Greenland, Mestervig	1882	KY773140	–	KY784477	KY772725	
	H379, C-F-50346	Greenland, Ella Isl.	1982	KY773141	–	KY784478	–	
		holotype , H302, O-72617	Norway, Oppland	1957	–	–	KY784412	KY772661
	<i>H. elastica</i>	epitype , H372, C-F-29130	Sweden, Uppland	1946	–	–	KY784471	–
		H066, O-253311	Sweden, Hallan	2009	KY772950	KY772858	KY784230	KY772476
		H329, C-F-51672	Russia, Sakha	–	–	–	KY784433	KY772684
H414, C-F Fungi Exs. Suec. 271		Sweden, Uppland	1935	–	–	KY784509	–	
H443, O-253310		Norway, Akershus	2009	KY773167	–	KY784531	KY772775	
<i>H. ephippoides</i>	H085, O-253267	Japan, Honshu	1983	KY772957	KY772867	KY784237	KY772484	
<i>H. fallax</i>	epitype , H339, C-F-84621	France, Savoie	1992	KY773117	–	KY784442	KY772693	
	H002, O-253350	Norway, Oppland	2001	KY772901	–	–	KY772429	
<i>H. fibrosa</i>	H018, O-253351	Norway, Oppland	2009	KY772913	KY772830	KY784195	KY772439	
	H032, O-253352	Norway, Oppland	2009	KY772923	–	–	KY772452	
	H162, O-280610	Norway, Hedmark	2006	KY773009	–	KY784292	KY772543	
	H163, O-242201	Norway, Møre og Romsdal	2001	KY773010	–	KY784293	–	
	H168, O-63684	Norway, Hedmark	1998	KY773015	–	KY784298	KY772548	
	H169, O-66873	Norway, Oppland	2002	KY773016	–	KY784299	KY772549	
	H219, O-253348	France, Savoie	1992	KY773050	–	KY784339	–	
	H221, O-253349	France, Savoie	1992	KY773052	–	KY784341	–	
	H244, O-360225	Norway, Troms	2005	KY773072	–	KY784362	KY772611	
	H256, O-253353	Norway, Oppland	1996	KY773078	–	KY784372	KY772621	
	H395, C-F-45484	Sweden, Lule Lappmark	1970	–	–	KY784492	KY772740	
	H402, O-253354	Norway, Oppland	1985	KY773150	–	KY784498	KY772745	
	H419, C-F-45301	Norway, Nordland	1979	–	–	KY784514	KY772757	
	H428, C-F-57377	Switzerland, Graubünden	1984	–	–	KY784522	KY772765	
	H430, C-F-92108	Canada, NW Territories	1974	KY773160	–	KY784524	KY772767	
	H139, O-63973	Norway, Hedmark	2000	–	–	KY784272	KY772522	
	H164, O-88570	Norway, Akershus	1988	KY773011	–	KY784294	KY772544	
	H166, O-185923	Norway, Vestfold	1985	KY773013	–	KY784296	KY772546	
H167, O-185919	Norway, Vestfold	1985	KY773014	–	KY784297	KY772547		
H240, O-291352	Norway, Sør-Trøndelag	2008	KY773069	KY772898	KY784358	KY772607		
H243, O-291377	Norway, Sør-Trøndelag	2009	–	KY772899	KY784361	KY772610		
H250, O-253313	Georgia, Kaukasus	1988	–	–	KY784367	KY772615		
H270, C-F-54475	Norway, Nordland	1975	–	–	KY784385	KY772633		
H343, C-F-92103	Iceland, Merkurhraun	1984	–	–	KY784446	KY772697		
H344, C-F-92102	Iceland, Borgarfjörður	1984	–	–	KY784447	KY772698		
H357, C-F-53774	Norway, Nordland	1972	KY773125	–	KY784458	KY772708		
H369, C-F-92109	Finland, Oulun Pohjanmaa	1981	KY773136	–	KY784469	KY772719		
H426, C-F-38089	Denmark, Falster	1998	KY773158	–	KY784520	KY772763		
<i>H. fistulosa</i>	isoepitype , H413, C-F Fungi Exs. Suec 3262	Sweden, Halland	1956	–	–	KY784508	–	
	H109, FH	USA, Massachusetts	1999	KY772966	–	KY784248	KY772497	
	H114, FH	USA, Vermont	2004	–	–	KY784252	–	
	H179, O-253315	Norway, Akershus	2001	–	–	KY784308	KY772558	
	H205, O-253314	Japan, Honshu	1983	KY773039	–	KY784329	KY772580	
	H476, C	Iceland, Austur-Skaftafellsysla	1981	–	–	KY784556	–	
	neotype , H241, O-291887	Norway, Hordaland	2009	KY773070	–	KY784359	KY772608	
<i>H. fusca</i>	H304, C-F-89381	Netherlands, Zuid-Holland	1983	–	–	KY784414	KY772663	
	H305, C-F-92122	Hungary, Kiskunsag National Park	1978	KY773101	–	KY784415	KY772664	
<i>H. griseoalba</i>	H306, C-F-92112	USA, Michigan	1973	–	–	KY784416	KY772665	
<i>H. helvellula</i>	epitype , H308, C-F-92128	Spain, Canary Islands, Hierro	1977	–	–	KY784418	KY772667	
	H278, C-F-45507	France, Manche	1977	KY773090	–	KY784393	KY772641	
	H309, C-F-45469	France, Region des Landes	1981	KY773103	–	KY784419	KY772668	
<i>H. hyperborea</i>	H389, C-F-54473	Norway, Nordland	1975	–	–	KY784486	KY772734	
	H491, C-F-45306	Finland, Kuusamo	1978	–	–	KY784569	KY772812	
<i>H. hypocrateriformis</i>	epitype , H301, C-F-45379	Sweden, Uppland	1948	–	–	KY784411	KY772660	
	H275, C-F-57126 (isotype of <i>H. pulchra</i>)	Switzerland, Graubünden	1982	–	–	KY784390	KY772638	
	H300, C-F-92131 (isotype of <i>H. cupuliformis</i>)	Sweden, Uppland	1936	–	–	KY784410	KY772659	
<i>H. juniperi</i>	H415, C-F-42193	Portugal, Minho	1996	–	–	KY784510	KY772754	
<i>H. lactea</i>	H262, C-F Fungi Exs. Suec. 1355	Sweden, Uppland	1939	–	–	KY784377	KY772626	
	H374, C-F-39379	Denmark, Zealand	1961	–	–	KY784473	KY772722	
<i>H. lacunosa</i>	epitype , H407, C-F Fungi Exs. Suec. 2065	Sweden, Femsjö	1948	KY773152	–	KY784503	KY772749	
	H039, O-253319	Norway, Oppland	2007	KY772930	KY772845	KY784213	–	
	H044, O-253320	Norway, Oppland	2009	–	–	–	KY772459	
	H045, O-253321	Norway, Oppland	2009	KY772934	–	KY784215	KY772460	
	H059, O-253316	Norway, Akershus	2009	KY772943	–	KY784223	KY772470	
	H150, O-280703	Norway, Hordaland	2005	KY772999	–	KY784283	KY772533	
	H153, O-285214	Norway, Sør-Trøndelag	2007	KY773002	–	KY784285	KY772536	
	H170, O-59885	Norway, Finnmark	1995	KY773017	–	KY784300	KY772550	
	H189, O-253322	Norway, Oppland	2001	KY773032	–	KY784316	KY772567	

Table 2 (cont.)

Species	Type/Sample ID/Fungaria ¹	Locality	Collection year	GenBank accession numbers ²				
				LSU	<i>tef</i>	<i>hsp</i>	<i>rpb2</i>	
<i>H. lacunosa</i> (cont.)	H327, C-F-34477	Russia, Krasnoyarsk Krai	1993	KY773112	–	KY784431	KY772682	
	H399, C-F-55985	Greenland, Thule	1987	KY773149	–	KY784496	KY772743	
	H470, O-253318	Norway, Hordaland	2014	–	–	KY784551	KY772798	
	H471, C-F-19329	Svalbard, Longyearbyen	1988	–	–	KY784552	KY772799	
	H474, C-F-53539	Norway, Finnmark	1986	–	–	KY784554	KY772801	
<i>H. leucomelaena</i>	H486, O-253317	Norway, Finnmark	1986	–	–	KY784565	KY772808	
	epitype , H404, C-F Fungi Exs. Suec. 952	Sweden, Gotland	1938	–	–	KY784500	–	
	H115, FH	USA, Massachusetts	2006	KY772970	KY772870	KY784253	JX943751³	
	H267, C-F-39492	Denmark, Jutland	1967	–	–	KY784382	KY772630	
	H447, C-F-92127	Chile, Santiago	1966	KY773168	–	KY784533	KY772777	
<i>H. leucophaea</i>	H450, C-F-38142	Denmark, Zealand	1998	KY773170	–	KY784534	KY772780	
	H274, C-F-45487	France, Porquerelles	1976	KY773088	–	KY784389	KY772637	
<i>H. levis</i>	epitype , H290, C-F-55188	Denmark, Mid Zealand	2001	KY773098	–	KY784403	KY772652	
	H264, C-F-39370	Denmark, Mid Zealand	1968	–	–	KY784379	KY772627	
	H265, C-F-39366	Denmark, Jutland	1979	–	–	KY784380	KY772628	
	H266, C-F-39367	Denmark, Zealand	1974	–	–	KY784381	KY772629	
	H393, C-F-40830	Denmark, East Jutland	2002	KY773148	–	KY784490	KY772738	
	H458, C	Denmark, NE Zealand	2013	–	–	KY784540	KY772787	
	H469, C-F-52988	Denmark, NE Zealand	1997	–	–	KY784550	KY772797	
	H480, C-F-45517	Germany, Hamburg	1973	–	–	KY784559	–	
	epitype , H412, C-F Fungi Exs. Suec. 3266	Sweden, Uppland	1960	–	–	KY784507	KY772753	
	H060, O-253323	Norway, Buskerud	2009	KY772944	KY772853	KY784224	–	
	H069, O-292075	Norway, Akershus	2009	–	KY772861	KY784231	KY772478	
<i>H. macropus</i>	H073, O-253326	Norway, Oslo	2009	KY772954	KY772863	KY784233	KY772480	
	H118, FH	USA, Massachusetts	2006	KY772972	–	–	KY772503	
	H119, FH	Canada, Alberta	1996	KY772973	KY772871	KY784255	KY772504	
	H120, FH	Canada, Quebec	1997	KY772974	–	KY784256	KY772505	
	H124, FH	USA, Massachusetts	1998	KY772977	–	–	KY772508	
	H141, O-168819	Norway, Telemark	2000	KY772990	–	KY784274	KY772524	
	H142, O-166155	Norway, Telemark	2004	KY772991	–	KY784275	KY772525	
	H157, O-370348	Norway, Akershus	2006	KY773004	–	KY784287	KY772539	
	H158, O-65347	Norway, Hedmark	2002	KY773005	–	KY784288	–	
	H159, O-220323	Norway, Hordaland	2001	KY773006	–	KY784289	KY772540	
	H160, O-283072	Norway, Hordaland	2006	KY773007	–	KY784290	KY772541	
	H161, O-223871	Norway, Møre og Romsdal	2003	KY773008	–	KY784291	KY772542	
	H165, O-220225	Norway, Møre og Romsdal	2001	KY773012	–	KY784295	KY772545	
	H228, O-253324	Norway, Oppland	1980	KY773058	–	KY784347	–	
	H238, O-291425	Norway, Rogaland	2009	KY773067	KY772896	KY784356	KY772605	
	H239, O-291391	Norway, Rogaland	2009	KY773068	KY772897	KY784357	KY772606	
	H257, O-253325	Norway, Oppland	2009	KY773079	–	KY784373	KY772622	
	H260, O-253327	Norway, Østfold	2013	KY773081	–	KY784375	KY772624	
	H351, C-F-56087	USA, Alaska	1980	–	–	KY784452	KY772703	
	<i>H. macrosperma</i>	H029, O-253328	Norway, Oppland	2007	KY772921	KY772838	KY784205	KY772449
		H047, O-253329	Norway, Oppland	2009	KY772936	KY772850	KY784217	KY772462
H050, O-253330		Norway, Oppland	2009	KY772938	KY772852	–	KY772464	
H053, O-253331		Norway, Oppland	2009	KY772939	–	–	KY772466	
<i>H. maculata</i>	H303, C-F-45400	USA, Alaska	1973	–	–	KY784413	KY772662	
<i>H. monachella</i>	epitype , H268, C-F-92121	Hungary, Szelid	1979	–	–	KY784383	KY772631	
	H269, C-F-92120	Hungary, Szelid	1965	KY773084	–	KY784384	KY772632	
<i>H. nannfeldtii</i>	H017, O-253337	Norway, Oppland	2007	KY772912	KY772829	KY784194	KY772438	
	H028, O-253339	Norway, Oppland	2007	KY772920	KY772837	KY784204	KY772448	
	H188, O-253340	Norway, Oppland	2005	KY773031	–	KY784315	KY772566	
	H212, O-253332	France, Savoie	1992	KY773044	KY772888	–	KY772585	
	H216, O-253333	France, Savoie	1992	KY773048	KY772891	KY784337	KY772589	
	H254, O-253341	Norway, Oppland	1996	KY773076	–	KY784370	KY772619	
	H318, C-F-92123	Norway, Nordland	1974	KY773106	–	KY784424	KY772674	
	H362, O-253342	Norway, Oppland	1996	KY773130	–	KY784463	KY772713	
	H367, O-253343	Norway, Oppland	1985	KY773134	–	KY784467	KY772717	
	H452, O-253334	Norway, Hordaland	2014	KY773172	–	KY784536	KY772782	
	H454, O-253335	Norway, Hordaland	2014	KY773174	–	KY784538	KY772784	
	H457, O-253336	Norway, Hordaland	2014	–	–	KY784539	KY772786	
	H479, O-253344	Norway, Oppland	1983	–	–	KY784558	KY772804	
	holotype , H027, O-253338	Norway, Oppland	2009	KY772919	KY772836	KY784203	KY772447	
	<i>H. nigra</i>	epitype , H063, O-253345	Sweden, Hallan	2009	KY772947	KY772855	KY784227	KY772473
H067, O-253346		Sweden, Hallan	2009	KY772951	KY772859	–	–	
H068, O-253347		Sweden, Hallan	2009	KY772952	KY772860	–	KY772477	
H1029, O-253404		Spain, La Rioja	2014	–	–	KY784573	KY772815	
H1030, O-253405		Spain, Basque Country	2007	–	–	KY784572	KY772816	
<i>H. oblongispora</i>	H132, O-166316	Norway, Oppland	2004	KY772983	–	KY784265	KY772515	
	H332, C-F-56844	Switzerland, Graubünden	1979	–	–	–	KY772687	
	H448, C-F-56914	Switzerland, Graubünden	1979	KY773169	–	–	KY772778	
<i>H. pallescens</i>	epitype , H138, O-66205	Norway, Møre og Romsdal	2003	KY772988	KY772878	KY784271	KY772521	
	H070, O-289039	Norway, Møre og Romsdal	2003	KY772953	KY772862	KY784232	KY772479	
	H136, O-220306	Norway, Hordaland	2001	KY772987	KY772877	KY784269	KY772519	
	H236, O-291458	Norway, Rogaland	2009	–	KY772895	KY784354	KY772603	
	H373, O-253355	Norway, Østfold	1992	KY773137	–	KY784472	KY772721	
<i>H. palustris</i>	H001, O-253357	Norway, Oppland	2001	–	KY772817	KY784182	KY772428	
	H019, O-253358	Norway, Oppland	2009	KY772914	KY772831	KY784196	KY772440	

Table 2 (cont.)

Species	Type/Sample ID/Fungaria ¹	Locality	Collection year	GenBank accession numbers ²					
				LSU	<i>tef</i>	<i>hsp</i>	<i>rpb2</i>		
<i>H. palustris</i> (cont.)	H043, O-253359	Norway, Oppland	2009	KY772933	KY772848	KY784214	KY772458		
	H181, O-253360	Norway, Oppland	1996	KY773025	KY772884	–	KY772560		
	H184, O-253361	Norway, Oppland	1996	KY773027	KY772887	–	KY772562		
	H195, O-253356	Japan, Honshu	1983	KY773033	–	KY784319	–		
	H350, C-F-55330	Finland, Kuusamo	1978	KY773123	–	KY784451	KY772702		
	H468, O-253362	Norway, Oppland	1982	–	–	KY784549	KY772796		
<i>H. panormitana</i>	epitype , H064, O-253363	Sweden, Hallan	2009	KY772948	KY772856	KY784228	KY772474		
	H130, O-171969	Norway, Møre og Romsdal	2001	KY772981	–	KY784263	KY772513		
	H137, O-284515	Norway, Hordaland	2007	–	–	KY784270	KY772520		
	H143, O-65394	Norway, Hordaland	2002	KY772992	–	KY784276	KY772526		
	H144, O-178718	Norway, Møre og Romsdal	2003	KY772993	–	KY784277	KY772527		
	H145, O-203499	Norway, Møre og Romsdal	2005	KY772994	–	KY784278	KY772528		
	H154, O-167560	Norway, Hordaland	2005	KY773003	–	KY784286	KY772537		
	H237, O-360894	Norway, Møre og Romsdal	2006	KY773066	–	KY784355	KY772604		
	isotype , H271, C-F-45305	Spain, Teruel	1988	KY773085	–	KY784386	KY772634		
<i>H. paraphysitorquata</i>	epitype , H061, O-253366	Sweden, Hallan	2009	KY772945	KY772854	KY784225	KY772471		
	H065, O-253367	Sweden, Hallan	2009	KY772949	KY772857	KY784229	KY772475		
	H196, O-253365	Norway, Vestfold	1981	–	–	KY784320	–		
	H204, O-253364	Japan, Honshu	1983	KY773038	–	KY784328	KY772579		
	H230, C-F ex GZU109.86	Nepal, Langtang	1986	KY773060	–	–	–		
	H418, C-F-45301	Denmark, Jutland	1968	–	–	KY784513	–		
	H420, C-F-45505	Norway, Vestfold	1981	–	–	KY784515	KY772758		
	H431, C-F-52986	Denmark N Jutland	1997	KY773161	–	KY784525	KY772768		
	<i>H. philonotis</i>	H005, O-253294	Norway, Oppland	2001	KY772903	KY772820	KY784185	–	
		H006, O-253295	Norway, Oppland	2007	KY772904	KY772821	KY784186	–	
		H015, O-253296	Norway, Oppland	2007	KY772910	KY772827	KY784192	KY772436	
		H023, O-253297	Norway, Oppland	2009	KY772916	KY772834	KY784199	KY772443	
		H037, O-253298	Norway, Oppland	2007	KY772928	KY772843	KY784211	–	
		H038, O-253299	Norway, Oppland	2007	KY772929	KY772844	KY784212	–	
		H048, O-253300	Norway, Oppland	2009	KY772937	KY772851	KY784218	KY772463	
H051, O-253301		Norway, Oppland	2009	–	–	KY784219	KY772465		
H193, O-253305, holotype of <i>H. dovrensis</i>		Norway, Oppland	1989	–	–	KY784318	KY772571		
H198, O-253302		Norway, Oppland	1989	–	–	KY784322	KY772573		
H199, O-253303		Norway, Oppland	1989	KY773035	–	KY784323	KY772574		
H200, O-253304		Norway, Oppland	1989	–	–	KY784324	KY772575		
H214, O-253291		France, Savoie	1992	KY773046	KY772889	KY784335	KY772587		
H218, O-253292		France, Savoie	1992	KY773049	KY772892	KY784338	KY772590		
H220, O-253293		France, Savoie	1992	KY773051	KY772893	KY784340	KY772591		
H361, C-F-57376	Switzerland, Graubünden	1984	KY773129	–	KY784462	KY772712			
H381, O-253289	Austria, Tirol	1990	KY773142	–	KY784479	KY772726			
H475, O-253290	Austria, Tirol	1990	–	–	KY784555	–			
holotype , H492, C-F-45481	Iceland, Hveragerdi	1959	–	–	KY784570	KY772813			
paratype , H272, C-F-45486	Iceland, Grøndalur	1959	KY773086	–	KY784387	KY772635			
<i>H. phlebophora</i>	H197, O-253368	Japan, Honshu	1983	KY773034	–	KY784321	KY772572		
	H273, C-F-45405	Iceland, Austur Skaftafellsysla	1981	KY773087	–	KY784388	KY772636		
<i>H. pubescens</i>	H251, O-253369	Norway, Østfold	1986	–	–	KY784368	KY772616		
	H333, C-F-56499	USA, Oregon	1991	–	–	KY784436	–		
	H334, C-F-56502	USA, Oregon	1991	KY773114	–	KY784437	KY772688		
<i>H. pulla</i>	holotype , H121, FH	Canada, Alberta	1994	KY772975	–	KY784257	KY772506		
	epitype , H149, O-69282	Norway, Møre og Romsdal	2008	KY772998	–	KY784282	KY772532		
<i>H. queletiana</i>	H259, O-253370	Norway, Østfold	2013	KY773080	–	KY784374	KY772623		
	neotype , H403, C-F-45303	Denmark, Zealand	1995	KY773151	–	KY784499	KY772746		
	<i>H. rivularis</i>	H025, O-253380	Norway, Oppland	2009	KY772918	–	KY784201	KY772445	
		H245, O-253381	Norway, Oppland	1996	–	–	KY784363	KY772612	
		H312, C-F-86705	Norway, Nordland	1975	–	–	KY784420	KY772669	
		H319, C-F-92124	Norway, Nordland	1972	–	–	KY784425	KY772675	
		H363, O-253382	Norway, Oppland	2001	KY773131	–	KY784464	KY772714	
		H365, O-253383	Norway, Oppland	1983	KY773132	–	KY784465	KY772715	
		H366, O-253384	Norway, Oppland	1983	KY773133	–	KY784466	KY772716	
		H368, O-253385	Norway, Oppland	1984	KY773135	–	KY784468	KY772718	
		H424, O-253386	Norway, Oppland	1982	KY773157	–	KY784519	KY772762	
		holotype , H276, C-F-59447	Norway, Nordland	1972	KY773089	–	KY784391	KY772639	
		holotype , H140, O-65348	Norway, Hedmark	2002	KY772989	KY772879	KY784273	KY772523	
		<i>H. semiobruta</i>	H307, C-F-45467	Spain, Valdepenas	1975	KY773102	–	KY784417	KY772666
			isotype , H277, C-F-45507	France, Rhone	1972	–	–	KY784392	KY772640
<i>H. silvicola</i>		H281, C-F-60841	Kyrgyz Republic, Tianshan Interior	1967	–	–	KY784395	KY772644	
	H282, C-F-57385	Switzerland, Graubünden	1984	KY773092	–	KY784396	KY772645		
	H283, C-F-56847	Switzerland, Graubünden	1979	KY773093	–	KY784397	KY772646		
	H489, O-253387	Switzerland, Graubünden	1984	–	–	KY784568	KY772811		
<i>H. solitaria</i>	epitype , H370, C-F Fungi Exs. Suec. 3267	Sweden, Uppsala	1942	–	–	KY784470	KY772720		
	H004, O-253374	Norway, Oppland	2001	KY772902	KY772819	KY784184	KY772430		
	H021, O-253375	Norway, Oppland	2009	–	KY772832	KY784197	KY772441		
	H080, O-253376	Norway, Oppland	1989	–	KY772864	–	–		
	H090, O-253371	France, Savoie	1992	KY772959	KY772868	KY784241	KY772488		
	H122, FH	Canada, Alberta	1996	KY772976	–	KY784258	KY772507		
	H171, O-129536	Norway, Akershus	1987	KY773018	–	KY784301	KY772551		
	H174, O-129533	Norway, Sør-Trøndelag	1987	KY773019	–	KY784303	KY772553		
	H176, O-58891	Norway, Oslo	1996	KY773021	–	KY784305	KY772555		

Table 2 (cont.)

Species	Type/Sample ID/Fungaria ¹	Locality	Collection year	GenBank accession numbers ²				
				LSU	<i>tef</i>	<i>hsp</i>	<i>rpb2</i>	
<i>H. solitaria</i> (cont.)	H186, O-253377	Norway, Oppland	2005	KY773029	–	KY784313	KY772564	
	H187, O-253378	Norway, Oppland	2005	KY773030	–	KY784314	KY772565	
	H215, O-253379	Norway, Sør-Trøndelag	1985	KY773047	KY772890	KY784336	KY772588	
	H252, O-253372	Georgia, Kaukasus	1988	–	–	KY784369	KY772617	
	H314, C-F-54683	Norway, Nordland	1981	KY773105	–	KY784421	KY772671	
	H315, C-F-54680	Norway, Nordland	1981	–	–	KY784422	KY772672	
	H316, C-F-54682	Norway, Nordland	1981	–	–	KY784423	KY772673	
	H326, C-F-34410	Russia, Khatanga	1993	–	–	KY784430	KY772681	
	H330, C-F-57390	Switzerland, Graubünden	1984	–	–	KY784434	KY772685	
	H340, C-F-34316	Iceland, Sudur-Mulasysla	1993	KY773118	–	KY784443	KY772694	
	H341, C-F-34321	Iceland, Nordur-Mulasysla	1993	KY773119	–	KY784444	KY772695	
	H353, O-129541	Norway, Oppland	1957	–	–	KY784454	KY772705	
	H358, O-253373	Norway, Hedmark	1980	KY773126	–	KY784459	KY772709	
	<i>H. sp.</i> 'INDIA'	H421, C-F-45704	India, Udhampur	1967	–	–	KY784516	KY772759
	<i>H. sp.</i> 'JAPAN 1'	H206, O-253388	Japan, Honshu	1983	KY773040	–	KY784330	KY772581
	<i>H. sp.</i> 'JAPAN 2'	H093, O-253389	Japan, Honshu	1983	KY772961	–	KY784243	KY772490
	<i>H. sp.</i> 'JAPAN 3'	H213, O-253390	Japan, Honshu	1991	KY773045	–	KY784334	KY772586
	<i>H. sp.</i> 'JAPAN 4'	H461, O-253391	Japan, Honshu	1983	–	–	KY784543	KY772790
		H478, O-253392	Japan, Honshu	1983	–	–	KY784557	KY772803
<i>H. sp.</i> 'JAPAN 5'	H466, O-253393	Japan, Honshu	1983	–	–	KY784547	KY772794	
<i>H. sp.</i> 'JAPAN 6'	H482, O-253394	Japan, Honshu	1983	–	–	KY784561	KY772806	
<i>H. sp.</i> 'PAPUA 1'	H432, C-F-45531	Papua New Guinea, Manki	1972	–	–	KY784526	KY772769	
<i>H. sp.</i> 'PAPUA 2'	H400, C-F-45434	Papua New Guinea, Manki	1971	–	–	KY784497	KY772744	
<i>H. sp.</i> 'USA 1'	H416, C-F-58799	USA, New York	1989	–	–	KY784511	KY772755	
<i>H. sp.</i> 'USA 2'	H103, FH	USA, California	1988	–	–	KY784246	KY772493	
<i>H. sp.</i> 'USA 3'	H376, C-F-92118	USA, Idaho	1972	–	–	KY784475	–	
<i>H. sp.</i> 'USA 4'	H104, FH	USA, Massachusetts	1998	KY772964	KY772869	KY784247	KY772494	
<i>H. sp.</i> 'USA 5'	H110, FH	USA, Iowa	2008	KY772967	–	KY784249	KY772498	
<i>H. sp.</i> 'USA 6'	H291, C-F-92104	USA, Michigan	1979	–	–	KY784404	KY772653	
<i>H. sp.</i> 'USA 7'	H377, C-F-92119	USA, Michigan	1940	KY773139	–	KY784476	KY772724	
<i>H. sp.</i> 'USA 8'	H429, C-F-92105	USA, Michigan	1956	–	–	KY784523	KY772766	
<i>H. stevensii</i>	H297, C-F-45350, isotype of <i>H. connivens</i>	USA, Michigan	1947	–	–	KY784408	KY772657	
	H394, C-F-92117	USA, Michigan	1969	–	–	KY784491	KY772739	
<i>H. subglabra</i>	topotype , H280, C-F-65405	USA, Michigan	1972	–	–	KY784394	KY772643	
<i>H. sublicia</i>	epitype , H417, C-F-39823	Denmark, Zealand	1993	KY773155	–	KY784512	KY772756	
	H148, O-70080	Norway, Akershus	1994	KY772997	KY772880	KY784281	KY772531	
	H229, O-253312	Norway, Akershus	1988	KY773059	–	KY784348	KY772597	
	H422, C-F-39826	Denmark, Zealand	1993	–	–	KY784517	KY772760	
	H423, C-F-53175	Denmark, Zealand	1999	KY773156	–	KY784518	KY772761	
<i>H. sulcata</i>	epitype , H152, O-68095	Norway, Oslo	2006	KY773001	KY772882	KY784284	KY772535	
	H1027, O-253406	Spain, La Rioja	2013	–	–	KY784571	KY772814	
<i>H. terrestris</i>	H284, C	Norway, Nord Trøndelag	1983	KY773094	–	KY784398	KY772647	
<i>H. vespertina</i>	H102, FH	USA, California	2013	KY772963	–	KY784245	KY772492	
	H116, FH	USA, Maine	2000	KY772971	–	KY784254	KY772502	

¹ C-F = Copenhagen Fungal Herbarium, Natural History Museum of Denmark, University of Copenhagen; O = Mycological Herbarium, Natural History Museum, University of Oslo; FH = Farlow Herbarium, Harvard University Herbaria and Libraries, Harvard University.

² GenBank accession numbers are provided for the following markers: partial 28S large ribosomal sub unit (LSU), translation elongation factor 1-alpha (*tef*), heat shock protein 90 (*hsp*) and RNA polymerase II (*rpb2*). Sequences included in the three-gene alignment are indicated in **bold**. Sequences included in the two-gene alignment of *hsp* and *rpb2* are indicated in *italics*. Sequences included in both alignments are in **bold italics**.

³ Sequences obtained from GenBank.

Phylogenetic inference

DNA sequences from each locus were aligned separately using MAFFT v. 7.0.17 (Katoh & Standley 2013) within Geneious R9.0. The alignments were then improved manually. Alignments of each partition were analysed individually by Maximum Likelihood (ML) and Bayesian Inference phylogenetic methods, as implemented in RAxML 7.2.8 (Stamatakis 2006) and MrBayes 3.2.2 (Ronquist & Huelsenbeck 2003) in Geneious. For the ML analyses, the GTRCAT approximation was used for each partition. Bootstrap analyses were performed with 1 000 pseudo-replicates. PartitionFinder v. 1.1.1 was used to find the best-fit models for Bayesian analyses (Lanfear et al. 2012). Bayesian inferences were performed using MrBayes, applying the GTR + GAMMA model for *hsp* and *rpb2* and the GTR + GAMMA + I model for LSU. Two independent runs, each with three cold and one heated Markov Chain Monte Carlo chains, were started from a random starting tree. The MCMC chains lasted for four million generations, saving trees every 1 000th generation. The posterior probabilities (BPP) were calculated after burn-in phase (400 trees), which was determined from the marginal likelihood scored of the initially sampled trees. The average

split frequencies of the two runs were < 0.01, indicating the convergence of the MCMC chains.

In order to obtain a balanced dataset for the phylogenetic analysis we attempted to include 2–3 individuals for each evolutionary unit. Thus, from the initial alignments and phylogenetic trees of all specimens we pruned the dataset, keeping as much as possible genetic and geographic diversity.

The continental distribution of species based on our included sample was visualized in a Venn diagram (Fig. 1) using the online tool Venny (Oliveros 2007–2015).

To understand and compare the diversity of the various species groups we analysed the average pairwise within-species and within-groups-of-species-diversity for each locus using Mega 6.06 (Tamura et al. 2013). These analyses were based on the same specimens as included in the final phylogenetic analyses. In order to further compare the phylogenetic informativeness (PI) of the different loci we produced a phylogenetic informativeness profile for each locus using the online tool PhyDesign (López-Giráldez & Townsend 2011). For these analyses an ultrametric tree based on the ML tree of three loci (*hsp*, *rpb2* and LSU) was constructed in the R package Ape (Paradis 2012,

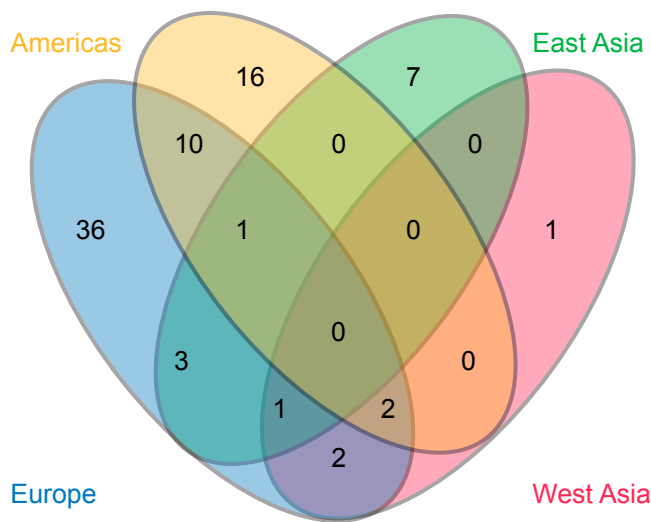


Fig. 1 Venn diagram of the localities where specimens have been collected, depicting the level of continental endemism and inter- and intracontinental distributions of *Helvella* in our sample set. Blue indicates species collected in Europe, yellow indicates species collected in North and South America, green indicates species collected in East Asia (Japan), red indicates species collected in West Asia (including India).

Paradis et al. 2004, R Core Team 2014). Separate analyses including more specimens from selected species groups were also analysed.

Nomenclature

Roughly 170 valid species names are available to *Helvella* spp. when excluding subspecific epithets (cf. Index Fungorum, <http://www.indexfungorum.org/>).

Taking into account the many new phylogenetic species that have been recognised among the earlier inferred morphospecies complexes of *Helvella* in this synopsis, we assume that many heterotypic synonyms listed in *Helvella* literature may prove to be ‘good’ species if their taxonomic status can be reassessed based on adequate type studies. As a consequence, we have been reluctant to accept early heterotypic synonyms of species if they are not resting on morphological and molecular comparisons of type specimens. At the end, we have compiled a list of 108 binomials not treated in this synopsis but referred to or retained in *Helvella* or its segregate genera by previous authors and also suspected by us to represent good species or taxonomic synonyms of *Helvella* species (Appendix 1).

It is against this background we typify the European names in designating lectotypes and epitypes, or neotypes, for many early *Helvella* names where the original material is an illustration (iconotype), does not exist, is poorly preserved, or will be much too old to yield useful DNA sequence data for an identification (cf. Richard et al. 2015). For epitype designations we use the criterion that the epitype shall originate from the original continent (and preferably the same climatic zone and habitat) as judged from the protologue, and that DNA sequence data should have been obtained from at least one protein-coding locus.

RESULTS

Sequence amplification and assembly

Four loci, which included a 515 bp region of the protein-coding gene *tef*, a 269 bp region of the protein-coding gene *hsp*, a 347 bp region of the protein-coding gene *rpb2* (including the 7–11 regions) and a 697 bp fragment at the 5’ end of LSU

(including the D1 and D2 regions), were sampled to delimitate phylogenetic species of *Helvella*.

Amplicons were not produced for all taxa. *Hsp* and *rpb2* were the most successful single-copy protein coding loci obtained from DNA extractions of old, dried fungarium material. The *tef* primers worked well on DNA extractions from freshly collected material but failed to regularly produce amplicons from DNA extracted from old fungarium material. For this reason *tef* was excluded from our ‘whole set’ analyses. Although, we would like to emphasize that an analysis of a small alignment (88 accessions of 26 taxa, 515 bp) of *tef* produced a tree that was concordant with the results of the other three loci (analyses not shown).

Based on initial analyses of *hsp* and *rpb2* sequences of a collection of 432 *Helvella* specimens, we selected 183 specimens, which together represented the full range of genetic diversity sampled, as representative for all independently evolving units in our dataset.

For the final analyses we produced two alignments: one including all species for the concatenated dataset of *hsp* and *rpb2* – consisting of 178 accessions and 616 bp –, and a second alignment including all species with an LSU sequence for the concatenated dataset of *hsp*, *rpb2* and LSU consisting of 118 accessions and 1 314 bp. All alignments were submitted to Dryad (<http://datadryad.org/>).

Phylogenies derived from the separate *hsp*, *tef*, *rpb2* and LSU datasets did not exhibit any incongruence. Incongruence was evaluated by presence of conflicting nodes with bootstrap support above 70 in the ML trees. Trees constructed from the combined four locus –, three locus – and two locus datasets produced a topology similar to those constructed from individual marker datasets. Nevertheless, the four loci discriminated clades at somewhat different level. *Hsp* and *rpb2* consistently yielded high levels of species discrimination power in all clades and in a multilocus combination were the two most informative loci for inferring species-level relationships/lineages in *Helvella*. LSU provided more variable levels of resolution in the different clades. For instance, *Helvella palustris* consistently formed a distinct clade with *H. philonotis* in the *hsp*, *rpb2* and *tef* gene trees, but showed no resolution in the LSU rDNA gene tree.

The phylogenetic Informativeness (PI) analyses (Appendix 2) and the diversity measures are presented in Table 3. This demonstrated that LSU had the highest PI overall and per site (Appendix 2). Moreover, LSU showed high PI that dropped quickly at a more recent time. *Hsp* and *rpb2* evolved at a more similar rate than LSU, as reflected in the PI values and diversity measures, and were informative for a wider evolutionary time span.

Inference of species phylogenies

We selected the maximum likelihood (ML) tree based on the *hsp* and *rpb2* concatenated alignment as representative for the species lineages in *Helvella* (Fig. 2), as this alignment included most of the taxa with more than one accession and the maximum likelihood and Bayesian methods produced concordant topologies (not shown). Support values from Bayesian posterior probability (BPP) analyses were added to the ML tree. In addition, ML bootstrap (BP) and BPP from the analyses of the three-locus alignment (including LSU) were added, since LSU gave additional support to some branches.

We recovered 55 *Helvella* species from Europe based on concordance of the single gene phylogenies and two- and/or three-gene phylogenies. In addition, 27 extralimital non-European species or single-specimen lineages were supported by genetic divergence from their sisters in two or three of the protein-coding gene trees. A lineage was considered to be

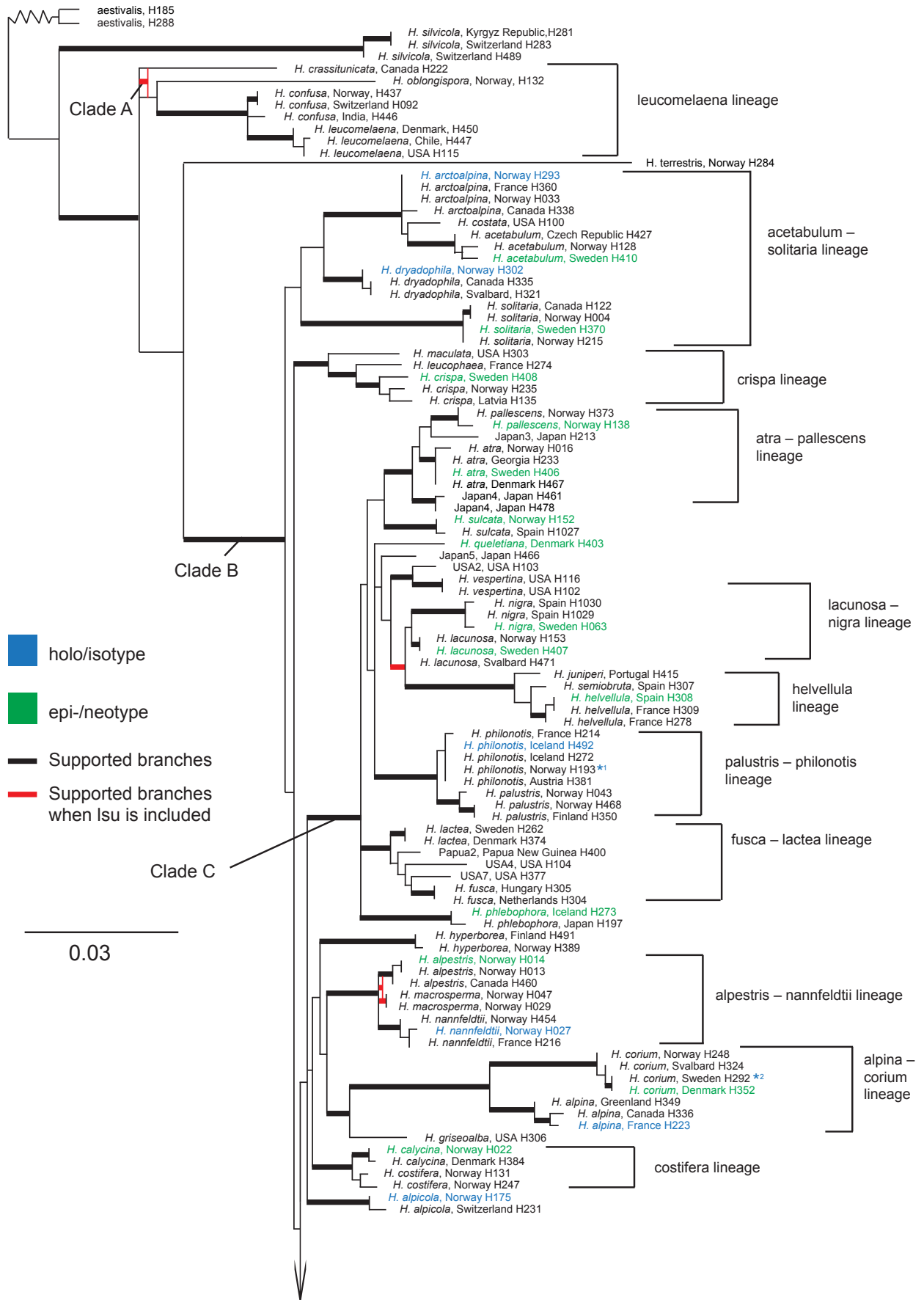
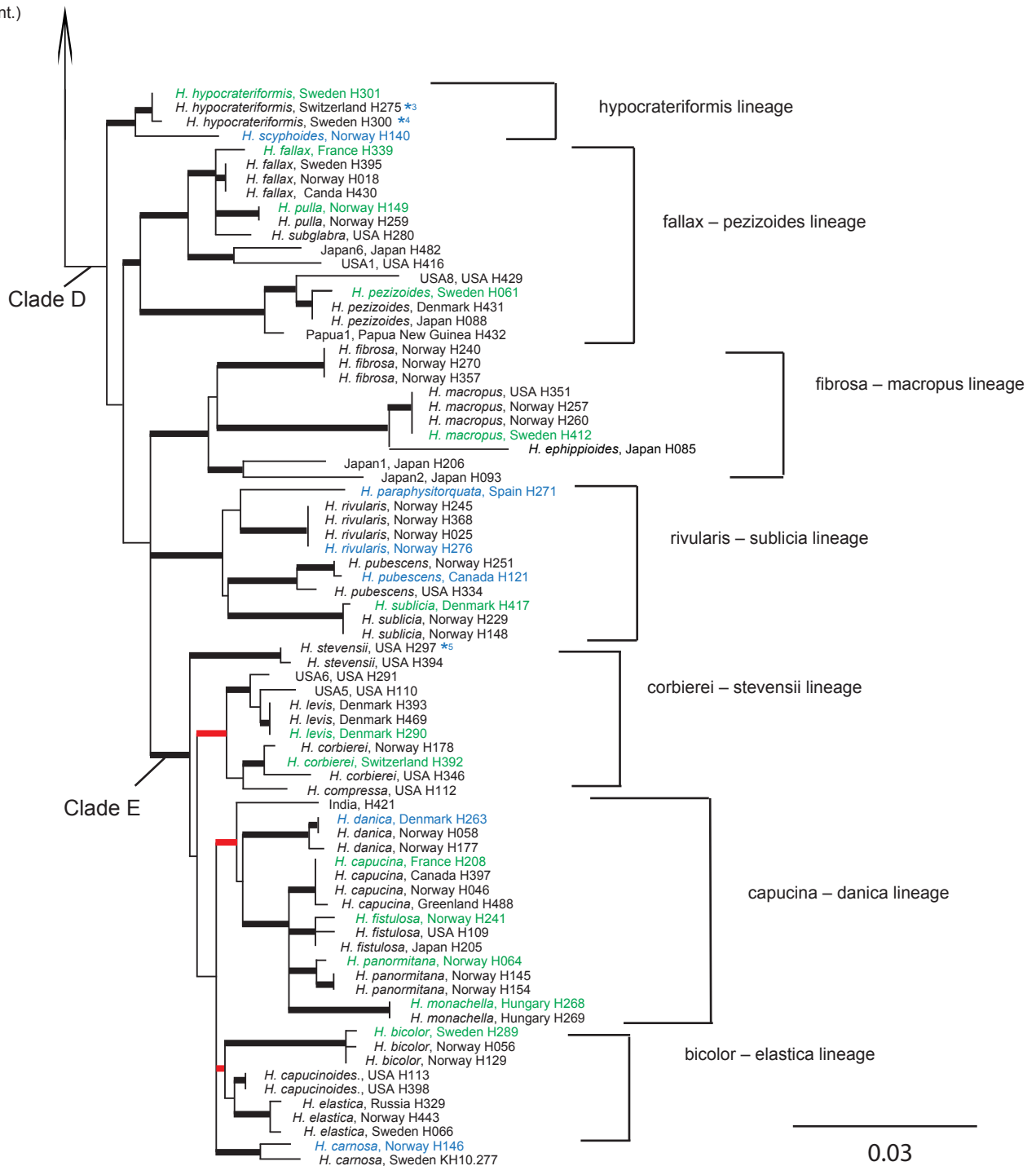


Fig. 2 Maximum Likelihood (ML) tree of European (and some extralimital) members of *Helvella* using parts of the RNA polymerase II (*rpb2*) and the heat shock protein 90 (*hsp*) loci. Branches supported by both ML bootstrap analyses (> 70) and posterior probability (> 0.95) from Bayesian inference are in **bold**. Branches that are supported only if part of the nuclear ribosomal large subunit (LSU) is added are **bold** and red. Sequences from holo-/isotype (blue) and epi-/neotype specimens (green) are colour-coded. Sequences from holo-/isotypes of synonymous taxa are indicated with blue asterix: *1 = holotype of *Helvella dovensis*; *2 = isotype of *Helvella arctica*; *3 = isotype of *Helvella pulchra*; *4 = isotype of *Helvella cupuliformis*; *5 = isotype of *Helvella connivens*.

Fig. 2 (cont.)



genealogical concordant if it was found in more than one locus and had BP and BPP support values greater than 70 % and 0.95, respectively.

Initial analyses suggested that *H. aestivalis* (R. Heim & L. Rémy) Dissing & Raitv. (1974) does not belong in the genus *Helvella*. However, blast searches, using LSU sequences as the query, indicated that this species is part of the *Helvellaceae*, and therefore was used as an outgroup to *Helvella* in our analyses. The placement of *H. aestivalis* will be resolved in a separate study, thus the species is not treated here.

In our phylogeny specimens of *H. silvicola* formed a well-supported group as sister to the rest of the *Helvella* species. The phylogenetic tree exposed some well-supported major clades and a number of resolved and unresolved infrageneric lineages. To improve the 'readability' of the tree, we have outlined and named 5 nested clades (A–E) and 18 lineages to be compared and discussed. The first lineage, named the leuco-

melaena lineage (clade A), encompasses the cosmopolitan *H. leucomelaena*, the European *H. oblongispora* and *H. confusa*, and the North American *H. crassitunicata*. Between this lineage and the rest of the helvellas encompassed in clade B, we find the morphologically highly divergent *H. terrestris*, which constitutes a very long branch of its own that may be subject to long-branch attraction. However, analysing a small subset of samples did not alter the placement of this species (analyses not shown). Within clade B we find a lineage, although unsupported, named the acetabulum-solitaria lineage (Fig. 2), which encompasses a species assemblage of *H. solitaria*, *H. dryadophila*, *H. acetabulum*, *H. arctoalpina* and the North American *H. costata*. A *crispa* lineage of *H. crispa*, *H. maculata* and *H. leucophaea* constitutes a species assemblage of its own nested outside a well-supported large lacunosa clade (clade C). The lacunosa clade includes 14 European and 8 non-European species and recovered many sister group relationships with

Table 3 Results from within clade, lineage or species nucleotide diversity in *Helvella*, for each of the three molecular markers.

Clades and lineages	LSU ¹		<i>hsp</i> ¹		<i>rpb2</i> ¹		two-gene tree ³	two-gene tree ³	three-gene tree ³	three-gene tree ³
	all ²	per site ²	all ²	per site ²	all ²	per site ²	BP ⁴	BPP ⁴	BP ⁴	BPP ⁴
entire alignment	22.0	0.044	16.4	0.061	19.0	0.064				
without outgroup	20.7	0.041	16.1	0.060	18.5	0.062				
acetabulum-solitaria lineage	20.7	0.046	16.3	0.061	8.6	0.029	64	0.908	84	1
alpestris-nannfeldtii lineage	22.5	0.049	2.7	0.010	1.05	0.003	96	1	100	1
alpina-corium lineage	8.7	0.017	7.3	0.027	5.0	0.017	100	1	100	1
atra-pallescens lineage	0	0	4.0	0.015	1.8	0.006		1	99	1
bicolor-elastica lineage	2.3	0.005	8.1	0.030	2.3	0.008	42	–	70	0.984
capucina-danica lineage	7.3	0.015	4.6	0.017	6.8	0.022	87	0.712	95	1
corbierei-stevensii lineage	7.0	0.014	4.5	0.017	4.4	0.014	–	0.938	97	1
costifera lineage	2.0	0.004	1.2	0.005	1.5	0.006	91	0.990	98	1
crispa lineage	5.0	0.010	5.6	0.021	6.0	0.020	98	1	100	1
elastica clade	7.7	0.015	7.4	0.027	8.5	0.028	90	1	99	1
fallax-pezizoides lineage	9.4	0.019	8.1	0.034	7.1	0.026	84	0.912	82	0.993
fibrosa-macropus lineage	8.2	0.016	9.1	0.038	8.9	0.034	81	1	88	0.998
fusca-lactea lineage	–	–	4.3	0.016	3.3	0.011	89	1	95	1
helvellula lineage	3.3	0.007	2.6	0.010	2.0	0.007	100	1	100	1
hypocrateriformis lineage	–	–	3.0	0.011	3.0	0.010	93	1	–	–
lacunosa-nigra lineage	8.7	0.017	4.5	0.017	4.1	0.014	61	0.932	36	–
lacunosa clade	10.8	0.021	9.4	0.035	8.9	0.026	99	1	100	1
leucomelaena lineage	16.9	0.034	11.1	0.041	9.0	0.026	–	–	84	0.998
palustris-philonotis lineage	0	0	2.1	0.008	2.0	0.007	100	1	98	1
rivularis-sublicia lineage	8.5	0.017	7.6	0.028	9.7	0.033	99	1	99	0.918
Species										
<i>H. acetabulum</i>	0	0	2.0	0.007	1.3	0.004	100	1	100	1
<i>H. aestivalis</i>	18.0	0.036	2.0	0.009	0	0	–	–	–	–
<i>H. alpestris</i>	5.0	0.010	1	0.004	0	0	76	0.999	100	1
<i>H. alpicola</i>	0	0	2.0	0.008	0	0	99	1	100	1
<i>H. alpina</i>	5.0	0.011	2.3	0.009	0.7	0.002	100	1	100	1
<i>H. arctoalpina</i>	2.0	0.004	0.0	0	1.0	0.003	–	–	100	1
<i>H. atra</i>	0	0	0.3	0.001	0.5	0.002	93	0.993	100	1
<i>H. bicolor</i>	0	0	0.7	0.002	0.7	0.002	100	1	100	1
<i>H. calycina</i>	1.0	0.002	1	0.004	0	0	95	0.999	98	1
<i>H. capucina</i>	0	0	0	0	0.5	0.002	96	1	100	1
<i>H. capucinoides</i>	–	–	0	0	0	0	–	–	–	–
<i>H. carnososa</i>	1.0	0.002	5.0	0.036	0	0	96	1	99	1
<i>H. confusa</i>	0	0	0.7	0.002	1.3	0.004	–	–	100	1
<i>H. corbierei</i>	–	–	2.7	0.01	1.3	0.004	69	0.992	89	1
<i>H. corium</i>	0	0	0.7	0.002	0.5	0.002	100	1	100	1
<i>H. costifera</i>	2.7	0.005	0	0	3.3	0.011	65	0.824	93	0.996
<i>H. crispa</i>	5.0	0.010	2.7	0.01	3.3	0.010	90	0.997	98	0.998
<i>H. danica</i>	0	0	0	0	1.3	0.004	100	1	100	1
<i>H. dryadophila</i>	1.0	0.002	0	0	0.7	0.002	100	1	100	1
<i>H. elastica</i>	0	0	1.3	0.005	0	0	97	1	100	1
<i>H. fallax</i>	0.7	0.001	0.7	0.002	0.7	0.002	99	–	89	0.940
<i>H. fibrosa</i>	1.0	0.002	0	0	0	0	100	1	100	1
<i>H. fistulosa</i>	3.3	0.007	2.0	0.007	0.7	0.002	94	1	99	1
<i>H. fusca</i>	–	–	0	0	0.0	0	100	1	–	–
<i>H. helvellula</i>	0	0	0	0	0	0.002	91	0.999	97	1
<i>H. hyperborea</i>	–	–	1.0	0.004	0	0	100	1	–	–
<i>H. hypocrateriformis</i>	–	–	0	0	0.7	0.002	99	0.971	–	–
<i>H. lactea</i>	–	–	0	0	0	0	100	0.998	–	–
<i>H. lacunosa</i>	0	0	1.3	0.005	0	0	92	0.624	100	1
<i>H. leucomelaena</i>	11.0	0.020	0	0	0.7	0.002	99	1	95	1
<i>H. levis</i>	1.0	0.002	0	0	0	0	98	0.889	100	1
<i>H. macropus</i>	0	0	0	0	0	0	97	0.952	100	1
<i>H. macrosperma</i>	0	0	0	0	0	0	96	–	100	0.999
<i>H. monachella</i>	–	–	0	0	0.0	0.0	100	1	–	–
<i>H. nannfeldtii</i>	7.0	0.015	1.3	0.005	0	0	84	1	100	1
<i>H. nigra</i>	0	–	0.7	0.002	0.7	0.002	100	1	–	–
<i>H. pallescens</i>	–	0	2.0	0.007	2.0	0.007	98	1	94	0.999
<i>H. palustris</i>	0	0	2.0	0.007	0	0	99	1	96	0.997
<i>H. panormitana</i>	1.3	0.003	0.7	0.002	1.3	0.004	86	1	99	1
<i>H. pezizoides</i>	0	0	0.5	0.002	0.5	0.002	100	0.997	100	1
<i>H. philonotis</i>	0	0	0.7	0.001	0	0	96	0.693	88	1
<i>H. phlebophora</i>	0	0	1.0	0.004	1.0	0.003	100	1	71	0.978
<i>H. pubescens</i>	5.0	0.010	0	0	1.0	0.003	100	1	100	1
<i>H. pulla</i>	0.0	0	0	0	0	0	100	1	100	1
<i>H. rivularis</i>	0.7	0.001	0	0	0	0	100	1	100	1
<i>H. semiobruta</i>	5.0	0.010	2.0	0.007	2.0	0.007	–	–	–	–
<i>H. silvicola</i>	–	–	2.0	0.007	0.7	0.002	100	1	–	–
<i>H. solitaria</i>	0	0	0	0	0.7	0.002	100	1	100	1
<i>H. stevensii</i>	–	–	0	0	0	0	99	1	–	–
<i>H. sublicia</i>	8.0	0.016	0.7	0.002	0	0	100	1	100	1
<i>H. sulcata</i>	–	–	1.0	0.004	0	0	100	1	–	–
<i>H. vespertina</i>	0	0	0	0	0	0	100	1	100	1
<i>H. sp. 'JAPAN 4'</i>	–	–	0	0	1.0	0.003	96	1	–	–

¹ partial 28S large ribosomal sub unit (LSU), heat shock protein 90 (*hsp*) and RNA polymerase II (*rpb2*).² 'all' indicates total pairwise nucleotide diversity, while 'per site' indicates pairwise nucleotide diversity per site.³ Two-gene tree denotes phylogenies based on a *hsp* and *rpb2* alignment, three-gene tree denotes phylogenies based on a *hsp*, *rpb2* and LSU alignment.⁴ BP denotes Maximum Likelihood Bootstrap Pseudoreplicates and BPP denotes Bayesian Posterior Probability. '–' denotes missing value.

high support: i.e., *H. lactea* (two-gene support: BPP = 0.996/BP = 99) with *H. fusca* (1/100) constituting a fusca-lactea lineage; *H. pallescens* (0.975/90) with *H. atra* (0.996/93) constituting an atra-pallescens lineage; *H. palustris* (1/95) with *H. philonotis* (0.885/73) constituting a palustris-philonotis lineage, *H. lacunosa* with *H. vespertina* and *H. nigra*, constituting a lacunosa-nigra lineage, and a *helvellula* lineage of *H. juniperi*, *H. helvellula* and *H. semiobruta*. The next two lineages to diverge are the alpestris-nannfeldtii lineage and the alpina-corium lineage, which include five species previously considered to constitute a single morphospecies, i.e., *H. corium* s.lat. The last lineage in clade B is the costifera lineage that includes *H. calycina* and *H. costifera*. The rest of the supported lineages are found within clade D. This clade encompasses lineages and species with cylindrical (not ribbed) stipes, i.e., a hypocrateriformis lineage, a fallax-peizoides lineage, an unsupported fibrosa-macropus lineage, a rivularis-sublicia lineage, and a well-supported elastica clade (clade E), in addition to several single species lineages from Oceania, North America and Asia. The elastica clade contains 10 European and 5 non-European species and a number of supported sister group relationships, i.e., a corbierei-stevensii lineage, a bicolor-elastica lineage, and a capucina-danica lineage.

Seven independent evolving lineages are represented by single collections in our phylogram, i.e., *H. scyphoides*, *H. semiobruta*, *H. juniperi*, *H. paraphysitorquata*, *H. leucophaea*, *H. queletiana* and *H. terrestris*, plus an additional 22 extralimital non-European singletons, which represent a combination of discrete morphological and molecular data. These single-specimen lineages are interpreted as putative species of *Helvella*.

Species diversity and distribution

Helvella is a highly diverse genus, however, very little within-species divergence of the three loci *hsp*, *rpb2* and LSU were observed (Table 3). Nevertheless, some species show more intraspecific diversity than others, e.g., *H. costifera* and *H. crispa* have highest within-species diversity. The diversity analyses also suggested that LSU evolved in a more uneven rate than *hsp* and *rpb2*. For some species, e.g., in *H. nannfeldtii* and *H. leucomelaena* (Table 3), LSU has evolved very quickly, but in others much slower, e.g., in *H. palustris* and *H. philonotis*. The *hsp* and *rpb2* mostly evolved at a similar rate. The inferred lineages also showed variable degree of genetic diversity. For instance, the acetabulum-solitaria lineage showed high diversity but the elastica lineage contained comparably low genetic diversity. This also matched the branch lengths in our two-gene tree.

The Venn diagram demonstrated that most species are endemic to one continent (Fig. 1). The Venn diagram of course reflects that this study has mainly focused on European species. Of the 55 species in Europe, 36 were found only in Europe. Of the 29 species collected in North America, 16 were endemic to North America, while 10 were shared between Europe and North America. One species was present in East Asia, Americas and Europe, while two species were present in West Asia, Americas and Europe. Of the intercontinental species, some shared identical sequences from the different continent, e.g., for collections of *H. pezizoides* from Denmark and Japan and *H. solitaria* from Canada and Norway.

TAXONOMY

Nomenclature and typification

We propose 29 lectotypes, 28 epitypes and two neotypes for European *Helvella* species and resurrect 12 old binomials to be applied to newly recovered species, i.e., two species de-

scribed by Schaeffer (1774), two species described by Bergeret (1783), one species described by Persoon (1799), two species described by Holmskjöld (1799), one species described by Albertini & Schweinitz (1805), one species described by Raddi (1807), one species described by Schweinitz (1822), one species described by Fries (1822), and one species described by Inzenga (1865). Seven species are described as new, i.e., *H. alpicola*, *H. alpina*, *H. carnosa*, *H. danica*, *H. nannfeldtii*, *H. pubescens* and *H. scyphoides*, and full descriptions are provided for 12 emended species where the current concepts encompassed several related or unrelated species. Citations to precise descriptions and illustrations of the accepted European *Helvella* species of our sample are given.

For some species, our taxon sampling and data acquisition (i.e., incomplete molecular datasets) are not yet ideal for a consummate description of the species. Two new species descriptions are based on morphology and DNA sequence information from only one specimen. Being fully aware that single specimen descriptions cannot reflect intraspecific variation, we still believe our data represent characters so discrete that it is considered highly unlikely they fall within the variation range of another species. We therefore find it justified keeping these entities on a formally recognized level of species.

We provide *hsp* sequences for 55 European and 27 extralimital species of *Helvella*, *tef* sequences for 25 European and two extralimital species, *rpb2* sequences for 55 European and 25 extralimital species, and LSU nrDNA sequences for 55 European and 11 extralimital and putative *Helvella* species. This includes partial sequences from one to three genetic loci for 14 holo- or isotypes and 30 newly designated neo- and epitypes of species recorded in this study. Heterotypic synonymies inferred from identical partial protein-coding gene sequences of type specimens are provided for four taxa, i.e., *H. arctica*, *H. cupuliformis*, *H. dovrensis* and *H. pulchra*.

In a situation where sufficient material has not been collected across the whole distributional area we add under Notes molecular specifics for each locus to the species descriptions. This is intended to help in specimen identification and to guide future re-assessment of useful characters for species discrimination within *Helvella* spp. in Europe and worldwide.

In the present synopsis, we refer to good illustrations and descriptions or describe de novo the *Helvella* species from Europe known by us. We also present an artificial key to the species based on morphological characters.

Morphology

Ascocarps (apothecia) in *Helvella* are either cupulate or capitate, sessile or usually distinctly stipitate; when cupulate, cup deeply cupulate to saucer-shaped to discoid (planar), sometimes cup laterally compressed; when capitate, cap regularly campanulate to bi- to trilobate to irregularly saddle-shaped with cap edge free or partly attached to stipe, apothecial margin (cup margin or cap edge) recurved (deflexed) or adnate (reflexed) towards the stipe and sometimes firmly fused with it; hymenium whitish to greyish to brownish to black when fresh, receptacle surface (apothecial underside) concolorous or discoloured, glabrous or pubescent; stipe when present terete or ribbed and furrowed, inside solid or hollow or chambered. In some cupulate species the ribbed stipe becomes much reduced so that almost sessile apothecia occur. Asci are cylindrical, 8-spored, operculate, with an aporhynchous or pleurorhynchous base. Ascospores ellipsoid to ellipso-fusoid, hyaline, generally unsculptured or minutely verrucose in fully mature ascospores, containing a large central guttule when mature, tetranucleate. Paraphyses filiform, septate, not much inflated, or inflated (enlarged) at tips to a clavate or subcapitate apex.

KEY TO EUROPEAN SPECIES OF HELVELLA

1. Apothecium with a ± prominent distinct stipe. 2
1. Apothecium sessile, stipe poorly differentiated or absent 13
2. Stipe ribbed and furrowed over entire length, internally solid or chambered, sometimes ribs present on receptacle surface 3
2. Stipe terete, even, internally solid or hollow, occasionally with grooves at base and/or apex, tissues well differentiated 30
3. Apothecium regularly cupulate to planar 4
3. Apothecium capitate, convex to saddle shaped or irregularly lobed 16
4. Stipe with ribs extending onto receptacle surface; ribs commonly branching and interconnected by cross-veins . . . 5
4. Stipe with blunt ribs not or scarcely continuing onto the receptacle surface 11
5. Hymenium light brown (6D5) to brown (6D8), sometimes with a violet tinge (11E5), drying brown (6-7D8) to dark brown (7F4-8). Receptacle surface light brown above, paler yellowish (4C7) to cream (4A3) below, delicately pubescent; ribs on receptacle surface branching, sharp-angled, rarely interconnected by cross-veins, not reaching the margin. Fruiting in spring (April to June). *H. acetabulum*
5. Hymenium grey (3-6D-E1-3) or light brown (5-6D6-8) to dark brown (6-9E-F5-8). Fruiting in summer and autumn (July to October) 6
6. Stipe long and slender, inflated above, with prominent blunt ribs extending half way up the receptacle surface. Hymenium light brown (5-6D6-8), drying darker (5-6E-F7-8), upper part of receptacle concolorous, lower receptacle surface yellowish white (3A2) to pale yellow (3A3-4); stipe and ribs light to greyish orange (5A-B4-6) *H. hyperborea*
6. Stipe low, 1–5 cm high, with prominent ± branching ribs extending onto the receptacle surface. 7
7. Apothecium light brown (5-6D6-8) to dark brown (6-9E-F5-8); ribs reaching lower to upper third of receptacle surface. In *Dryas* vegetation in arctic-alpine habitats 8
7. Apothecium grey (3-6D) or pale greyish brown (6E3), ribs prominent, reaching or almost reaching the cup edge. Not in *Dryas* vegetation 9
8. Hymenium brown (6D-E5-8) to dark brown (6-9E-F5-8), receptacle surface paler, drying blackish. Ribs blunt, double-edged, with little branching, reaching lower third of the receptacle surface *H. dryadophila*
8. Hymenium dark brown (6-9E-F5-8), drying brownish black (5-9H8); receptacle surface paler brown, sharp-angled, rarely interconnected by cross-veins, reaching upper half of receptacle surface in fully expanded specimens *H. arctoalpina*
9. Apothecium with prominent blunt to angular ribs and grooves on underside of apothecium. Hymenium brown when dried (6D7-8), receptacle covered by greyish white pruina (B1) *H. oblongispora*
9. Hymenium grey (E1-2) to brownish (6E5-8), exterior of cup (receptacle) pubescent 10
10. Hymenium greyish (6-7E1-3), drying dark greyish brown (6E3), stipe distinct with 5–6 prominent yellowish white blunt-edged ribs (4A2-3) extending onto receptacle, ribs not interconnected *H. costifera*
10. Hymenium brownish (6-8E5-8), receptacle greyish brown (6E3), stipe distinct with 5–8 prominent blunt-edged yellowish grey (4B2-3) ribs extending onto receptacle, in old fruit bodies ribs interconnected by shallow concentric parallel connections *H. calycina*
11. Hymenium black (19-24H8) or greyish black (19-24H1). Apothecium at first regularly cupulate, then laterally compressed with a ± recurved margin; hymenium black (20-21H8), receptacle and stipe greyish black (H1), with ± 'warts' (tufts of hyphoid hairs); stipe short, often compressed, with two to four grooves and blunt-edged shallow ribs that continue shortly onto the receptacle, stipe pale greyish (B1) towards the base *H. philonotis*
11. Hymenium brown (5-9D-E5-8) or greyish brown (6-7E3-4) 12
12. Apothecium 1.8–8 cm broad; stipe 1–8 cm long, 0.5–2 cm broad. Hymenium dark brown (6-9E-F5-8) to brownish black (5-9H8); stipe white to pale yellow (1-4A1-3), with 4–7 regular blunt ribs; when mature apothecia laterally compressed and sometimes recurved and irregular in shape, receptacle paler, greyish to greyish brown; frequently under *Salix*. (High elevation specimens have been distinguished as *H. ulvinenii*.) *H. solitaria*
12. Apothecium 1–3.5 cm broad; stipe 0.5–4 cm long, 0.4–1.3 cm broad. Hymenium greyish brown (6-7E3-4) to dark brown (5-9E5-6), receptacle paler; stipe yellowish white to yellowish grey (2-4A-B2-3), with 2–4 regular, blunt ribs *H. confusa*
13. Apothecium sessile or with a short, narrow stipe, rabbit-ear shaped, 2–4.5 cm broad, 3–6 cm high; hymenium brownish red (10D-E7-8); receptacle surface glabrous, brownish orange (6C6-8), towards the base pale yellow to white (4A1-3) *H. silvicola*
13. Apothecium cupulate or planar, hymenium and exterior brown (6D-E5-8) to dark brown (6-9E-F5-8) or black 20-21H8; stipe short (sessile) and indistinct, with grooves 14
14. Apothecium cupulate to planar with an irregular lobed apothecial margin; hymenium and outside black (H8) *H. helvellula*
14. Apothecium cupulate with a crenate margin; hymenium greyish brown to dark chocolate brown (6D-F3-8) . . . 15
15. Receptacle copper brown (7-8C-D8); hymenium dark chocolate brown (6-8E-F8), without ribs on receptacle surface. In *Dryas* vegetation in arctic-alpine habitats *H. aestivalis*
15. Receptacle light brown to brown (6D-E3-5), turning pale brown (5-6C-D4-6) to whitish when dried, with conspicuous blunt ribs and grooves on lower half. Under conifers, usually *Pinus* *H. leucomelaena*
16. Hymenium white to cream (3-5A1-2) or golden to brownish yellow (5B-C7-8); receptacle surface villose; edge of cap free or in part fused with stipe 17
16. Hymenium grey, brown or black; receptacle surface smooth or at most finely sub-pubescent; edge of cap free or in part fused with stipe 21
17. Hymenium white to cream (3-5A1-2), receptacle surface pubescent 18
17. Hymenium golden to brownish yellow (5B-C7-8), receptacle surface finely pubescent *H. leucophaea*
18. Apothecium saddle-shaped to irregularly lobed, edge of cap free 19
18. Apothecium saddle-shaped to irregularly lobed, edge of cap adnate and fused with stem at 3–4 points 20
19. Apothecium irregularly lobed, receptacle surface pubescent, light greyish to brownish orange (5-6B-C4-5); stipe robust, with sharp, partly anastomosing longitudinal ribs. Asci 270–320 µm long *H. crispa*

19. Apothecium saddle-shaped, margin reflexed towards the stipe, hymenium white to pale yellow (3-4A1-3), drying brownish orange (5-6C5-7); stipe short and broad, with longitudinal distantly interconnected ribs. Asci 240–260 μm long *H. lactea*
20. Apothecium saddle-shaped to campanulate; hymenium and stipe white to pale grey (3-5A-B1-2), drying brownish yellow (5B-C7-8); stipe long and slender, with four to five longitudinal distant ribs. Asci 280–310 μm long *H. pallescens*
20. Apothecium irregularly lobed to saddle-shaped; receptacle surface smooth, lacking raised veins, stipe lacunose *H. lacunosa* (albino)
21. Hymenium brown (6D-E5-8) to dark brown (6-9E-F5-8) when fresh, drying darker; stipe white 22
21. Hymenium grey (B-F1-2) or black (H8) when fresh . . . 23
22. Apothecium irregularly lobed, cap edge partly attached to stipe; stipe robust (broad), lacunose, with prominent, longitudinal ribs, extending onto receptacle surface and here forming elevated, branching veins *H. fusca*
22. Apothecium hemispherical in shape; stipe with sharp, elevated ribs extending onto and ending blunt on the receptacle surface, occasionally with a few veins from termination points; fruiting in spring *H. queletiana*
23. Apothecium saddle-shaped or irregularly lobed, edge of cap partly fused with stipe; stipe with 4–8 prominent, longitudinal, parallel ribs 24
23. Apothecium convex, flat hemispherical or saddle-shaped; edge of cap free. 25
24. Apothecium dark grey to black (F-H1-8), bi- to trilobate, cap edge remaining adnate towards stipe in mature specimens; hymenium black, often undulate-rugose, receptacle concolorous or dark greyish black (F-G1); stipe with 3–6 parallel ribs and grooves *H. palustris*
24. Apothecium convex to flat hemispherical; stipe greyish white (B1), contrasting the shining black hymenium (H8); with conspicuous sharp-edged longitudinal ribs extending onto receptacle surface and here building a network of radiating, raised veins *H. phlebophora*
25. Apothecium short-stipitate to medium-sized, cap saddle-shaped with lobes reflexed towards the stipe, up to 2 cm across; hymenium black (H8); stipe to 1.5 cm tall, with 3–4 inconspicuous, rounded ribs and grooves, subglabrous, grey to greyish black (B-F1-2), whitish below. Growing with *Cistus* and *Pinus* in the Mediterranean region. *H. semiobruta*
25. Apothecium long-stalked; medium-sized to large; cap margin partly fused with stem at 3–6 points 26
26. Apothecium hemispherical to slightly saddle-shaped, sometimes cap edge in part deflexed; hymenium black (H8), stipe grey above (5-7C-E1-2), whitish below, with 3–6 prominent longitudinal, blunt-edged, parallel ribs, partly attached to cap margin at 2–3 points. Growing with *Juniperus* in the Mediterranean region *H. juniperi*
26. Apothecium saddle-shaped to irregularly lobed; hymenium dark grey to black, stipe concolorous or slightly paler than hymenium, with 4–8 longitudinal, \pm anastomosing parallel ribs partly attached to apothecial margin at 3–6 points, \pm lacunose 27
27. Apothecium from 1–4 cm broad, from 3–6 cm high; hymenium black (H8); stipe slightly paler than hymenium, with 4–6 partly anastomosing longitudinal ribs, slightly lacunose *H. sulcata*
27. Apothecium large, from 1.5–6 cm broad, 3–15 cm high; hymenium black (H8) or brownish black (5-7F-G6-8) to dark violet brown (10-12F7-8); stipe robust (broad), lacunose, with prominent, anastomosing parallel ribs 28
28. Apothecium large, saddle-shaped; hymenium dark grey (F1) to greyish black (G1) when fresh, drying darker; stipe concolorous or slightly paler, lacunose, with 4–6 partly double-edged ribs, attached at 4–6 points to the adnate apothecial margin *H. nigra*
28. Hymenium black or dark violet brown; stipe concolorous or grey to whitish 29
29. Apothecium 1–5 cm broad, 3–12 cm high, saddle-shaped or irregularly lobed; hymenium and stipe blackish with a dark violet brown tinge (10-12F-H7-8), stipe with 4–7 sharp-edged, partly double-edged ribs, attached at 3–4 points to the reflexed apothecial margin *H. atra*
29. Apothecium large, 3–6 cm broad, 4–15 cm high, saddle-shaped or irregularly lobed, hymenium black (H8), often wrinkled-folded; stipe pale grey to white, lacunose, with 5–8 sharp-edged, commonly double-edged ribs, attached at 4–6 points to the apothecial margin; parts of margin free and often deflexed *H. lacunosa*
30. Apothecium cupulate to planar 31
30. Apothecium convex, bi- to trilobate saddle-shaped, or irregularly lobed 43
31. Apothecium stipitate-cupulate to discoid, cup 0.4–0.8 cm diam, stipe 0.3–0.8 cm high, 0.1–0.2 cm broad; hymenium purplish grey (12-14D3) to dark greyish black (F-G1), outside concolorous or paler, pubescent; stipe greyish to whitish. Ascospores fusoid, 50–60 \times 10–15 μm *H. terrestris*
31. Apothecium larger 32
32. Hymenium and receptacle black (H8) 33
32. Hymenium grey (D-F1-2), greyish brown (5-11D-F1-2) or yellowish brown (5C-D4-8); receptacle surface and stipe pubescent or villose 37
33. Apothecium 1–5 cm across, at first regularly cupulate, later slightly compressed and folded with irregular lobed margin; receptacle surface villose, sometimes with whitish scales ('warts') of fascicled hyphoid hairs towards apothecial margin; stipe black, 0.5–5 cm high, 0.2–0.7 cm broad, pubescent, occasionally with 2–3 irregular ribs extending onto the base of the receptacle *H. corium*
33. Apothecium regularly cupulate to discoid, 0.5–2 cm across; stipe black or whitish below 34
34. Apothecium short-stipitate, regularly cupulate to slightly irregular and compressed when post-mature, receptacle surface and stipe subtomentose; stipe greyish black above, white below, 0.5–2.0 cm high, 0.2–0.3 cm broad, deeply buried in soil, sometimes with a few inconspicuous furrows *H. nannfeldtii*
34. Stipe entirely black 35
35. Stipe slender, 1–3.5 cm high, 0.2–0.5 cm broad, terete when fresh, with some inconspicuous furrows when dried, subpubescent *H. alpina*
35. Stipe relatively short, 0.4–1.5 cm high, 0.2–0.4 cm broad, terete, cylindrical, densely tomentose 36
36. Hairs dark brownish black, partly fascicled and partly scattered, distributed on receptacle surface, up to 200 μm long. Asci 270–310 \times 12–16 μm ; ascospores 18.5–22.5 \times 11.0–13.8 μm ; paraphyses clavately enlarged at tips *H. alpestris*
36. Hairs dark brownish black, mostly aggregated in conspicuous, pyramidal fascicles, hairs up to 300 μm long at the apothecial margin. Asci 290–330 \times 16–20 μm ; ascospores 18.5–22.5 \times 11.5–13.8 μm ; paraphyses irregularly gnarled and slightly bent at tips *H. macrosperma*

37. Hymenium grey (D-F1-2) or dark greyish brown (5-11D-E2-3), receptacle surface and stipe villose; ascospores verruculose after discharge 38
37. Hymenium yellowish brown (5-6C-D4-8) or grey (D-E1-2) to dark greyish brown (6D-E2-3) or black when fresh, receptacle and stipe pubescent 39
38. Apothecium 1–3 cm across, hymenium grey (5-7C-E1-2); stipe long and slender, 3–7 cm high, solid. Ascospores ellipso-fusoid (acuminate), to 27 µm long . . . *H. macropus*
38. Apothecium 0.5–2.0 cm across, hymenium dark greyish brown (5-6E-F1-6); stipe 1.5–4 cm long, pale grey to brownish. Ascospores ellipsoid with rounded ends, to 23 µm long *H. fibrosa*
39. Apothecium 1.0–3.0 cm across; hymenium and receptacle surface yellowish brown (5-6C-D4-8) drying dark brown (6F5-8); stipe cream to whitish, usually shorter than cup diam. *H. hypocrateriformis*
39. Apothecium regularly cup-shaped to discoid, cup 0.5–3.5 cm across, hymenium grey, brown or greyish black . . 40
40. Hymenium greyish black (F-G1); receptacle dark greyish (E-F1), receptacle and stipe densely tomentose; stipe greyish to greyish white below, 0.2–0.3 cm broad, 0.5–1.8 cm high, with 2–3 shallow grooves at base *H. alpicola*
40. Hymenium grey or brown 41
41. Cup 0.5–2.0 cm across; hymenium grey (D-E1-2) to dark greyish brown (6D-E2-3), receptacle surface conspicuously villose, concolorous; stipe 1.5–3.5 cm long, greyish above, yellowish white below *H. rivularis*
41. Cup 1.5–3.5 cm across; hymenium pale greyish yellow (3-4B-C4-8) to pale brown (5-6D4-8) to brown, turning dark brown when dried 42
42. Apothecium cupulate to discoid; cap 2–3.5 cm across; hymenium greyish yellow (3-4B-C4-8) when fresh, drying dark yellowish brown (5F5); receptacle pale grey (B1-2), delicately pubescent; stipe light grey to whitish, pubescent, 1.5–3 cm high *H. pubescens*
42. Apothecium cupulate; hymenium dark brown (5-6F5-8) when dried, receptacle and stipe greyish (E1) to whitish, tomentose *H. scyphoides*
43. Cap remaining reflexed (adnate) towards the stipe . . 44
43. Cap saddle-shaped or irregularly lobed with a ± deflexed margin 50
44. Cap grey or black; receptacle and stipe concolorous or paler. 45
44. Cap and stipe with contrasting colours; hymenium grey, brown or brownish black; stipe white to yellowish . . . 46
45. Apothecium dark grey to black (F1-H1), slender, up to 6 cm high, cap 1–3 cm across, in mature specimens cap bi- to trilobate and reflexed towards stipe (connivent saddle-shaped); receptacle surface greyish (E-F1-2) when dried, subtomentose at margin, becoming almost glabrous towards stipe attachment; stipe solid, greyish, paler towards base, pubescent below *H. fallax*
45. Apothecium pale grey to medium grey (C-E1), saddle-shaped, bilobate, apothecial margin reflexed throughout development, receptacle and stipe concolorous, pubescent, attached to deeply decayed wood *H. pulla*
46. Cap regularly bi- to trilobate to campanulate; hymenium greyish brown (5-8D-E3) to light brown (5-6D4-8) to dark brown (5-6E5-8) to brownish black (6-9F-G6-8); flesh (receptacle tissues) gelatinous. 47
46. Cap campanulate or bilobate; hymenium brownish yellow (5C6-8) to light brown (5-6D4-8) to brown (6-7D5-8), drying darker; flesh not gelatinous 49
47. Apothecium long and slender, 3–15 cm in length, cap bi- to trilobate to campanulate; hymenium greyish brown to light brown to brown, stipe whitish to cream 48
47. Apothecium short-stipitate, cap campanulate to bi- to trilobate, hymenium dark brown to brownish black (6E-G6-8), stipe up to 2.5 cm high, solid, glabrous, broadly attached to cap underside, pure white when fresh, drying yellowish *H. capucina*
48. Hymenium light brown to brown (5-7D4-8); sometimes decoloured; receptacle glabrous *H. elastica*
48. Hymenium greyish brown (5-8D-E3), receptacle subpubescent *H. panormitana*
49. Cap campanulate; hymenium brownish yellow (5C6-8), apothecia commonly clustered *H. danica*
49. Cap regularly bilobate; hymenium brown (5-6E4-8), drying brownish black (6F-G5-8); receptacle surface delicately pubescent; stipe yellowish when dried *H. carnosa*
50. Receptacle surface pubescent to villose, apothecial margin partly inrolled (deflexed) over hymenium 51
50. Receptacle surface glabrous. 54
51. Apothecium white to cream when fresh, drying light brown *H. corbierei*
51. Apothecium grey, brown or black. 52
52. Apothecium grey; cap irregularly saddle-shaped, at first deflexed, in fully expanded specimens often campanulate or bilobate with reflexed margin; hymenium and receptacle greyish brown (6D-E2-3); stipe paler grey (B-C1-2) towards base. *H. sublicia*
52. Apothecium dark brown or black 53
53. Apothecium irregularly saddle-shaped and lobed, hymenium brown to dark brown (6E-F6-8), drying blackish, stipe consisting of 2–3 terete strands, free or fused at top half, whitish above, brownish below, delicately pubescent *H. paraphysitorquata*
53. Apothecium saddle-shaped, occasionally with a deflexed margin, in mature specimens cap occasionally bilobate and reflexed towards stipe (connivent saddle-shaped), 0.5–1.5 cm across; receptacle surface pubescent to villose; stipe 0.3–0.5 cm thick, up to 5 cm high, at first solid, then partly hollow (fistulose), pubescent above, glabrous below *H. pezizoides*
54. Cap regularly saddle-shaped to campanulate to irregularly lobed; light brown (5-6D6-8) to brown (5-9D-E5-8) to dark brown (6-9E-F5-8) 55
54. Cap bi- to trilobate, hymenium brown (6D-E7-8) apothecial margin free and reflexed towards stipe (adnate), stipe terete, solid or hollow *H. fistulosa*
55. Hymenium greyish yellow (3B-C6-7) to brownish yellow (5C6-8), drying pale brown (5-6D4-6); cap regularly saddle-shaped, lobes deflexed; stipe at first solid, then hollow. Ascospores broadly ellipsoid, 17–21 × 13.5–17 µm *H. levis*
55. Hymenium dark brown (6-7E-F7-8) or blackish (6-7G-H7-8) 56
56. Hymenium dark brown (6-7E7-8), drying blackish; cap regularly saddle-shaped or with irregularly deflexed lobes; stipe solid or hollow, 2–6 cm long, 0.3–0.6 cm broad. Ascospores ellipsoid, 19–22 × 11–13.5 µm *H. bicolor*
56. Hymenium dark brownish black to black (6-7G-H7-8), cap complex saddle-shaped with irregularly deflexed lobes; stipe robust, hollow, 2–6 cm long, 0.5–2 cm broad. Ascospores ellipsoid, 21–24 × 13–15 µm; preferable habitat sand dunes *H. monachella*



Fig. 3 Photos of fresh (a–b) and dried (c–h) apothecia. a. *H. arctoalpina* (O-253395); b. *H. solitaria* (O-253396); c. *H. acetabulum* (C-Fungi Exs. Suec. 3261); d. *H. dryadophila* (O-72617, holotype); e. *H. hyperborea* (C-F-45306); f. *H. confusa* (C-F-70807, isotype); g. *H. costifera* (O-253397 ex TROM-F11436); h. *H. arctoalpina* (O-72616, holotype). — Scale bars = 1 cm. — Photos: a–b: T. Schumacher; c–h: I. Skrede.

Helvella acetabulum (L.) Quél., Hymenomyc., Fasc. Suppl. (Alençon): 102. 1874 — Fig. 3c

Basionym. *Peziza acetabulum* L., Sp. Pl. 2: 1181. 1753; Fr., Syst. Mycol. 2: 44. 1822.

Synonyms. *Octospora acetabulum* (L.) Timm, Fl. Megapolit.: 260. 1788.

Aleuria acetabulum (L.) Gillet, Champ. France Discomyc.: 36. 1879.

Paxina acetabulum (L.) Kuntze, Revis. Gen. Pl. 2: 864. 1891.

Acetabula acetabulum (L.) Underw. & Earle, Alabama Agric. Exp. Sta. Agric. Coll. Bull. 80: 200. 1897.

Phleboscypus acetabulum (L.) Clem., Crypt. Form. Coloradens.: 298. 1907.

Fungioides acetabuliforme Vaill., Bot. Par.: 57. 1727, nom. inval.

Macrosocyphus acetabuliforme Gray, Nat. Arr. Brit. Pl. 1: 672. 1821.

Lectotype. Vaill., Bot. Par. t. 13, f. 1. 1727, selected by Dissing (1966b).

Epitype designated here: SWEDEN, Östergötland, Gryt parish, Säterön, 14 June 1945, J.A. Nannfeldt 7885 (C-Fungi Exs. Suec. 1354, ‘*Helvella acetabulum* (L.: Fr.) Quél.’). MycoBank MBT375375

Peziza sulcata Pers., Syn. Meth. Fung. 2: 643. 1801; Fr., Syst. Mycol. 2: 44. 1822.

Acetabula sulcata (Pers.) Fuckel, Jahrb. Nassauischen Vereins Naturk. 23–24: 330. 1870 (‘1869–1870’).

Paxina sulcata (Pers.) Kuntze, Revis. Gen. Pl. 2: 864. 1891.

Lectotype designated here: Pers., Syn. Meth. Fung. 2, t. 5, f. 1. 1801. MycoBank MBT375686.

Misapplied name

– *Acetabula sulcata* sensu Boud., Icon. Mycol., livr. 16: no 357, pl. 246. 1907 (preliminary text with ‘circulaires’) (= ? *Helvella solitaria* P. Karst.).

Illustrations — Dissing (1964: f. 2), Harmaja (1977b: f. 1–2).

Description of the species — Harmaja (1977b: 48).

Specimens examined/sequenced. CZECH REPUBLIC, Vändra, 4 Aug. 1960, A. Raitviir [H427] (C-F-45314). — ICELAND, Nordur-Mulasysla, Hengifossargil, 6 Aug. 1983, J. Vesterholt [H261] (C-F-21174; ‘*H. hyperborea* Harmaja’ det. Harmaja). — NORWAY, Møre og Romsdal, Fræna, Skotten, road side on calcareous ground, 15 m asl, 3 June 2004, J.B. Jordal [H126] (O-178001); Møre og Romsdal, Fræna, Talstadhesten, road side on calcareous ground, c. 310 m asl, 11 June 2004, J.B. Jordal [H127] (O-178005); Vestfold, Sande, Mørkassel, along road under *Quercus*, 10 m asl, 28 May 2006, O. Karlsen [H128] (O-284420); Vestfold, Nøtterøy, Torød, on mossy grass garden, 20

May 2005, A. Aronsen [H133] (O-286533); Østfold, Halden, Kjeøya, moldy deciduous forest on calcareous soil, 8 June 2001, I.-J. Seem & J. Iversby [H134] (O-64925); Oppland, Dovre, Grimsdalen, at Buåi, on the ground in subalpine birch forest, 29 July 1984, T. Schumacher & K. Østmo TS 99.84 [H226] (O-253213), TS 100.84 [H225] (O-253212); *ibid.*, 7 July 1982, TS 142.82 [H287] (O-253215); Dovre, Grimsdalen, Kattuglehøi, southern slope, 19 July 1983, T. Schumacher & K. Østmo TS 33.83 [H286] (O-253214); Finnmark, F.-E. Eckblad 19.61 [H485] (O-253211). — SWEDEN, Östergötland, Gryt parish, Säterön, close to *Quercus*, 14 June 1945, J.A. Nannfeldt 7885 [H410] (C-Fungi Exs. Suec. 1354 epitype); Öland, Böda parish, Byerum, by the road to Bränslögårdarna, 31 May 1967, R. Schöld-ström [H409] (C-Fungi Exs. Suec. 3261).

Notes — Harmaja (1976, 1977b, 1979) was particularly insightful when he concluded there were more recognisable species in the *H. acetabulum* morphospecies complex than previously thought. We inferred a highly-supported lineage of *H. acetabulum* and the morphologically and molecularly related *H. arctoalpina* and *H. costata*, and *H. dryadophila* (Table 3). *Helvella costata*, an apparent distinct American taxon of the *H. acetabulum* morphospecies complex, also fruits in spring and is here adopted for a genetically divergent specimen from California, USA (see Extralimital species below). The five collections of *H. acetabulum* from the Czech Republic, Sweden and Iceland, plus some 11 additional collections from Norway, share three unique single nucleotide polymorphisms (SNPs) within *hsp*, two in *rpb2* and one within the LSU (see alignment: Dryad). The *tef* sequence was identical among five collections from different corners of Norway (see alignment: Dryad).

Helvella alpestris Boud., Bull. Soc. Bot. France 41: CCXL. 1894 — Fig. 4c, f

Synonyms. *Cyathipodia corium* var. *alpestris* (Boud.) Boud., Hist. Classif. Discomyc. Europe: 39. 1907.

Leptopodia alpestris (Boud.) Grelet, Bull. Soc. Bot. Centre-Ouest, Nouv. sér. 3: 86. 1934.

Holotype. SWITZERLAND, Zermatt, Grand St. Bernard, Aug. 1894 (PC), not examined. *Epitype* designated here: NORWAY, Oppland, Dovre, Grimsdalen, Jegerhøi, 1 Aug. 2007, T. Schumacher TS 45.07 (O-253221). MycoBank MBT375376.

Misapplied names

– *Helvella corium* forma *alpestris* (Boud.) J. Favre, *Ergebn. Wiss. Untersuch. Schweiz. Nationalparkes* 5 (33): 27. 1955 (= ? *H. philonotis* Dissing).
 – *Leptopodia murina* Boud. var. *alpestris* (Boud.) R. Heim & L. Rémy, *Bull. Soc. Mycol. France* 48: 58. 1932 (= ? *H. alpina* Skrede, T. Carlsen & T. Schumacher.).

Illustrations — Boudier (1895: pl. 2, f. 2), Dissing (1966a: f. 11j).

Apothecia shallow stipitate-cupulate to -discoid, cup 0.5–1.8 cm broad, stipe terete, solid, c. 0.2–0.4 cm broad, 0.4–1.5 cm high, hymenium and outside black, receptacle and stipe densely tomentose. **Medullary excipulum** of *textura intricata*, hyphae 2–5 µm broad. **Outer excipulum** of brown-walled globose to angular cells, 10–20 µm diam, gradually arranged perpendicularly to the surface and forming a layer of closely packed cells extending into dark brown-walled multicellular, scattered hyphoid hairs or form bundles from the excipulum exterior, hairs generally 40–150 µm, at the margin to 200 µm long, cells 10–15 µm broad, 10–40 µm long. **Asci** pleurorhynchous, 270–310 × 12–16 µm. **Ascospores** ellipsoid, 18.5–22.5 × 11.0–13.8 µm. **Paraphyses** filiform, 2–2.5 µm broad, septate, brownish almost from base, colour increasing in intensity towards the gnarled, clavate tips, 4.5–6.0 µm broad.

Specimens examined/sequenced. CANADA, Nunavut, Kitikmeot Region, above Bloody Falls, on moist, seasonally wet sand in shallow gully in sand hills, 19 July 2014, J.M. Saarela, P.C. Sokoloff, R.D. Bull 4182 [H460] (O ex DAOM-574891). — NORWAY, Oppland, Dovre, Grimsdalen, Jegerhøi, 1 Aug. 2007, T. Schumacher TS 45.07 [H014] (O-253221 epitype); Dovre, Grimsdalen, Tverrådalen, 6 Aug. 2009, T. Carlsen, I. Skrede & T. Schumacher TS 11.09 [H042] (O-253224); *ibid.*, 15 Aug. 1997, T. Schumacher [H246] (O-253219); *ibid.*, 31 July 2007, T. Schumacher TS 33.07 [H036] (O-253223); *ibid.*, 1. Aug. 2007, T. Schumacher TS 20.07 [H013] (O-253220); *ibid.*, 7 Aug. 2009, T. Carlsen, I. Skrede & T. Schumacher TS 06.09 [H031] (O-253222); *ibid.*, 7 Aug. 2009, T. Carlsen, I. Skrede & T. Schumacher TS 11.09 [H042] (O-253224); Grimsdalen, Tverrgjellbekken, on silt and moss underneath *Salix arbuscula*, 26 July 1984, T. Schumacher & K. Østmoe TS 70.84 [H483] (O-253225).

Notes — The holotype of *H. alpestris* from Zermatt in Switzerland, located in PC and depicted by Dissing (1966a), is old and presumably unsuitable for DNA extraction. It is here supported with an epitype specimen from an alpine locality in Norway, adding sequences of *hsp*, *tef*, *rpb2* and LSU as molecular characteristics to the species. Based on morphology and molecular data, *H. alpestris* is sister species to *H. macrosperma* from which it diverges in one substitution in *hsp*, four substitutions in *tef*, one substitution in *rpb2* and seven substitutions in LSU.



Fig. 4 Photos of fresh (f) and (a–e) dried apothecia. a. *H. corium* (C-F-92111, holotype of *H. arctica*); b. *H. nannfeldtii* (O-253343); c. *H. alpestris* (O ex DAOM574891); d. *H. macrosperma* (O-253330); e. *H. alpina* (O-253228, holotype); f. *H. alpestris* (O-253400). — Scale bars = 1 cm. — Photos: a–e: I. Skrede; f: T. Schumacher.

Helvella alpicola Skrede, T. Carlsen & T. Schumach., *sp. nov.* — MycoBank MB820315; *Hsp* barcode GenBank KY784304; *Rpb2* barcode GenBank KY772554; Fig. 5c, e

Etymology. From Latin 'thriving in mountainous areas'.

Holotype. NORWAY, Nordland, Saltdal, Junkerdalsura, 27 Aug. 1988, A.E. Torkelsen 180.88 (O-185924).

Apothecia stipitate-cupulate, cup 0.5–1.5 cm broad, hymenium greyish black (G1), receptacle dark greyish (E-F1), receptacle surface and stipe densely tomentose, stipe greyish to whitish below, 0.2–0.3 cm broad, 0.5–1.8 cm high, with 2–3 shallow grooves at base. *Medullary excipulum* of loose *textura intricata*, hyphae 2–5 µm broad, hyaline. *Outer excipulum* of *textura angularis*, cells 10–27 µm diam, the strong pubescence of the outer receptacle surface due to long fascicled tufts of multiseptate, subhyaline, hyphoid hairs, 60–250 µm long; individual cells cylindrical to drum-shaped, 20–40 × 10–25 µm, with conspicuous brown pigments at septa. *Asci* pleurohynchous, 290–330 × 15–18 µm. *Ascospores* ellipsoid, 20–22.6 × 11.8–13.5 µm. *Paraphyses* c. 2.5 µm below, septate, brownish, gradually enlarged to 5–6 µm at the clavate tips.

Specimens examined/sequenced. NORWAY, Nordland, Saltdal, Junkerdalsura, 27 Aug. 1988, A.E. Torkelsen 180.88 [H175] (O-185924 holotype). — SWITZERLAND, Graubünden, Inn at Resgia, on soil at the river, 26 Aug. 1984, H. Dissing [H231] (O-253226).

Notes — *Helvella alpicola* possesses a tomentose receptacle covered by short-celled hyphoid hairs (Fig. 5c, e). It resembles *H. rivularis* in shape and colour. The species is recorded from two distant localities, e.g., in Northern Norway (Arctic) and the Swiss Alps. The sequenced specimens are invariable

in *rpb2*, but differ in two *hsp* sites. *Helvella alpicola* forms a divergent lineage in our phylograms.

Helvella alpina Skrede, T. Carlsen & T. Schumach., *sp. nov.* — MycoBank MB820322; *Hsp* barcode GenBank KY784343; *Rpb2* barcode GenBank KY772593; Fig. 4e

Etymology. From Latin 'occurring in mountainous regions'.

= ? *Helvella murina* Boud. var. *alpestris* R. Heim & L. Rémy, Bull. Soc. Mycol. France 48: 58. 1932.

Holotype. FRANCE, Savoie, Plan des Evettes, 26 Aug. 1992, T. Schumacher F15.92 (O-253226).

Apothecia regularly cupulate-stipitate, black all over, cup 0.8–2.0 cm across, receptacle surface subpubescent, commonly with white crystalline deposits at the margin, stipe slender, 0.2–0.3 cm thick, 1.0–3.5 cm long, solid to hollow, occasionally with a few longitudinal grooves. *Medullary excipulum* of *textura intricata*, hyphae 2–5 µm broad, hyaline. *Outer excipulum* of *textura angularis*, cells 10–25 µm diam, intermixed with subhyaline to brown-walled hyphae, turned perpendicularly to receptacle surface and forming scattered 3–8-celled, brown-walled, branching hyphoid hairs, 30–100 µm long, individual cells ovoid to subglobose, up to 20 µm broad. *Asci* aporhynchous, 220–290 × 14–18 µm. *Ascospores* ellipsoid, 16.6–19.2 × 11.5–13.2 µm. *Paraphyses* 2.0–2.8 µm broad, septate, brownish along the whole length, gradually enlarged to 4.0–6.5 µm at the subcapitate tips.

Specimens examined/sequenced. CANADA, British Columbia, Whistler National Park, on the ground under *Salix* in subalpine spruce forest, 13 Aug. 1994, T. Schumacher [H336] (O-253227). — FRANCE, Savoie, Plan des



Fig. 5 Photos of fresh (e) and dried (a–d) apothecia. a. *H. hypocrateriformis* (C-F-92131, isotype of *H. cupuliformis*); b. *H. scyphoides* (O-65348, holotype); c. *H. alpicola* (O-185924, holotype); d. *H. rivularis* (C-F-59447, holotype); e. *H. alpicola* (O-253402). — Scale bars = 1 cm. — Photos: a–d: I. Skrede; e: T. Schumacher.

Evettes, 26 Aug. 1992, *T. Schumacher* F15.92 [H223] (O-253226 holotype). – GREENLAND, Qeqertarsuaq, Godhavn, the plain E of the Arctic station, in moss carpet of *Paludella squarrosa* with *Salix arctophila*, 11 Aug. 1977, *P.M. Petersen* [H349] (C-F-63820).

Notes — This new species may have been described from the French Alps as a variety (var. *alpestris*) of *H. murina* (Heim & Rémy 1932). There are, however, no authentic specimens left to support this assumption (Dissing, pers. comm). Macromorphologically, *H. alpina* resembles *H. corium* and *H. alpestris*, but has a more slender stipe two to three times longer than cap height and width. The receptacle appears smooth to the naked eye but is covered with minute, scattered distributed hyphoid hairs using a 10× hand lens. *Helvella alpina* and *H. corium* form a highly divergent lineage in our phylogeny characterised by black, stipitate-cupulate apothecia and asci with an aporhynchous ascus base. Asci and ascospores of the two species are in the same range, but apothecial shape, hairs and habitat easily distinguish them. The three collections from arctic and alpine localities in Greenland, France and Canada share identical *rpb2* sequences, but vary in three *hsp* sites.

Helvella arctoalpina Harmaja, *Karstenia* 17: 58. 1977 — Fig. 3a, f

Holotype. NORWAY, Hordaland, Eidfjord, Dyranut, 1 Aug. 1959, *F.-E. Eckblad* (O-72616).

Synonyms. *Acetabula barlae* Boud., *Hist. Classif. Discomyc. Europe*: 40. 1907.

Paxina barlae (Boud.) Seaver, *North Amer. Cup-fungi (Operculates)*: 205. 1928.

Helvella dalgeri Donadini, *Bull. Soc. Linn. Provence* 36: 136. 1985 '1984'. *Lectotype*. FRANCE, Nice, Feb. 1883, *D. Barla*, selected by Dissing 1966a.

Illustrations — Boudier (1905–1910: pl. 245, as *Acetabula barlae*), Harmaja (1977b: f. 3–4), Schumacher & Mohn Jensen (1992: 13).

Descriptions of the species — Harmaja (1977b: 48), Schumacher & Mohn Jensen (1992: 13).

Specimens examined/sequenced. CANADA, Ellesmere Island, Alexandra Fjord, 23 July 1984, *H. Dissing* [H338] (C-F-56722); *ibid.*, [H337] (C-F-56723). – FRANCE, Savoie, Val d'Isere, 2550 m asl, in *Dryas* association, 31 Aug. 1992, *T. Schumacher* [H360] (O-253229). – GREENLAND, Ella Island, St. Elvdal, most calcareous sand in *Dryas* association, 6 Aug. 1982, *H. Dissing* & *S. Sivertsen* [H359] (C-F-50652). – ICELAND, Nordur-Mulasysla, Hengifossargill, in dry heath vegetation with *Dryas octopetala*, 6 Aug. 1993, *H. Knudsen* [H342] (C-F-34334). – NORWAY, Hordaland, Eidfjord, Dyranut, in *Dryas* carpets, 1 Aug. 1959, *F.-E. Eckblad* [H293] (O-72616 holotype); Ulvik, Finse, Bio 101 peak, in *Dryas* association, 24 July 2014, *T. Schumacher* [H472] (O-253231); *ibid.*, 29 July 2014, *T. Schumacher* [H456] (O-253230); Oppland, Lom, Høyrokampen, in *Dryas* association, 1400–1440 m asl, 29 Aug. 1957, *F.-E. Eckblad* [H354] (O-174714); Oppland, Dovre, Grimsdalen, Tverråi, along the slopes in *Dryas* vegetation, 27 July 1984, *T. Schumacher* & *K. Østmoe* D 83.84 [H083] (O-253239); *ibid.*, 16 Aug. 1996, *S. Landvik* & *T. Schumacher* TS 199.96 [H084] (O-253240); *ibid.*, 16 Aug. 2001, *T. Schumacher* [H003] (O-253232); *ibid.*, 2. Aug. 2007, *T. Schumacher* TS 13.07 [H011] (O-253233); *ibid.*, *T. Schumacher* TS 27.07 [H012] (O-253234); *ibid.*, 7 Aug. 2009, *T. Carlsen*, *I. Skrede* & *T. Schumacher* TS 2.09 [H030] (O-253236); *ibid.*, TS 7.09 [H033] (O-253237); *ibid.*, TS 8.09 [H040] (O-253238); Grimsdalen, Tverrgjelet, in moist *Dryas* vegetation, 26 July 1984, *T. Schumacher* & *K. Østmoe* D 75.84 [H356] (O-253244); *ibid.*, 20 Aug. 1997, *T. Schumacher* 35.97 [H255] (O-253403); *ibid.*, 15 Aug. 2001, *T. Schumacher* [H182] (O-253243); *ibid.*, 8 Aug. 2009, *T. Carlsen*, *I. Skrede* & *T. Schumacher* TS 24.09 [H026] (O-253235); Grimsdalslytta, 3 Aug. 1966, *A. Danielsen* & *A.-E. Torkelsen* [H086] (O-253241); *ibid.*, [H087] (O-253242); Nordland, Ballangen, Håfjellet, on calcareous soil along path, 26 July 2008, *D. Holtan* & *P.G. Larsen* PL 41.2008 [H173] (O-69063).

Notes — The sequenced specimens from Canada and Greenland have one common *rpb2* nucleotide character that separates them from the European specimens. European specimens are genetically uniform. Dissing (1966a) examined a specimen

of *Acetabula barlae* in PC, which he considered to be a suitable lectotype specimen, and referred it to his concept of *H. acetabulum*. He noted that “the very characteristic dark greenish olive colours, seen in fresh specimens of *H. acetabulum*, are not mentioned in Boudier’s otherwise detailed description” (Dissing 1966a). In our opinion, Boudier’s plate of *A. barlae* (Boudier 1905–1910: pl. 245) depicts a typical specimen of *H. arctoalpina*, as does Favres record of *A. barlae* from the Swiss Alps (Favre 1955: pl. 4, f. 1). *Helvella arctoalpina* and *H. acetabulum* form a well-supported sublineage of the acetabulum-solitaria lineage in our phylogeny. *Helvella arctoalpina* differs from *H. acetabulum* by one substitution in *rpb2*, six in *hsp*, three in *tef* and 10 in LSU.

Helvella atra Oeder, *Fl. Dan.* 3 (9): 7. 1770 — Fig. 6f

Basionym. *Helvella atra* Oeder, *Fl. Dan.* 3, fasc. 9: 7. 1770; *Fr., Syst. Mycol.* 2: 19. 1822.

Synonym. *Leptopodia atra* (Oeder) Boud., *Icon. Mycol.*, liste prélim.: 2. 1904.

Lectotype. Oeder, *Fl. Dan.* 3 (9): t. 534, f. 1. 1770 ('*Elvela*'), selected by Filippa & Baiano (2011). *Epitype* designated here: SWEDEN, Uppland, Uppsala, about 300 m NW of Grindstugan, 13 July 1938, *S. Lundell* (C-Fungi Exs. Suec. 2066 '*H. lacunosa* Afzel. ex Fr. – dwarfed form'). MycoBank MBT375395.

Illustrations — Oeder (1770: pl. 534, f. 1), Filippa & Baiano (2011: f. 9–10, f. 11 as *H. lacunosa*).

Apothecia stipitate-capitate, saddle-shaped or irregularly lobed, 1–4 cm broad, 3–12 cm high, cap margin adnate and attached to stipe at 3–4 points; hymenium and stipe blackish with a dark violet brown tinge (10-12F-H7-8), even or wrinkled; receptacle surface greyish brown to black, smooth, with inconspicuous ribs on outer surface; stipe 0.5–2.5 cm broad, naked, with 4–7 sharp-edged, partly double-edged ribs, attached at 3–4 points to the reflexed apothecial margin greyish brown to black, paler towards base, ribs prominent, sharp, partly anastomosing and double-edged, with ‘holes’ (lacunae) between ribs, stipe chambered inside. *Medullary excipulum* of *textura intricata*, hyphae 3–5 µm broad. *Outer excipulum* of *textura globulosa-angularis*, cells 8–15 µm diam, hyaline, heavily staining in CB, outermost cells club-shaped, 10–30 × 5–15 µm. *Asci* pleurohynchous, 260–10 × 14–18 µm. *Ascospores* ellipsoid, 15.5–18.5 × 10–12.5 µm. *Paraphyses* straight, septate, subhyaline to light brown below, increasingly brown above, 3–4 µm broad, clavate to 6.5 µm at tips.

Specimens examined/sequenced. DENMARK, Zealand, Møn, Ulvshale, 13 June 1999, *T. Læssøe* [H467] (C-45782). – GEORGIA, Caucasus, Kasbeghi, Gvethi valley, sandy soil along path, 200 m asl, 13 July 1988, *E. Johannesen* [H233] (O-253245); *ibid.*, [H375] (O-253246). – NORWAY, Oppland, Dovre, Grimsdalen, at Buài, on sandy soil along the road, 12 Aug. 1981, *T. Schumacher* & *K. Østmoe* 165.81 [H465] (O-253252); Grimsdalen, Jegerhøi towards Verkenseter, 1 Aug. 2007, *T. Schumacher* TS 43.07 [H016] (O-253251); Sør-Trøndelag, Oppdal, Loslia, in calcareous pasture land above tree limit, 995 m asl, 20 Aug. 2009, *J.B. Jordal* [H481] (O-291384); Nordland, Bodø, Sjunkhatten National Park, Steigtindvann, at the trail, 23 June 2010, *L. Ryvarden* [H462] (O-294033); Nordland, Steigen, Liland, Bru, 21 July 2006, *N. Hagen* 74.06 [H151] (O-281641); *ibid.*, Andøy, Slettneset, in sand dunes on calcareous soil, 13 Sept. 2005, *P.H. Larsen* 234 [H464] (O-360146); Finnmark, *F.-E. Eckblad* 64.61 [H487] (O-253248); Finnmark, *F.-E. Eckblad* 99.61 [H484] (O-253247). – SWEDEN, Uppland, Uppsala, about 300 m NW of Grindstugan, 13 July 1938, *S. Lundell* [H406] (C-Fungi Exs. Suec. 2066 epitype).

Notes — *Helvella atra* was originally described and depicted in *Flora Danica* (Oeder 1770), but redescribed two years later by Zoega (1772) based on a specimen from Iceland collected by J. König. The illustration and descriptions leave little doubt that the fungus belongs to the *H. lacunosa* morphospecies complex, as also concluded by Dissing (1964, 1966b). Fries (1822) adopted Oeder’s name for a broadly defined species



Fig. 6 Photos of fresh (b–c) and dried (a, d–f) apothecia. a. *H. lacunosa* (C-Fungi Exs. Suec. 2065, epitype); b. *H. lacunosa* (O-253398); c. *H. palustris* (O-253399); d. *H. philonotis* (C-F-45481, holotype); e. *H. nigra* (O-253345, epitype); f. *H. atra* (C-Fungi Exs. Suec. 2066, epitype). — Scale bars = 1 cm. — Photos: a, d–f: I. Skrede; b–c: T. Schumacher.

which included Königs fungus (Oeder 1770, Zoega 1772 – erroneously referred to as published by König) as well as *H. atra* in the sense of Afzelius (1783) and Holmskjöld (1799), and *H. nigricans* (Persoon 1796, 1801). In our opinion Afzelius' and Holmskjöld's '*H. atra*' and Persoon's *H. nigricans* represent a distinct species for which we have adopted the binomial *H. fallax* (see this species below). Dissing selected Holmskjöld's plate (1799: pl. 25) as the lectotype of *H. atra*, but should better have used Oeder's plate as an interpretive legitimate type, since *H. atra* Oeder represents the older sanctioned homonym (cf. ICN Articles 53.1, 53.2, 15. Note 1 (ICN 2012)). We therefore re-instate Oeder's plate as a lectotype and supports it with an epitype. Although a specimen from Iceland would have been the ideal epitype, we have selected a specimen from Sweden, widely distributed as an exsiccate specimen, to represent this species. The sequenced specimens from subalpine Norway have one *rpb2* site polymorphism that separates them from the rest of the sequenced specimens. Two LSU sequences in GenBank [KC122770, KC122771] treated as *H. lacunosa* in Landeros et al. (2015) cluster with *H. atra* (cf. Appendix 3).

Helvella bicolor Raddi, Mem. Mat. Fis. Soc. Ital. Sci. 13, 2: 354. 1807 '1806' — Fig. 7e, i

Lectotype designated here: Raddi, Mem. Mat. Fis. Soc. Ital. Sci. 13, 2: 362, pl. 13, f. 10. 1807. MycoBank MBT375687. *Epitype* designated here: SWEDEN, Gästrikland, Göskegruvan i Hofors, calcareous soil under *Picea*, 9 Sept. 1978, E. Sundström (C-F-45334). MycoBank MBT375464.

Synonyms. *Helvella albella* Quél., Compt. Rend. Assoc. Franc. Avancem. Sci. 24: 621. 1896 '1895' ('*Elvela*')
Leptopodia albella (Quél.) Boud., Icon. Mycol., liste prélim.: 2. 1904.

Lectotype designated here: Quél., Compt. Rend. Assoc. Franc. Avancem. Sci. 24: t. 6, f. 16. 1896 ('*Elvela*'). MycoBank MBT375688.

Illustrations — Raddi (1807: pl. 13, f.10), Dissing (1966b: f. 37, as *H. albella*).

Description of the species — Dissing (1966b: 136, as *H. albella*).

Specimens examined/sequenced. NORWAY, Vestfold, Lardal, Nerli, coniferous forest with *Betula* and *Populus*, 29 July 2000, P. Marstad [H147]

(O-105346); Hedmark, Åmot, Kvannbekken National Reserve, calcareous river cleft, 30 Aug. 2002, T.S. Nilsen [H129] (O-65375); Akershus, Eidsvoll, Eidsvollbygningen, 16 Sept. 2009, I. Skrede TS 40.09 [H057] (O-253254); Akershus, Hurdal, 15 Sept. 2009, I. Skrede TS 41.09 [H056] (O-253253). — SWEDEN, Gästrikland, Göskegruvan i Hofors, on calcareous soil under *Picea*, 9 Sept. 1978, E. Sundström [H289] (C-F-45334 epitype).

Notes — The original description and illustration of *H. bicolor* Raddi (1807), which fully cover the present concept of *H. albella* of Quélet's (1896), seems to have escaped recognition by earlier mycologists, including Fries (1822, 1832) and Dissing (1966b). We have chosen the plate and figure of Raddi's (1807) as a lectotype and supported it with an epitype from Sweden, adding partial sequences from *hsp*, *rpb2* and LSU to the species characteristics. According to Dissing (1966b), there is no authentic material of *H. albella* left in PC. The five collections studied by us have one polymorphic *rpb2* and one polymorphic *hsp* site among them. A number of synapomorphies in the *hsp* and *rpb2* loci separates the species from the sisters of the bicolor-*elastica* lineage of the *elastica* clade (clade E).

Helvella calycina Skrede, T. Carlsen & T. Schumacher, *nom. nov.*
 — MycoBank MB820325

Etymology. From Latin 'trumpet-like'.

Basionym. *Boletus calyciformis* Battarra, Fungorum Arimin.: 25. 1759; Fr., Syst. Mycol. 2: 45. 1822.

Synonyms. *Peziza calyciformis* (Battarra) Fr., Syst. Mycol. 2: 45. 1822.

Acetabula calyciformis (Battarra) Sacc., Syll. Fung. 8: 61. 1889.

Paxina calyciformis (Battarra) Kuntze, Revis. Gen. Pl. 2: 864. 1891.

— non *Helvella calyciformis* Batsch, Elench. Fung., cont. Prim. (Halle): 27. 1786 ('*Elvela*') = *Peziza calycina* α (var.) Fr., Syst. Mycol. 2: 91. 1822.

Lectotype designated here: Battarra, Fungorum Arimin.: t. III, f. C, 1759. MycoBank MBT375689. *Epitype* designated here: NORWAY, Oppland, Dovre, Grimsdalen, Storberget, 8 Aug. 2009, T. Carlsen, I. Skrede & T. Schumacher TS 16.09 (O-253255). MycoBank MBT375389.

Illustration — Dissing (1966b: f. 16, as *H. costifera*).

Apothecia at first short-stipitate-cupulate, when expanding more irregularly folded, 2.0–7.5 cm broad, 1.5–4.5 cm high. *Hyme-*

nium brownish (6-8E5-8), receptacle surface greyish brown 6E3), slightly pubescent, stipe with 5–8 prominent blunt-edged yellowish grey ribs (4B2-3) extending onto receptacle but not reaching the margin, ribs apically dichotomously branched and interconnected by shallow concentric parallel connections in old fruit bodies making receptacle surface ‘wrinkled’. *Medullary excipulum* of hyaline *textura intricata*, hyphae c. 3–5 µm broad. *Outer excipulum* of *textura prismatica* to *textura angularis*, outermost cells with brown walls. *Asci* pleurorhynchous, 240–280 × 11–14 µm. *Ascospores* ellipsoid, 14.5–17.6 × 9.5–12.0 µm. *Paraphyses* 2.5–3.5 µm broad, straight, septate, gradually enlarged to 4–5 µm at the tips.

Specimens examined/sequenced. DENMARK, Klim Bjerg, Klim W of Fjeritlev, 18 Oct. 1993, J. & T. Læssøe & A. Møller [H382] (C-F-21122); *ibid.*, 16 July 1999, P.B. Hansen & J. Vesterholt JV 153.99 [H384] (C-F-41038); Northeast Jutland, Hjørring, under *Picea* in Klitplantage (Rubjerg Knude Plantage), 4 Aug. 1998, D. Boertmann DB 98007 [H387] (C-F-71286). – NORWAY, Oppland, Dovre, Grimsdalen, Storberget, 8 Aug. 2009, T. Carlsen, I. Skrede & T. Schumacher TS 16.09 [H022] (O-253255 epitype).

Notes — *Helvella calycina* is here typified based on the basionym *Boletus calyciformis* Battarra (1759). Fries adopted *Peziza calyciformis* for this cupulate, prominently ribbed autumnal species of Battarra’s and compared it with the vernal *Peziza acetabulum* (Fries 1822). Later, he described *Peziza costata* (Fries 1851), which was recombined in *Helvella* under

the new legitimate name of *H. costifera* by Nannfeldt (Lundell & Nannfeldt 1953). Neither Fries nor Nannfeldt considered *Boletus calyciformis* as a possible earlier name for *Peziza costata* (= *Helvella costifera*). We now know there are at least two prominently ribbed cupulate *Helvella* species that occur in Europe sympatrically in autumn, i.e., *H. costifera* and *H. calycina*. Three specimens of *Helvella* from Mexico referred to as *Helvella* aff. *costifera* (JX993057, JX993058, JX993059; cf. Appendix 3) are, judged from the published LSU sequence, concluded to represent *H. calycina*. *Helvella calycina* differs from its sister species *H. costifera* in two consistent *rpb2* and one *hsp* substitution plus some inconstant polymorphies, including one *hsp* and five *rpb2* sites.

Helvella capucina Quél., Bull. Soc. Bot. France 24: 327. 1878 ‘1877’ — Fig. 7g

Synonym. *Leptopodia capucina* (Quél.) Boud., Hist. Classif. Discomyc. Europe: 37. 1907.

Lectotype. Quél., Bull. Soc. Bot. France 24: t. 6, f. 3. 1878, selected by Van Vooren (2010). *Epitype* designated here: FRANCE, Savoie, Val d’Isère, Gorges du Mal, 2300 m asl, on river bed, 31 Aug. 1992, T. Schumacher (O-253256). MycoBank MBT375396.

Illustrations — Dissing (1964: f. 3), Schumacher & Mohn Jensen (1992: 15).



Fig. 7 Photos of dried apothecia. a. *H. panormitana* (O-253363, epitype); b. *H. carnosa* (O-68100, holotype); c. *H. levis* (C-F-55188, epitype); d. *H. elastica* (C-F-29130, epitype); e. *H. bicolor* (O-105346); f. *H. danica* (O-253288); g. *H. capucina* (O-253256); h. *H. fistulosa* (O-253315); i. *H. bicolor* (C-45334, epitype). — Scale bars = 1 cm. — Photos: I. Skrede.

Descriptions of the species — Dissing (1964: 113), Schumacher & Mohn Jenssen (1992: 15).

Specimens examined/sequenced. CANADA, Northwest Territories, Keewatin district, Rankin Inlet, NW of airstrip, on sandy ground with moss, 21 Aug. 1971, E. & M. Ohenoja 43.1971 [H397] (C-F-92107); Nunavut, Kitikmeot Region, above Bloody Falls, at Coppermine River, 19 July 2014, J.M. Saarela, P.C. Sokoloff & R.D. Bull 4183 [H459] (O- ex DAOM 574890). — FRANCE, Savoie, Val d'Isère, Gorges du Mal, 2300 m asl, on river bed, 31 Aug. 1992, T. Schumacher F 74.92 [H208] (O-253256 epitype); Savoie, Val d'Isère, Plan des Evettes, 2500 m asl, on river terrace, 26 Aug. 1992, R. Fellner F 1.82 [H211] (O-253257). — GREENLAND, Mestervig, around Blyminen, on naked soil in river bed, 14 Aug. 1982, H. Dissing & S. Sivertsen [H488] (C-F-50768). — NORWAY, Oppland, Dovre, Grimsdalen, Buài, at the river, 17 Sept. 1983, T. Schumacher & K. Østmo D164.83 [H082] (O-253262); Grimsdalen, Tverrgjelet, on silt along Tverrgjebekken, 4 Aug. 1989, T. Schumacher G 39.89 [H201] (O-253264); *ibid.*, G.40.89 [H202] (O-253265); *ibid.*, 16 Aug. 1996, S. Landvik & T. Schumacher SL 202.96 [H089] (O-253263); Grimsdalen, Veslegrimsa, on river bed, 8 Aug. 2009, T. Carlsen, I. Skrede & T. Schumacher TS 20.09 [H046] (O-253261); Grimsdalen, Tverrådalen, on moist silt on river slope, 1 Aug. 2007, T. Schumacher TS 14.07 [H035] (O-253260); Grimsdalen, Grimsa at Storberget, on river terrace, 3 Aug. 2007, T. Schumacher TS 38.07 [H034] (O-353259); Grimsdalen, Jegerhøi SE toward Verkenseter, on soil along path, 3 Aug. 2007, T. Schumacher TS 50.07 [H009] (O-253258). — SWITZERLAND, Graubünden, Las Palüds, 1750 m asl, on soil, 29 Aug. 1984, H. Dissing [H203] (O-253266).

Notes — The species is genetically uniform; the Greenland collection has one *hsp* substitution not found in the rest of the specimens, which are identical. The species appears to be restricted to the arctic-alpine biome. *Helvella pygmaea*, originally described from Northern Norway (Sommerfelt 1826), and the name sanctioned by Fries (1828), presumably represents an older name for this species, however, there is neither an original illustration nor material of *H. pygmaea* left in Sommerfelt's herbarium in O to support this assumption.

Helvella carnosa Skrede, T. Carlsen & T. Schumacher, *sp. nov.*
— MycoBank MB820323; *hsp* barcode GenBank KY784279; *rpb2* barcode GenBank KY772529; Fig. 7b

Etymology. From Latin 'fleshy in consistency'.

Holotype. NORWAY, Oslo, Malmøykalven, 13 Oct. 2006, O. Smith (O-68100).

Apothecia stipitate-capitate, regularly bilobate, cap 0.5–1.5 cm broad, apothecial margin inflexed (adnate); hymenium brown (5F-6E4-8), drying brownish black (6F-G5-8); receptacle surface delicately pubescent; stipe hollow, 3–4 cm high, by 0.3–0.5 cm broad, yellowish and slightly compressed when dried. *Medullary excipulum* of dense *textura intricata*, hyphae 3–5 µm broad. *Outer excipulum* of subhyaline to light brown *textura angularis*, cells 20–35 × 10–30 µm, outermost cells club-shaped turning out perpendicularly to the surface forming clusters of loose, short-celled, hyaline hyphoid hairs heavily stained in CB. *Asci* pleurorhynchous, 270–300 × 13–15 µm. *Ascospores* ellipsoid, 18.0–19.8 × 11.8–12.6 µm. *Paraphyses* straight, c. 3 µm broad, light brown along the whole length, at tips clavately enlarged to 5–8 µm.

Specimen examined/sequenced. NORWAY, Oslo, Malmøykalven, 13 Oct. 2006, O. Smith [H146] (O-68100 holotype).

Notes — This new species of the *elastica* clade is described based on a single specimen from Norway. The molecular specifics are supported with *hsp*, *rpb2* and LSU GenBank sequences of a second specimen from Sweden (cf. Fig. 2). *Helvella carnosa* resembles *H. bicolor* in colour, but has a subpubescent exterior and smaller asci and ascospores. In summary, five *rpb2*, eight *hsp* and eight LSU substitutions separate it from *H. elastica*; 11 *rpb2*, six *hsp* and eight LSU substitutions from *H. danica*; 11 *rpb2* and six *hsp* substitutions from *H. fistulosa*; six *rpb2*, 16 *hsp* and 11 LSU substitutions from

H. bicolor; and 11 *rpb2*, seven *hsp*, and 10 LSU substitutions from *H. panormitana*.

Helvella confusa Harmaja, *Karstenia* 17: 43. 1977 — Fig. 3g

Holotype. DENMARK, Northern Jutland, Klitmøller, 15 May 1965, K. Toft & H. Dissing ('*H. solitaria*') (H). *Isotype* (C-F-70807 '*H. solitaria*').

Synonym. ? *Helvella pedunculata* Harmaja, *Karstenia* 18: 57. 1978.

Holotype. FINLAND, Pohjois-Pohjanmaa, Kiiminki, Keski kylä, 2 July 1975, E. & M. Ohenoja (OULU), not examined.

Misapplied name

— *Helvella solitaria* sensu Dissing, *Dansk Bot. Ark.* 25: 41. 1966.

Illustration — Dissing (1966b: f. 10, as *H. solitaria*).

Descriptions of the species — Dissing (1966b: 42, as *H. solitaria*), Harmaja (1977a: 43, 1979: 36).

Specimens examined/sequenced. DENMARK, Northern Jutland, Klitmøller, on calcareous soil under *Picea*, 15 May 1965, K. Toft & H. Dissing [H477] (C-F-70807 isotype); *ibid.*, in coniferous tree plantation, 12 June 1981, T. Læssøe 0110 [H438a] (C); Northern Jutland, Nystrup Plantage, Klitmøller, 31 May 1986, D. Boertmann [H438] (C-F-71647). — INDIA, Kupwara, Lolab Valley, on soil in coniferous forest, 2 May 1967, K.S. Thind [H446] (C-F-45513). — NORWAY, Østfold, Fredrikstad, Kråkerøy, Fuglevik, roadside with spruce, elm and birch, 20 June 1987, R. Kristiansen [H192] (O-253270); Onsøy, Engalsvik, in spruce forest on gravelly sand, 20 June 1981, R. Kristiansen [H253] (O-253271); Buskerud, Gol, in moss along rivulet, 9 June 2014, K. Sæbø [H437] (O-253268); Oppland, Lunner, Søndre Oppdalen, on calcareous ground, 12 July 1987, T.E. Brandrud [H439] (O-129435); Aust-Agder, Grimstad, Landvik, in rich deciduous forest at the road, 24 Apr. 1998, I.-L. Fonneland [H155] (O-71947); Dovre, Grimsdalen, Tollevschaugen, in pine forest reserve, 4 Aug. 2007, T. Schumacher & T. Vrålstad TS 077.07 [H008] (O-253269); Nordland, Rana, Ørtfjellmoen bridge, spring vegetation in calciphilic spruce forest, 20 Aug. 1979, S. Sivertsen [H320] (C-92125); *ibid.*, 24 Aug. 1981, H. Dissing [H386] (C-F-55016); Nordland, Rana, Dunderland, in river bed, 31 Aug. 1998, H. Dissing & S. Sivertsen AAS 08.98 [H313] (C-F-58808). — SWEDEN, Uppland, Älvkarleby parish, 3 km NE of Gårdskär, on gravelly roadside among bark debris in coniferous forest, 30 June 1965, O. Eriksson & N. Lundquist [H279] (C-F-92132 Fungi Exs. Suec. 3268 '*H. solitaria* P. Karst.'). — SWITZERLAND, Graubünden, Mota Jüda, Val Plavna, 1600 m asl, along path, 30 Aug. 1979, H. Dissing [H331] (C-F-56845); Las Palüds, 1750 m asl, on soil, 29 Aug. 1984, H. Dissing [H092] (O). — USA, Oregon, Sahale Falls, Hood River Meadows, road to Cloud Cap, road side on soil, 9 July 1991, H. Dissing [H449] (C-F-56513).

Notes — We have adopted the binomial *H. confusa* for this widespread species. Harmaja (1977a) argued that Dissing had misunderstood Karsten's concept of *H. solitaria* and introduced the name *H. confusa* for this species. A Danish specimen that was depicted in Dissing (1966b: f. 10), was selected as the holotype (Harmaja 1977a), a specimen re-examined here by us. Later, Harmaja (1978) erected an additional taxon, *H. pedunculata*, to include parts of the specimens previously cited as *H. solitaria* sensu Dissing. Dissing (1966b) noted the close relationship between *H. confusa* (as *H. solitaria*) and *H. leucomelaena*, but kept them separate based on colour, anatomy and ascospore characteristics. The distinct sulcate stipe in *H. confusa* was maintained as a feature distinguishing it from *H. leucomelaena* (Dissing 1966b).

We obtained partial sequences from *hsp*, *rpb2* and LSU as molecular specifics to the species circumscription. Two unique *rpb2* substitutions separate the non-European from the European specimens, which on their hand are identical. The Indian and North American specimens are separated by one *rpb2* substitution. A specimen from Spain [JX 993070] published as *H. leucomelaena* by Landeros et al. (2015), shares the LSU nrDNA sequence of *H. confusa* (cf. Appendix 3). Four *rpb2*, three *hsp* and five LSU substitutions distinguish *H. confusa* from the sister species *H. leucomelaena*.

Helvella corbierei (Malençon) Van Vooren & Frund, Bull. Mycol. Bot. Dauphiné-Savoie 198: 9. 2010

Basionym. *Leptopodia corbierei* Malençon, Bull. Soc. Mycol. France 43: 95. 1927.

Lectotype. Malençon, Bull. Soc. Mycol. France 43: t. 6, f. 7, selected by Van Vooren & Frund (2010). *Epitype* designated here: SWITZERLAND, Graubünden, Ramosch, along the river Inn at Resgia, 7 Sept. 1982, *H. Dissing* (C-F-57133). MycoBank MBT375397.

Misapplied name

– *Helvella stevensii* sensu Dissing, Dansk Bot. Ark. 25: 125. 1966.

Illustrations — Malençon (1927: pl. 6, f. 7), Dissing (1966b: f. 34, as *H. stevensii*), Van Vooren & Frund (2010: 7).

Description of the species — Van Vooren & Frund (2010: 6).

Specimens examined/sequenced. NORWAY, Oppland, Dovre, Grimsdalen, along the road at Storberget, 16 Aug. 2001, *T. Schumacher* [H178] (O-253273); *ibid.*, 17 Aug. 2001, *T. Schumacher* [H191] (O-253274); Nordland, Rana, Krogstrand, 40 km E Mo i Rana, in small stream, 7 Sept. 1972, *H. Dissing* [H390] (C-F-53800). – SWITZERLAND, Graubünden, Ramosch, along the river Inn at Resgia, 7 Sept. 1982, *H. Dissing* [H392] (C-F-57133 *epitype*); *ibid.*, 26 Aug. 1984, *H. Dissing* [H232] (O-253275); Schmelboden, along road and river Landwasser to Brombänz, 2300 m asl, 4 Sept. 1982, *L. Petrini* & *H. Dissing* [H391] (C-F-57087). – USA, Oregon, National Forest Lane Co., Mac Donald Forest, Benton Co., on moss grown trunk along stream, 6 July 1991, *H. Dissing* Oregon 40.91 [H346] (C-F-56503).

Notes — Van Vooren & Frund (2010) adopted the binomial *H. corbierei* for this species, a disposition approved by us. *Helvella corbierei* represents the European *H. stevensii* sensu Dissing (Dissing 1966b, 2000). To support the lectotype (iconotype) selected by Van Vooren & Frund (2010), we have designated an epitype specimen from Switzerland in order to stabilize the use of the name. The sequenced specimens share identical *rpb2* sequences and vary in one *hsp* site. The specimen from Western USA (Oregon) deviates from the European collections by two *rpb2* and three *hsp* substitutions. Two specimens from North America referred to as *H. compressa* by Landeros et al. (2015) belong here (cf. Appendix 3).

Helvella corium (O. Weberb.) Masee, Brit. Fungus-Fl. 4: 463. 1895 — Fig. 4a

Basionym. *Peziza corium* O. Weberb., Pilze Nord-Deutschl. 1: 7. 1873.

Synonyms. *Aleuria corium* (O. Weberb.) Gillet, Champ. France Discomyc. 2: 39. 1880.

Scypharia corium (O. Weberb.) Quél., Enchir. Fung.: 83. 1886.

Lachnea corium (O. Weberb.) W. Phillips, Man. Brit. Discomyc. 204. 1887.

Macropodia corium (O. Weberb.) Sacc., Syll. Fung. 8: 159. 1889.

Fuckelina corium (O. Weberb.) Kuntze, Revis. Gen. Pl. 2: 852. 1891.

Sarcoscypha corium (O. Weberb.) J. Schröt., Krypt.-Fl. Schlesien (Breslau) 3: 59. 1893.

Cyathipodia corium (O. Weberb.) Boud., Icon. Mycol., liste prélim.: 2. 1904.

Leptopodia corium (O. Weberb.) Boud., Hist. Classif. Discomyc. Europe: 239. 1907.

Cowlesia corium (O. Weberb.) Nieuwl., Amer. Midl. Naturalist 4: 380. 1916.

Paxina corium (O. Weberb.) Seaver, North Amer. Cup-fungi (Operculates): 208. 1928.

Holotype. POLAND, Georgenberg Landeck, May 1870, *Weberbauer* (WRSL), not examined. *Epitype* designated here: DENMARK, Mid Zealand, Kirke Hvalsø, Brødlesgård, 2 July 1984, *U. Søchting* (C-F-71638). MycoBank MBT375398.

Helvella arctica Nannf., Svensk Bot. Tidskr. 31: 60. 1937.

Cyathipodia arctica (Nannf.) M.M. Moser in Gams, Kl. Krypt.-Fl. (Stuttgart) 2a: 89. 1963.

Paxina arctica (Nannf.) E.K. Cash, J. Wash. Acad. Sci. 44(2): 45. 1954.

Holotype. SWEDEN, Torne Lappmark, Jukkasjärvi, E of Abiskoajok, Aug. to Sept. 1928, *J.A. Nannfeldt* 1523 (UPS). *Isotype* (C-F-92111- Fung. Exs. Suec. 369 as '*H. arctica* Nannf.').

Illustrations — Nannfeldt (1937: pl. 1–2), Dissing (1966b: f. 19), Schumacher & Mohn Jenssen (1992: 17).

Description of the species — Nannfeldt (1937: 56, 60 as *H. arctica*).

Specimens examined/sequenced. DENMARK, Mid Zealand, Kirke Hvalsø, Brødlesgård, 2 July 1984, *U. Søchting* [H352] (C-F-71638 *epitype*). – NORWAY, Hordaland, Ulvik, Finse, at railway station, 29 July 2014, *T. Schumacher* [H453] (O-253279); Finse, Blåisen, on 1960 moraine, 11 Aug. 1996, *K. Høiland* [H248] (O-253277); *ibid.*, 27 July 2014, *T. Schumacher* [H451] (O-253278); Troms, Tromsø, Ringheim, on sandy soil, 23 July 1989, *A. Holst Jensen* & *S. Sæstad* [H434] (O-253280). – RUSSIA, Tjumenskaja oblast, northern Urals, Labytangi, with *Salix* on rich clay, 14 Aug. 1990, *H. Knudsen* [H294] (C-F-16568); Ural Mts, Krasnij Khamel, 40 km W of Labytangi, 20 July 1992, *H. Kotiranta* [H328] (C-F-34476). – SVALBARD, Bunsow Land N Longyearbyen, around Gipselva, among *Dryas* and *Salix polaris*, 10 Aug. 1985, *H. Dissing* [H324] (C-F-55580); Kongsfjord, Ny-Ålesund, Hollenderhaugen at Thiisbukta, on silt near the shore, 3 Aug. 1986, *G. Gulden* & *K.M. Jenssen* GG 142.86 [H242] (O-362201); Kongsfjord, Ny-Ålesund, at the Bay river, 5 Aug. 1988, *T. Schumacher* [H436] (O-253281). – SWEDEN, Torne Lappmark, Jukkasjärvi, E of Abiskoajok, Aug. to Sept. 1928, *J.A. Nannfeldt* 1523 [H292] (C-F-92111-Fung. Exs. Suec. 369 isotype of *H. arctica* Nannf.).

Notes — Traditionally, *H. corium* has been interpreted as a highly variable species colonizing a range of habitats and biomes on the European continent. We have examined a selection of specimens curated as *H. corium* in the fungaria of (O) and (C) and have discovered five phylogenetic species, viz. *H. corium* s.str., *H. alpina*, *H. nannfeldtii*, *H. alpestris* and *H. macrosperma*. The *H. corium* morphospecies complex forms two well-supported lineages, i.e., an alpina-corium lineage and an alpestris-nannfeldtii lineage. *Helvella corium* and *H. alpina* differ in 10 *hsp* and 10 *rpb2* substitutions. The alpina-corium lineage has morphological features that separate it from the alpestris-nannfeldtii lineage, i.e., smaller asci (< 300 µm in length), an aporhynchous ascus base, and ascospores less than 20 µm long, compared to asci exceeding 300 µm in length, a pleurohynchous ascus base, and ascospores up to 23 µm in length in the alpestris-nannfeldtii lineage. Macromorphologically, the most notable features that separate *H. corium* and *H. alpina* are apothecium size and stipe length; in *H. corium* the breadth of the apothecium and the stipe length are approximately 1 : 1 and the tomentum of hyphoid hairs forms macroscopical 'warts', while in *H. alpina* the apothecia are slender with a stipe two to three times longer than apothecium breadth and with a receptacle surface of scattered distributed short hairs. *Helvella corium* occurs from sea level to high altitude elevations, while the black 'look-alike' *H. alpina* has a more restricted distribution at higher altitudes (subalpine and alpine zone) of Northern and Central Europe and Canada. The holotype of *H. corium* in WRSL is old and presumably unsuitable for molecular identification and is therefore supported by an epitype from Denmark. The sequenced specimens of *H. corium* from Norway, Denmark, Svalbard and Russia show variation in one *rpb2* and one *hsp* character.

Helvella costifera Nannf., in Lundell & Nannfeldt, Fungi Exsicc. Suecici Fasc. 41–42: 37, no. 2061. 1953 — Fig. 3h

Basionym. *Peziza costata* Fr., Acta Reg. Soc. Sci. Ups., Ser. 5, 1: 120. 1851.

Synonym. *Acetabula costifera* (Nannf.) Benedix, Westfälische Pilzbrieft 5: 113. 1965.

Holotype. SWEDEN, Uppland, Uppsala, Botanical Garden, E. Fries sub nomen *Peziza costata* Fr. (UPS), not examined. *Epitype* designated here: SWEDEN, Uppland, Uppsala, Carolinaparken, 9 July 1948, *J.A. Nannfeldt* no. 9956 (C-Fungi Exs. Suec. 2061). MycoBank MBT375399.

Misapplied name

– *Acetabula ancilis* sensu Boud., Icon. Mycol., livr. 7: no 181, pl. 244. 1906 (preliminary text with 'circulaires').

Illustration — Landeros et al. (2012: f. 23).

Apothecia regularly stipitate-cupulate, cup 1.5–4 cm broad, 1–4 cm high, hymenium greyish (6-7E1-3), drying dark greyish brown (6E3), receptacle surface subpubescent, concolorous with hymenium when fresh, when dried pale greyish brown; stipe distinct, hollow, with 5–6 prominent yellowish white blunt-edged ribs (4A2-3) extending onto receptacle, ribs dichotomously branched apically, not interconnected, remaining whitish in dried specimens. *Outer excipulum* of *textura prismatica* to *textura angularis*, outermost cells with light brown walls. *Asci* pleurohynchous, 230–270 × 12–15 µm. *Ascospores* broadly ellipsoid, 14.2–16.6 × 10.6–13.6 µm. *Paraphyses* 2.0–3.2 µm broad, straight, septate, gradually enlarged to 4.5 µm at tips.

Specimens examined/sequenced. DENMARK, Zealand, Copenhagen, Frederiksberg Park, 7 July 1984, J. Vesterholt JV 615.84 [H383] (C-F-92113). — NORWAY, Akershus, Bærum, Øverland Arboretum, 27 July 2007, P.A. Bergersen [H131] (O-68514); Oppland, Dovre, Grimsdalen, Kvannbekken at Gravhøi, 12 Sept. 1982, T. Schumacher & K. Østmoe 507.82 [H347] (O-253284); Grimsdalen, Tverråi, 940 m asl, Aug. 1985, T. Schumacher [H209] (O-253282); Vågå, Brunskardsknappene, 1180–1200 m asl, on soil, 29 Aug. 1998, S. Kjølnér [H247] (O-253283); Sør-Trøndelag, Oppdal, Vinstradalen at Ryphuskollen, on rich calcareous soil, 11 Aug. 1984, T. Schumacher & K. Østmoe TS 15.84 [H227] (O-253285); Finnmark, Cirgojokka, Vassbotndalen, Bjørnelva to Scaccavaggi, in *Dryas* vegetation, 25 Aug. 1986, H. Dissing [H388] (C-F-53529); *ibid.*, 27 Aug. 1986, H. Dissing [H385] (C-F-53538). — SWEDEN, Uppland, Uppsala, Carolinaparken, 9 July 1948, J.A. Nannfeldt 9956 [H298] (C-Fungi Exs. Suec. 2061 epitype).

Notes — We have identified two widespread species of the *H. costifera* morphospecies complex, i.e., *H. costifera* and *H. calycina* nom. nov. (= *Boletus calyciformis* Battarra), separated by one *hsp* and two *rpb2* substitutions. Dissing (1966b) included both species in his concept of *H. costifera* stating that “collections with a darker, brownish colour have been seen from Norway”. Some of these specimens also have a whitish margin, due to colourless hyphae in the outer excipulum. These latter specimens apply to *H. calycina* (see this species above). Landeros et al. (2012) examined an isolectotype specimen of *H. costifera* and the holotype specimen of *H. hyperborea*, and placed them into synonymy based on morphological features. We have found good reasons to keep these two species apart (see *H. hyperborea*).

Helvella crispa (Scop.) Fr., Syst. Mycol. 2: 14. 1822 — Fig. 8c

Basionym. *Phallus crispus* Scop., Fl. Carniol., ed. 2, 2: 475. 1772; Fr., Syst. Mycol. 2: 14. 1822.

Synonym. *Costapeda crispa* (Scop.) Falck, Sluzowce Monogr., Suppl. 3: 401. 1923.

Lectotype. P. Micheli, Nov. Pl. Gen., t. 86, f. 7, 1729, selected by Dissing (1966b). *Epitype* designated here: SWEDEN, Blekinge parish, Karlskrona, Wämö, 5–14 Oct. 1946, S. Lundell & S. Wikland (C-Fungi exs. Suec. 2062). MycoBank MBT375400.

Helvella pallida Schaeff., Fung. Bavar. Palat. Nasc. 4: 112. 1774.

Helvella crispa a. (forma) *pileo albo, pallescente* Fr., Syst. Mycol. 2: 14. 1822 (*Helvella 'albida'* Schaeff. = *lapsus calami* for *H. pallida* Schaeff.).

Lectotype designated here: Schaeff., Fung. Bavar. Palat. Nasc. 3: t. 282. 1772 ('Elvela vicesima nona'). MycoBank MBT375690.

Helvella alba Bergeret, Phytanom. Univ. 1: t. 145. 1783 (= *H. crispa* a. (forma) fide Fries (1822)).

Helvella nivea Schrad., J. Bot. 2: 66. 1799 (= *H. crispa* a. (forma) fide Fries (1822)).

Illustrations — Boudier (1905–1910: pl. 225), Dissing (1966b: f. 21).

Description of the species — Dissing (1966b: 85).

Specimens examined/sequenced. ENGLAND, Surrey, Oxshott Heath, roadside, 16 Oct. 1994, E.W. Brown [H105] (FH). — LATVIA, Riga, on soil, 6 Sept. 1982, D. Pfister [H107] (FH). — NORWAY, Akershus, Asker, Leangbukta, under pine and beech, 15 Oct. 2004, P. Marstad 326.04 [H135] (O-187744); Nordland, Andøy, Oksbåsen, sand dunes at sea shore, 13 Sept. 2005, B.H. Larsen 235 [H235] (O-360158). — SWEDEN, Blekinge parish, Karlskrona, Wämö, 5–14 Oct. 1946, S. Lundell & S. Wikland [H408] (C-Fungi Exs. Suec. 2062 epitype); Öland, Böda parish, Byerum, along wayside in forest, 24 Aug. 1960, R. Schöldström [H405] (C-Fungi exs. Suec. 3263); Halland, Spendshult, rich soil, 17 Sept. 2009, L. Walter & A. Molia [H062] (O-253287).

Notes — We have selected an epitype specimen from Southern Sweden that deviates from the Latvian and North Norwegian specimens in two *rpb2* characters.

Helvella danica Skrede, T. Carlsen & T. Schumach., *sp. nov.* — MycoBank MB820330; *hsp* barcode GenBank KY784378; *rpb2* barcode GenBank KY772627; Fig. 7f

Etymology. From Latin 'described from Denmark'.

Holotype. DENMARK, Jutland E, Hobro Østerskov, 18 Sept. 2008, J. Heilmann-Clausen (C-F-85205).

Misapplied names

— *Helvella esculenta* sensu Hornem., Fl. Dan., fasc. 26: pl.1559. 1816.
— *Helvella pulla* sensu Rostr. in Lange, Nomenclator 'Florae Danicae': 54. 1887.

Illustration — Hornemann (1816: pl.1559, as *H. esculenta*).

Apothecium stipitate-capitate, small to medium-sized, cap campanulate or slightly irregularly lobate, 1.2–3.0 cm broad, of similar height, hymenium brownish yellow (5C6-8), receptacle surface white to yellowish, smooth; stipe short, 0.5–0.8 cm broad, 1.5–3.5 cm high, whitish to yellowish, hollow, often with



Fig. 8 Photos of dried apothecia of 'white' *Helvella* spp. a. *H. lactea* (C-Fungi Exs. Suec. 1355); b. *H. pallescens* (O-66205, epitype); c. *H. crispa* (O-18774). — Scale bars = 1 cm. — Photos: I. Skrede.

grooves towards the base. *Medullary excipulum* of loosely interwoven *textura intricata*, hyphae 3–5 µm broad. *Outer excipulum* of isodiametric *textura angularis* to *textura globulosa*, innermost cells angular, subhyaline, turning out in rows of clavate to subglobose cells perpendicularly to receptacle surface, cells heavily stained in CB. *Asci* pleurorhynchous, 300–340 × 14–16 µm. *Ascospores* ellipsoid, 19.5–22.4 × 12.2–13 µm. *Paraphyses* subhyaline, 3–5 µm broad, septate, broadly cylindrical in upper part, generally broadest below tips (spadiceiform), to 10–14 µm broad.

Specimens examined/sequenced. DENMARK, Jutland E, Hobro Østerskov, 18 Sept. 2008, J. Heilmann-Clausen [H263] (C-F-85205 holotype); Zealand, Gentofte, Insulin Mosen, rich soil together with *Parascutellinia carneosanguinea* and *H. elastica*, 18 Sept. 1974, D. Boertmann [H396] (C-F-64512). – NORWAY, Akershus, Eidsvoll, at Eidsvollbygningen, in garden, 16 Sept. 2009, I. Skrede & T. Schumacher [H058] (O-253288); Finnmark, Alta, Altaelva at Lille Raipas, on sandy soil in upper inundation zone, 7 Aug. 1983, H. Edvardsen & K. Høiland [H177] (O-129543). – RUSSIA, St. Petersburg, near town, on soil, 28–29 Aug. 1982, D. Pfister [H111] (FH).

Notes — This short-stipitate, campanulate, medium-sized species with brown hymenium and white stipe of the *elastica* clade (clade E) appears to have been overlooked by early taxonomists, except Hornemann (1816) who depicted the species in *Flora Danica*, but misapplied the binomial *H. esculenta* for this species. *Helvella danica* is distinguishable macromorphologically by the short stipe and often clustered growth habit of the medium brown (hymenium) and white (stipe) apothecia, by large asci and ascospores, and by a distinctive shape (spadiceiform) of the paraphyses under the microscope. The species resembles *H. bicolor* and *H. capucina* when fresh; the two latter species have a darker brown hymenium. Our sample of *H. danica* constitutes a well-supported sublineage of the *elastica* clade (clade E), separated from a sublineage of *H. fistulosa*, *H. panormitana*, *H. monachella* and *H. capucina* of the *capucina-danica* lineage by four *hsp* and eight *rpb2* substitutions.

Helvella dryadophila Harmaja, *Karstenia* 17: 58. 1977 — Fig. 3d

Holotype. NORWAY, Oppland, Lom, Høyrokampen, 29 Aug. 1957, F.-E. Eckblad (O-72617)

Illustration — Harmaja (1977b: f. 5).

Description of the species — Harmaja (1977b: 48).

Specimens examined/sequenced. CANADA, Ellesmere Island, Alexandra Fjord, near Fox hill, in moss among *Dryas* and *Salix arctica*, 1 Aug. 1984, H. Dissing [H335] (C-F-56772). – GREENLAND, Ella Island, E of Lauge Kock's house, near Lange sea, on soil with *Dryas*, 4 Aug. 1982, H. Dissing & S. Sivertsen [H379] (C-F-50346); Mestervig, behind Nyhavn, in sand at the riverside, 17 Aug. 1982, H. Dissing & S. Sivertsen [H378] (C-F-52701). – NORWAY, Oppland, Lom, Høyrokampen, 29 Aug. 1957, F.-E. Eckblad [H302] (O-72617 holotype); Dovre, Grimsdalen, Tverrgjelet, in *Dryas* association on moist slopes, 16 Aug. 1996, S. Landvik & T. Schumacher SL 201.96 [H183] (O-253308); *ibid.*, 20 Aug. 1997, S. Landvik & T. Schumacher TS 35.97 [H180] (O-253307); *ibid.*, 21 Aug. 2005, T. Schumacher [H190] (O-253309); *ibid.*, 2 Aug. 2007, T. Schumacher [H010] (O-253306). – SVALBARD, Bunsow Land, in *Dryas* association, 10 Aug. 1985, H. Dissing [H323] (C-F-55578); *ibid.*, [H321] (C-55579); *ibid.*, [H322] (C-F-55597); Kongsfjord, Gluudneset, 'Gåsebu', 2 Aug. 1986, G. Gulden & K. Mohn Jenssen GG 111.86 [H234] (O-363304).

Notes — The sequenced specimens, including collections from Svalbard, Greenland, Norway and Canada, vary in one *rpb2* site. Abbott & Currah (1997) compared the type specimens of *H. dryadophila*, *H. arctoalpina* and *H. verruculosa*, and placed them in synonymy under the latter, older name. Landeros et al. (2012) studied the types of *H. dryadophila* and *H. verruculosa* and concluded they were conspecific. However, they did not study the type of *H. arctoalpina*. Since the older name *H. verruculosa* may apply to either of the two, i.e., *H. arctoalpina* or

H. dryadophila, it is unclear to us to which name Saccardo's species applies. We have therefore avoided using the binomial *H. verruculosa* in the present synopsis (see Appendix 1).

Helvella elastica Bull., *Herb. France* 6: t. 242. 1785 — Fig. 7d

Basionym. *Helvella elastica* Bull., *Herb. France* 6: t. 242. 1785; Fr., *Syst. Mycol.* 2: 21. 1822.

Synonyms. *Leptopodia elastica* (Bull.) Boud., *Icon. Mycol.*, liste prélim.: 2. 1904 (preliminary text with 'circulaires').

Tubipeda elastica (Bull.) Falck, *Mykol. Untersuch. Ber.* 1: 401. 1923.

Lectotype. Bull., *Herb. France* 6: t. 242, f. A–B, D–G. 1786, selected by Abbott & Currah (1997). *Epitype* designated here: SWEDEN, Uppland, Älvkarleby parish, Billudden, N Källvik, on bare sandy soil, 29 Sept. 1946, G. Sandberg & R. Santesson (C-F-29130 Fungi Exs. Suec. 2064 'H. elastica Bull. ex Fr.'). MycoBank MBT375401.

Illustration — Bulliard (1786: t. 242, f. A–B, D–G).

Apothecia stipitate-capitate, cap 1.0–3.5 cm broad, 1.5–3.0 cm high, at first irregularly lobed to bilobate with an adnate apothecial margin adhered to stipe, then sometimes irregularly folded with margin free from stipe; hymenium light brown to brown (5-7D4-8), sometimes decoloured, receptacle surface subpubescent, whitish to yellowish, concolorous with stipe; stipe terete, 0.5–1.2 cm broad, 3–15 cm high, solid to hollow, depressed and flat when dry. *Subhymenium* and *medullary excipulum* of highly gelatinous hyphae, embedded in an amorphous gelatinous matrix, hyphae c. 3 µm broad. *Outer excipulum* of angular cells up to 40 × 30 µm diam, outermost cells giving rise to 2–4-celled club-shaped extensions making up the subpubescent surface. *Asci* pleurorhynchous, 330–360 × 15–17 µm. *Ascospores* oblong ellipsoid, 19–22 × 10.6–12.2 µm. *Paraphyses* c. 3 µm broad below, septate, light brown in colour, at tips irregular clavate to 6–10 µm broad.

Specimens examined/sequenced. NORWAY, Nannestad, Åsgreina, Damvegen, in mossy garden, 30 Aug. 2009, Ø. Stensrud TS 35.09 [H443] (O-253310). – RUSSIA, Sakha, Khangalasskiy Ulus, Sasabyt River 2 km NW Bestyakh, under *Larix* on calcareous soil, *H. Knudsen* [H329] (C-F-51672). – SWEDEN, Uppland, Älvkarleby parish, Billudden, N Källvik, on bare sandy soil, 29 Sept. 1946, G. Sandberg & R. Santesson [H372] (C-F-29130 Fungi Exs. Suec. 2064 'H. elastica Bull. ex Fr.' epitype); Uppland, Vassunda parish, Örsand, close to lake Mälaren, 27 Oct. 1935, E. Krantz [H414] (C-Fungi Exs. Suec. 271 'H. elastica Bull. ex Fr.'). Halland, Halmstad, Almberget, 16 Sept. 2009, G. Holden [H066] (O-253311).

Notes — *Helvella elastica*, as circumscribed here, represents a much narrower species concept than commonly outlined in literature. As the name indicates, the species is elastic due to the gelatinous receptacle and stipe tissues. The gelatinous matrix of the excipulum also characterises the morphologically similar but genetically divergent *H. panormitana* and *H. capucina*. Dissing (1966b) included *H. panormitana*, *H. fistulosa*, as well as the American *H. capucinoidea* (1912), *H. gracilis*, and *H. adherens* (Peck 1902) in his broad concept of *H. elastica*. Zhuang (2004) described a new species of the *elastica* group, i.e., *H. jimsarica* from China, distinguished from *H. elastica* on the basis of larger ascocarps and occurrence on rotten wood. *Helvella elastica* deviates from the putative North American *H. capucinoidea* in two *rpb2* characters (see this taxon under non-European taxa). A published LSU sequence from Estonia [AJ 972411] referred to as *H. albella*, is suggestive of *H. elastica* (Landeros et al. 2015) (cf. Appendix 3).

Helvella fallax Qué., *Bull. Soc. Bot. France* 23: 331. 1876 — Fig. 9a

Lectotype designated here: Qué., *Bull. Soc. Bot. France* 23: t. 3, f. 15. 1876. MycoBank MBT375691. *Epitype* designated here: FRANCE, Savoie, Bonneval-sur-Arc, Rau du Chalanson, 2300–2500 m asl, 2 Sept. 1992, E. Horak (C-F-84621). MycoBank MBT375402.

Synonym. Helvella nigricans Pers., *Observ. Mycol.* 1: 72. 1796, nom. illeg. (homonym).

– non *Helvella nigricans* Schaeff., *Fung. Bavar. Palat. Nasc.* 4: 102. 1774 ('*Elvela*') (= *H. lacunosa* Afzel.).

Misapplied names

- *Helvella atra* sensu Fr., *Syst. Mycol.* 2: 19. 1822.
- *Helvella atra* sensu Holmsk., *Beata Ruris Otia Fung. Dan.* 2: 47. 1799.
- *Helvella atra* sensu Dissing, *Dansk Bot. Ark.* 25: 121. 1966.
- *Leptopodia atra* sensu Boud., *Icon. Mycol., liste prélim.*: 2. 1904.

Illustrations — Holmskjöld (1799: pl. 25, as *H. atra*), Boudier (1905–1910: pl. 238, as *L. atra*), Filippa & Baiano (2011: f. 13–15, as *H. atra*).

Descriptions of the species — Holmskjöld (1799: 47 as *H. atra*), Dissing (1964: 112, 1966b: 121 as *H. atra*).

Specimens examined/sequenced. CANADA, Northwest Territories, District of Keewatin, Baker Lake NE, sandy river shore with *Salix herbacea*, 16 Aug. 1974, E. & M. Ohenoja [H430] (C-F-92108 ex Herb. Univ. Ouluensis). – FRANCE, Savoie, Bonneval-Sur-Arc, Rau du Chalanson 2300–2500 m asl, 2 Sept. 1992, E. Horak [H339] (C-F-84621 epitype); Savoie, Val d'Isère, Gorges du Mal, on river terrace, 2250 m asl, 31 Aug. 1992, T. Schumacher F 76.92 [H219] (O); Savoie, Les Vallions, Nat. Park Vanoise, on river terrace, 2600 m asl, 28 Aug. 1992, T. Schumacher F 28.92 [H221] (O). – NORWAY, Hedmark, Løten, Rokoberget, 17 Oct. 2006, R. Haugan, S06005 [H162] (O-280610); Hedmark, Kongsvinger, Bogeråsen, in spruce forest, 6 Aug. 1998, I. Tangen & K.H. Amundsen [H168] (O-63684); Oppland, Dovre, Grimsdalen, Tverrådalen, 13 Aug. 1985, T. Schumacher [H402] (O-253354); *ibid.*, 12. Aug. 1996, A. Holst Jensen [H256] (O-253353); *ibid.*, 7 Aug. 2009, T. Carlsen, T. Schumacher & I. Skrede TS 10.09 [H018] (O-253351); Grimsdalen, Veslegrimsa, on river terrace, 8 Aug. 2009, T. Carlsen, T. Schumacher & I. Skrede TS 19.09 [H032] (O-253352); Grimsdalen, 16 Aug. 2001, T. Schumacher [H002] (O-253350); Oppland, Lom, N Bøvertjønnen, 950 m asl, 20 July 2002, R.Y. Berg [H169] (O-66873); Møre og Romsdal, Sunndal, Sunndalsfjorden N Hisdalen, under *Corylus*, 11 Sept. 2001, J.B. Jordal [H163] (O-242201); Nordland, Rana,

Hammarnes, 15 km N Mo i Rana, rich mouldy soil, 18 Aug. 1979, H. Dissing [H419] (C-F-54652); Troms, Gratangen, Finnesletta, calcareous pasture land, 10 Sept. 2005, B.H. Larsen [H244] (O-360225). – SWEDEN, Lule Lappmark, Gällivarre Parish, 6 km SE Ritsemjokk train station, moist fen at rivulet with Sphagnum and dwarf willows, 22 Aug. 1970, G. Lohammar [H395] (C-F-45484). – SWITZERLAND, Graubünden, Albula Pass, near Crap Alv, 2040 m asl, 30 Aug. 1984, T. Schumacher [H428] (C-F-57377).

Notes — We have adopted the binomial *H. fallax* for this species, a species described and depicted from France by Quélet (1876). *Helvella nigricans*, which was referred to as a synonym of *H. atra* by Fries (1822, 1832), represents an older illegitimate name (homonym) for the species. Persoon (1796) compared his fungus with *H. atra* sensu Afzel., leaving no doubt about which fungus he had in hand. Fries' broad concept of *H. atra*, including *H. atra* J. König, *H. atra* sensu Holmsk. (1799) and Afzelius (1783) and *H. nigricans* Pers. as well, was not accepted by Dissing (1966b), who adopted Holmskjöld's concept of *H. atra* as an available name for the present species. Since Fries (1822, 1832) clearly assigned and credited König to the sanctioned epithet of '*atra*', we have reserved *H. atra* for König's fungus and adopted Quélet's name (i.e., *H. fallax*) for the illegitimate *H. nigricans*. *Helvella fallax* is here lectotypified by Quélet's original figure, supported with an epitype specimen from France that provides partial sequences from four genes, e.g., *hsp*, *tef*, *rpb2* and LSU as molecular specifics to the species. The sequenced specimens of *H. fallax* from France have identical LSU and *hsp* sequences, but deviate from the rest of the collections from Northern Europe in one *rpb2* and three LSU substitutions. A collection from Estonia [AJ 972413] recorded by Landeros et al. (2015, as *H. atra*) is also nested here (cf. Appendix 3).



Fig. 9 Photos of dried apothecia. a. *H. fallax* (O-253401); b. *H. fibrosa* (O-185919); c. *H. macropus* (O-65347); d. *H. pulla* (O-69282, epitype); e. *H. sublicia* (C-F-53175). — Scale bars = 1 cm. — Photos: I. Skrede.

Helvella fibrosa (Wallr.) Korf, Mycotaxon 103: 311. 2008 — Fig. 9b

Basionym. *Peziza fibrosa* Wallr., Fl. Crypt. Germ. 2: 498. 1833 (typus: *Octospora villosa* Hedw.).

Synonyms. *Macropodia fibrosa* (Wallr.) Sacc., Syll. Fung. 8: 160. 1889. *Octospora villosa* Hedw., Descr. Micro-anal. Musc.: 54. 1789.

Peziza macropus var. *villosa* (Hedw.) Pers., Syn. Meth. Fung. 2: 646. 1801.

Peziza macropus β (var.) *hirta* (Hedw.: Fr.) Fr., Syst. Mycol. 2: 57. 1822. *Fuckelina villosa* (Hedw.) Kuntze, Revis. Gen. Pl. 2: 852. 1891.

Cyathipodia villosa (Hedw.) Boud., Icon. Mycol., liste prélim.: 2. 1904.

Leptopodia villosa (Hedw.) Arnould, Bull. Soc. Mycol. France 9: 111. 1893.

Helvella villosa (Hedw.) Dissing & Nannf., Svensk Bot. Tidskr. 60: 330. 1966, nom. illeg. (homonym)

Helvella dissingii Korf, Mycotaxon 31: 381. 1988.

Lectotype. Hedw., Descr. Micro-anal. Musc.: t. 19, f. B, no. 3. 1789, selected by Dissing & Nannfeldt (1966). *Epitype.* SWEDEN, Halland, Onsala parish, Presse, Björkhamra, 8 July 1956, *F. Karlvall* 6944 - Fungi Exs. Suec. 3262 '*H. chinensis*' (Velen.) Nannf. & L. Holm (UPS), selected by Korf (2008). *Peziza sublicia* Holmsk., Beata Ruris Otia Fung. Dan. 2: 26. 1799.

Lectotype designated here: Holmsk., Beata Ruris Otia Fung. Dan. 2: pl. 10. 1799. MycoBank MBT375692.

Illustration — Dissing & Nannfeldt (1966: pl. 2, as *H. villosa*).

Descriptions of the species — Dissing & Nannfeldt (1966: f. 3, pl. 2, as *H. villosa*), Dissing (1966b: 67, as *H. villosa*), Weber (1972: 171, as *H. villosa*).

Specimens examined/sequenced. DENMARK, Falster, Gedesby, in garden under *Corylus*, 7 July 1998, *P. Corfixen* [H426] (C-F-38089). — FINLAND, Oulun Pohjanmaa, Haukipudas, Niemeläntörmä, Höyhtyä farm, 26 July 1981, *T. Ulvinen* [H369] (C-F-92109). — GEORGIA, Kaukasus, Kasbhegi, Gvethi valley, sandy soil with herbs, along trail, 2000 m asl, 13 July 1988, *E. Johannesen* [H250] (O-253313). — ICELAND, Rang., Merkurhraun, forest near Merkihvoll, among moss on gravel in *Betula* forest, 26 Aug. 1984, *S.A. Elborne* [H343] (C-F-92103); Borg., Borgarfjörður, Hafnarskógur, 18 Aug. 1984, *H.F. Gøtzsche* [H344] (C-F-92102). — NORWAY, Akershus, Bærum, Kalvøya, on calcareous soil under *Corylus*, 28 Aug. 1988, *T. Schumacher* [H164] (O-88570); Vestfold, Sande, Bekkestranda, 12 Sept. 1985, *P. Marstad* 135.85 [H166] (O-185923); Vestfold, Tønsberg, Sem, Slagentangen, 11 Sept. 1985, *P. Marstad* [H167] (O-185919); Hedmark, Stange, Roa nordre, pasture land, 22 Sept. 2000, *S. Sivertsen, P.G. Larsen, T.S. Nilsen, A. Mollia & T. Pouli* [H139] (O-63973); Sør-Trøndelag, Oppdal, Vinstradalen, Nordistusetar at the road, rich pasture land, 28 Aug. 2008, *J.B. Jordal* [H240] (O-291352); Oppdal, Loslia, rich pasture land, 1000 m asl, 20 Aug. 2009, *J.B. Jordal* [H243] (O-291377); Nordland, Rana, Rausandsaksla, 15 km E Mo i Rana, calcareous soil, 11 Sept. 1975, *T. Schumacher* [H270] (C-F-54475); Rana, Store Røvatn, 20 km NE of Mo i Rana, on calcareous soil under *Salix*, 6 Sept. 1972, *H. Dissing* [H357] (C-F-53774). — SWEDEN, Halland, Onsala parish, Presse, Björkhamra, 8 July 1956, *F. Karlvall* 6944 '*H. chinensis*' (Velen.) Nannf. & L. Holm' isoeotype [H413] (C-Fungi Exs. Suec. 3262).

Notes — *Helvella fibrosa* apparently has a worldwide distribution. It has been confused with *H. macropus* on many occasions (cf. Dissing & Nannfeldt 1966). Korf (2008) gave an extensive treatment of name use and nomenclature of this characteristic species. There exist several 18th century descriptions and coloured iconographs of *H. fibrosa*, although being presented with other binomials, i.e., in Hedwig (1789: 54, pl. 19, f. B, no. 3, as *Octospora villosa*), Persoon (1796: 26, pl. 1, f. 2, as *Peziza macropus* var. β. *lacunosa*) and Holmskjöld (1799: 26, pl. 10, as *Peziza sublicia*). The hymenium is darker (greyish brown) and the receptacle surface less villose in *H. fibrosa* compared to *H. macropus*. Moreover, the ascospores are broadly ellipsoidal and not acuminate as in *H. macropus*. The material studied by us is invariable in *hsp* and *rpb2* sequences, except for the Georgian specimen that deviates in one *rpb2* bp character. Häffner (1987), Abbott & Currah (1997) and Landeros et al. (2015) placed *H. pallidula* in synonymy with *H. chinensis* (= *H. fibrosa*), a disposition which needs to be re-assessed based on molecular data. *Helvella* 'Japan 1' and *Helvella* 'Japan 2' are

morphologically similar to *H. fibrosa*, but deviates in a number of *rpb2* and *hsp* characters.

Helvella fistulosa Alb. & Schwein., Consp. Fungorum Lusat.: 299. 1805 — Fig. 7h

Basionym. *Helvella fistulosa* Alb. & Schwein., Consp. Fungorum Lusat.: 299. 1805; Fr., Syst. Mycol. 2: 21. 1822.

Synonyms. *Leptopodia fistulosa* (Alb. & Schwein.) Boud., Hist. Classif. Discomyc. Europe: 37. 1907.

Helvella elastica forma *fistulosa* (Alb. & Schwein.) Rehm, in Winter, Rabenh. Krypt.-Fl., ed. 2 (Leipzig) 1.3 (lief. 53): 1184. 1895.

Neotype designated here: NORWAY, Hordaland, Ulvik, Ossete, Nipane, on lime-phyllite gravel, 5 Sept. 2009, *G. Flatabø* [H241] (O-291887). MycoBank MBT375403.

Apothecia medium-sized, 0.5–1 cm broad, 1–2 cm high, bi- to trilobate to irregularly lobed, margin reflexed and free; hymenium brown (6D-E7-8), outside subpubescent, yellowish, concolorous with stipe; stipe terete, solid or hollow, inflated and occasionally reddish brown when dried, 0.3–0.6 cm broad, by 2–7 cm high. *Medullary excipulum* of loosely interwoven *textura intricata*, hyphae 3–4 μm broad. *Outer excipulum* a mixture of broad-celled *textura intricata*, hyphae 6–10 μm broad and *textura angularis*, angular cells 20–35 μm diam, towards surface cells more club-shaped, to 40–50 μm long, forming 3–4-celled, ramified extensions on the excipulum exterior. *Asci* pleurorhynchous, 300–320 × 14–17 μm. *Ascospores* ellipsoid, 19.0–21.5 × 12–13.2 μm. *Paraphyses* straight, c. 3 μm broad below, subhyaline, septate, clavate to subcapitate to 6–8 μm at the tips.

Specimens examined/sequenced. ICELAND, Austur-Skaftafellssýsla, Skaf-tafell, 20 Aug. 1981, *H.F. Gøtzsche* HFG 81.32 [H476] (C-F-45406). — JAPAN, Honshu, Tochigi, Okunikko, Chuzenjikohan, Asegata, on soil in forest, 25 Aug. 1983, *T. Schumacher* [H205] (O-253314). — NORWAY, Akershus, Bærum, path-way in forest, 16 Aug. 2001, *T. Schumacher* [H179] (O-253315); Hordaland, Ulvik, Ossete, Nipane, on lime-phyllite gravel, 5 Sept. 2009, *G. Flatabø* [H241] (O-291887 neotype). — USA, Massachusetts, Worcester county, Lancaster, Devens Reserve Forces Training Area, on soil and debris in hemlock-Northern hardwood forest, 9 July 1999, *B. Neill, G. Valiant, W. Metclaf, M. Jacobs, D. Pfister, K. Griffith* D-435 [H109] (FH); Vermont, Windsor county, Norwich, on soil in hemlock forest with some pines and occasional hardwoods, 29 Apr. 2004, *K. Griffith* [H114] (FH).

Notes — *Helvella fistulosa* is morphologically almost indistinguishable from *H. danica*, however, molecular data clearly discriminate between the two: five *hsp*, six *rpb2* and eight LSU substitutions separate the species. We have selected a collection from Norway as a neotype for this intercontinental species, here supplied with partial sequences of *hsp*, *rpb2* and LSU. The North American, European and Japanese specimens vary by one *rpb2* bp substitution.

Helvella fusca Gillet, Champ. France Discomyc. 1: 9. 1879

Synonyms. *Helvella fusca* var. *bresadolae* Boud., Icon. Mycol., liste prélim.: 2. 1904.

Helvella fusca var. *gyromitroides* Chénant., in Pelé & Chénantais, Bull. Soc. Sci. Nat. Ouest France, sér. 4, 1: 75. 1921.

— non *Helvella elastica* (Bull.: Fr.) var. *fusca* Bull., Herb. France 2: 299. 1791.

Helvella elastica (Bull.: Fr.) c. *fusca* Bull.: Fr., Syst. Mycol. 2: 21. 1822. — non *Helvella sulcata* a. (var.) *fusca* Afzel., Kongl. Vetensk. Acad. Nya Handl. 4: 305, t. 10, f. 1. 1783 (= *Helvella sulcata* a. (forma) *fusca* Afzel.: Fr., Syst. Mycol. 2: 16. 1822).

Lectotype. Gillet, Champignons de France, Discom., t. 4. 1879, selected by Landeros & Korf (2012). *Epitype.* ITALY, Al Deserto, 21 May 1898, *Bresadola* (S-F-124428), selected by Landeros & Korf (2012), not examined.

Illustrations — Gillet (1879: pl. 4), Dissing (1966b: f. 23), Landeros & Korf (2012: f. 1–4).

Descriptions of the species — Dissing (1966b: 92), Landeros & Korf (2012: 434).

Specimens examined/sequenced. HUNGARY, Kiskunsag National Park, Bugac, in populeto (*Populus canescens*, *P. alba*), 11 May 1978, *M. Babos* & *A. Friesz* [H305] (C-F-92122). — NETHERLANDS, Zuid-Holland, Oostvoorne, in sandy dunes, 14 May 1983, *C. Bas* [H304] (C-F-89381).

Notes — *Helvella fusca* is a spring and early summer species characterized by a stipitate saddle-shaped apothecium, brownish hymenium, and a white, lacunose stipe with ribs extending and ramifying onto the receptacle surface. It grows in association with *Populus* and is presumed to be an ectomycorrhizal partner with this host. Dissing (1966b) referred *H. fusca* to his section *Crispae* based on the saddle-shaped apothecium and the pubescent outside, a disposition that get no support from our phylogeny. The description of *H. fusca* in Abbott & Currah (1997) probably applies to *H. maculata*, as also concluded by Landeros & Korf (2012). Landeros et al. (2015) recently supplied a LSU nrDNA sequence from the epitype specimen of *H. fusca*, which deviates in two bp substitutions from the above cited specimens from Hungary (cf. Appendix 3).

Helvella helvellula (Durieu) Dissing, Rev. Mycol. 31: 204. 1966

Basionym. *Peziza helvellula* Durieu, Expl. Sci. Algerie 1: t. 27, f. 11. 1849.

Synonyms. *Geopyxis helvellula* (Durieu) Sacc., Syll. Fung. 8: 65. 1889.

Acetabula helvellula (Durieu) Maire, Bull. Soc. Hist. Nat. Afrique N. 8: 176. 1917.

Lectotype designated here: Durieu, Expl. Sci. Algerie 1: t. 27, f. 11. 1849. MycoBank MBT375693. *Epitype* designated here: SPAIN, Canary Islands, Hierro, 4.5 km toward Taibique, SW San Andres, on mossy soil, 7 Jan. 1977, *R.P. Korf*, *R. Fogel*, *G.L. Hennebert* & *L.M. Kohn* (C-F-92128 Mycoflora of Macaronesia 1412). MycoBank MBT375404.

Misapplied names

– *Acetabula clypeata* sensu Boud. Bull. Soc. Mycol. France 3: 146. 1887.
– *Paxina clypeata* sensu Linder in Polunin, Bull. Natl. Mus. Canada, Biol. ser. 26, 97: 257. 1947.

Illustration — Boudier (1905–1910: pl. 247, as *Acetabula clypeata*).

Description of the species — Dissing (1966b: 45).

Specimens examined/sequenced. FRANCE, Cote Atlantique, Region des Landes, Mimizan, with *Pinus maritima*, March 1981, *F. Candoussau* [H309] (C-F-45469); Dpt. Manche, Carteret au nord de phare, 15–25 m asl, 20 Apr. 1977, *R. Schumacker* 770420/01 [H278] (C-F-45506). — SPAIN, Canary islands, Hierro, 4.5 km toward Taibique, SW San Andres, on mossy soil, 7 Jan. 1977, *R.P. Korf*, *R. Fogel*, *G.L. Hennebert* & *L.M. Kohn* [H308] (C-F-92128 'Mycoflora of Macaronesia 1412' epitype).

Notes — This cupulate, black, subsessile Mediterranean species was described by Durieu (1849) based on a specimen from Morocco collected by Montagne. There are no specimens of this species in Montagne's Herbarium in Paris (PC) (Dissing 1966a). The species is here typified with the original plate of Durieu's, supported by a widely distributed epitype specimen from the Canary Islands, Spain. According to Dissing (1966a), materials in Boudier's herbarium, described and depicted as *Acetabula clypeata* (Boudier 1905–1910: pl. 247) represent *H. helvellula*. In our phylogeny *H. helvellula* clusters with *H. juniperi* and *H. semiobruta* in a well-supported divergent lineage of the lacunosa clade (clade C).

Helvella hyperborea Harmaja, Karstenia 18: 57. 1978 — Fig. 3e

Holotype. FINLAND, Kuusamo, Juuma, Jäkälävuoma, 27 Aug. 1970, *H. Harmaja* (H), not examined.

Illustrations — Harmaja (1979: f. 1–2), Landeros et al. (2012: f. 27).

Description of the species — Harmaja (1979: 35).

Specimens examined/sequenced. FINLAND, Kuusamo, Liikasenvaara, slope of hill Korvasvaara, 23 Aug. 1978, *H. Harmaja* [H491] (C-F-45306). — NORWAY, Nordland, Rana, Rausandaksla, 15 km E Mo i Rana, on calcareous soil, 11 Sept. 1975, *T. Schumacher* [H389] (C-F-54473).

Notes — *Helvella hyperborea* belongs in the morphospecies complexes of *H. acetabulum* and *H. costifera*/*H. calycina*, but is clearly distinct judged from the *hsp* and *rpb2* barcode sequences; altogether 12, 11 and 19 *rpb2* substitutions distinguish it from the morphologically similar *H. costifera*, *H. calycina* and *H. acetabulum*, respectively. The specimens from Nordland in Northern Norway and Kuusamo in Finland share identical *hsp* and *rpb2* sequences. Landeros et al. (2012) studied the morphology of the type specimen of *H. hyperborea* and placed it in synonymy with *H. costifera*. A few additional collections from the Nordic countries, determined and referred to as *H. hyperborea* by Harmaja (annotations on herbarium specimens), have been sequenced by us and are referred to *H. acetabulum*, *H. calycina* or *H. costifera*. The above cited collection from Finland was photographed in fresh condition and depicted as the archetypic *H. hyperborea* in Harmaja (1979: f. 1). An attempt to sequence the holotype specimen of *H. hyperborea* awaits future studies.

Helvella hypocrateriformis Schaeff., Fung. Bavar. Palat. Nasc. 4: 102. 1774 ('*Elvela*') — Fig. 5a

Synonyms. *Peziza hypocrateriformis* (Schaeff.) Wallr., Fl. Crypt. Germ. 2: 498. 1833, nom. illeg. (homonym).

– non *Peziza hypocrateriformis* Bergeret, Phytomom. Univ. 1: t. 169. 1783 (= *Helvella macropus* (Pers.) P. Karst.).

Macropodia hypocrateriformis (Schaeff.) Sacc., Syll. Fung. 8: 159. 1889.
Cyathipodia hypocrateriformis (Schaeff.) Boud., Hist. Classif. Discomyc. Europe: 39. 1907.

Lectotype designated here: Schaeff., Fung. Bavar. Palat. Nasc. 2: t. 152. 1763 ('*Elvela quinta*'). MycoBank MBT375694. *Epitype* designated here: SWEDEN, Uppland, Uppsala, Stadsskogen, 21 July 1948, *R. Molander* (C-F-45378). MycoBank MBT375405.

Helvella cupuliformis Dissing & Nannf., Svensk Bot. Tidskr. 60: 326. 1966.
Cyathipodia cupuliformis (Dissing & Nannf.) J. Breitenb. & F. Kränzli., Champ. Suisse 1. Ascomycetes: 58. 1981.

Holotype. SWEDEN, Uppland, Uppsala, Kåbo, 30 July 1936, *K.G. Ridelius* - Fungi Exs. Suec. 3264 (UPS). *Isotype.* *ibid.* (C-F-92131).
= *Helvella pulchra* Dissing, Biblioth. Mycol. 150: 17. 1993.

Holotype. SWITZERLAND, Graubünden, Ramosch, Resgia, along the river Inn, 7 Sept. 1982, *H. Dissing* Sch 82-151 (ZT), not examined. *Isotype.* (C-F-57126).

Illustrations — Schaeffer (1763: pl. 152, as '*Elvela quinta*'), Dissing (1966b: f. 17, as *H. cupuliformis*), Dissing & Nannfeldt (1966: pl. 1, as *H. cupuliformis*).

Descriptions of the species — Dissing & Nannfeldt (1966: 326, as *H. cupuliformis*), Dissing (1966b: 71 as *H. cupuliformis*; 1993: 17, as *H. pulchra*).

Specimens examined/sequenced. SWEDEN, Uppland, Uppsala, Stadsskogen, near Kåbo, 21 July 1948, *R. Molander* [H301] (C-F-45379 epitype); *ibid.*, 30 July 1936, *K.G. Ridelius* [H300] (C-F-92131, Fungi Exs. Suec. 3264 isotype of *H. cupuliformis*). — SWITZERLAND, Graubünden, Ramosch, along the river Inn, at the bridge near Resgia, under *Picea*, 1100 m asl, 7 Sept. 1982, *H. Dissing* [H275] (C-F-57126 isotype of *H. pulchra*).

Notes — *Helvella hypocrateriformis* was referred to as a *Peziza* similar to *P. macropus* (= *H. macropus*) and *P. macropus* var. *hirta* (= *H. fibrosa*) by Fries (1832). Based on Schaeffer's plate (1763: pl. 152) and Fries' recognition of Schaeffer's fungus as a species close to *H. fibrosa*, we conclude that *H. hypocrateriformis* represents an older, available name for *H. cupuliformis*. We have resurrected Schaeffer's name for this fungus, selecting Schaeffer's plate as lectotype supported with a sequenced

epitype specimen from Sweden. The synonymies of *H. pulchra* and *H. cupuliformis* with *H. hypocrateriformis* are established here based on *hsp* and *rpb2* sequence comparisons; the iso-types of *H. pulchra* and *H. cupuliformis* share identical *hsp* and *rpb2* sequences, while the selected epitype of *H. hypocrateriformis*, collected in the same area as the type specimen of *H. cupuliformis*, deviates from the latter in one *rpb2* bp character. Landeros et al. (2015) supplied an LSU sequence from paratype material of *H. cupuliformis* in UPS, which deviates from the isoparatype of *H. cupuliformis* in C sequenced by us. This latter specimen is selected here as an epitype of *H. hypocrateriformis*, thus merging the concepts of *H. hypocrateriformis* and *H. cupuliformis*. Zhuang (2004) erected a variety 'crassa' for Chinese specimens of *H. cupuliformis* with large ascocarps and somewhat broader ascospores than the type variety. This variety probably deserves specific rank.

Helvella juniperi M. Filippa & Baiano, Riv. Micol. 42: 100. 1999

Holotype. ITALY, Viareggio, (LU), 16 Mar. 1996, Baiano, Filippa & Garofoli (MCVE-501), not examined.

Illustration — Filippa & Baiano (1999: 100).

Description of the species — Filippa & Baiano (1999: 100).

Specimen examined/sequenced. PORTUGAL, Minho, S of S. Bartolomeu do Mar N of Esposende, in sandy soil under *Cistus salvifolius* in the dunes, 15 Nov. 2000, P. Boisen Hansen [H415] (C-F-42193).

Notes — This morphologically distinct species of the *helvellula* lineage of the *lacunosa* clade (clade C) deviates from the sessile *H. helvellula* in two *rpb2* and five *hsp* substitutions, and from *H. semiobruta* in three *rpb2* and five *hsp* substitutions.

Helvella lactea Boud., Icon. Mycol., liste prélim.: 2. 1904 — Fig. 8a

Lectotype. FRANCE, Meaux, June 1902, D. Dumée (PC), selected by Dissing (1966a), not examined.

Illustrations — Dissing (1966a: f. 9b, f. 3, 7e–f; 1966b: f. 29).

Descriptions of the species — Dissing (1966a: 206; 1966b: 108).

Specimens examined/sequenced. DENMARK, Zealand, Dyrehaven, N of Copenhagen, rich soil in deciduous forest, 27 Aug. 1961, H. Dissing [H374] (C-F-39379). – SWEDEN, Uppland, Uppsala, Botanical garden, in sparse loamy lawn, under oaks and hazels, 25 July – 2 Aug. 1939, N. Hylander [H262] (C-Fungi Exs. Suec. 1355).

Notes — Dissing selected a lectotype in Boudier's herbarium in PC which morphologically matched material from Sweden and Denmark studied by him. The description and illustrations of *H. lactea* in Dissing (1966b) is representative of the narrowed concept of *H. lactea*, as reassessed here. Two specimens listed by Dissing (1966b) from Sweden and Denmark have been sequenced by us. We conclude there are two similar species that have been commonly affiliated to the broad concept of *H. lactea*, i.e., *H. lactea* and *H. pallescens*. It may well be that Boudier had the two species in hand when recording *H. lactea* and illustrating parts of the type material in Icones (Boudier 1905–1910). This conclusion rests on the observation that the slender white specimen depicted on plate 226 of the 'Icones' is more indicative of *H. pallescens* than *H. lactea* s.str. We also studied a North American white counterpart to *H. lactea*, referred to as *Helvella* 'USA 5' in the present synopsis (see non-European species), which differs by seven *rpb2* and five *hsp* substitutions.

Helvella lacunosa Afzel., Kongl. Vetensk. Acad. Nya Handl. 4: 303. 1783 — Fig. 6a–b

Basionym. *Helvella lacunosa* Afzel., Kongl. Vetensk. Acad. Nya Handl. 4: 303. 1783; Fr., Syst. Mycol. 2: 15. 1822.

Synonyms. *Helvella lacunosa* Fr., Observ. Mycol. 2: 301. 1818, nom. illeg. (homonym).

Costapeda lacunosa (Afzel.) Falck, Sluzowce Monogr., Suppl. (Paryz) 3: 401. 1923.

Helvella lacunosa Afzel. a. (forma) *major* Fr., Syst. Mycol. 2: 15. 1822 (= *H. mitra* Schaeff., where epithet 'mitra' is an unintentional 1822 error for epithet 'nigricans').

Helvella nigricans Schaeff., Fung. Bavar. Palat. Nasc. 4: 102. 1774 ('Elvela')

– non *Helvella nigricans* Pers., Observ. Mycol. 1: 72. 1796 (= *H. fallax* Qué.).

Lectotype designated here: Schaeff., Fung. Bavar. Palat. Nasc. (*Ratisbonae*) 2: t. 154. 1763 ('*Elvela septima*'). MycoBank MBT375733. *Epitype* designated here: SWEDEN, Femsjö parish, Femsjö, N of Skatåker, 4 Oct. 1948, S. Lundell & G. Haglund (C-Fungi Exs. Suec. 2065). MycoBank MBT375406.

Illustrations — Schaeffer (1763: pl. 154, as *H. nigricans*), Boudier (1905–1910: pl. 228).

Apothecia stipitate-capitate, saddle-shaped, bi- to trilobate, cap 3–6 cm broad, 2–4.5 cm high, apothecial margin reflexed or slightly deflexed when fully mature, attached to stipe at 4–8 points; hymenium black (G-H8), even or wrinkled; receptacle dark grey to greyish black (F-G8), drying blackish, smooth; stipe whitish to greyish, 4–15 cm long, 1.5–3(–6) cm broad, naked, chambered inside and outside with 5–8 sharp-edged, commonly double-edged and partly anastomosing ribs and deep 'holes' (lacunae) inbetween. *Medullary excipulum* of *textura intricata*, hyphae 3–5 mm broad. *Outer excipulum* of intermixed broad-celled *textura intricata* and *textura globulosa-angularis*, outermost cells club-shaped with brownish walls, 10–30 × 5–15 µm, with short 2–4-celled hyaline outgrowths. *Asci* pleuro-rhynchous, 250–290 × 14–17 µm. *Ascospores* narrowly ellipsoid, 17.0–19 × 9–11.5 µm. *Paraphyses* straight, subhyaline to light brown below, increasingly brown above, 3–4 µm broad, septate, clavate to 6–8 µm at the tips.

Specimens examined/sequenced. GREENLAND, Thule, Airbase, N river at Dundas road, clayey silt along coast, 4 Aug. 1987, H. Dissing [H399] (C-F-55985). – NORWAY, Akershus, Ullensaker, Aurtjern, albino morphotype, 12 Sept. 2009, Ø. Stensrud [H059] (O-253316); Hordaland, Ulvik, Finse, Bio 101-peak, 28 July 2014, T. Schumacher [H470] (O-253318); Kvam, Treskåra, Gjerde – Oma, mixed deciduous forest, 24 Aug. 2005, W. Holm WH 7 [H150] (O-280703); Oppland, Dovre, Grimsdalen, along road at Storberget, 20 Aug. 2001, T. Schumacher [H189] (O-253322); *ibid.*, 8 Aug. 2009, T. Carlsen, I. Skrede & T. Schumacher [H044] (O-253320), [H045] (O-253321); Grimsdalen, Tollevschaugen, 3 Aug. 2007, T. Schumacher [H039] (O-253319); Sør-Trøndelag, Ørland, Storfosna, Haugan, in garden, 6 Oct. 2007, R. Haugan, S07415 [H153] (O-285214); Finnmark, Nordkapp, Magerøya, Kobbholen, among *Dryas*, 12 Aug. 1995, L. Ryvarden 38048 [H170] (O-59885); Vassbotndalen, from Bjørnelva to Skacca vaggi, in subalpine birch forest, 400 m asl, 27 Aug. 1986, S. Sivertsen 44.86 [H474] (C-53539); Finnmark, F.-E. Ecckblad 189b.61 [H486] (O-253317). – RUSSIA, River Kotuy Khan at junction with river Kotuy, under *Larix gmelinii*, 19 Aug. 1993, S.A. Hanssen [H327] (C-F-34477). – SVALBARD, Longyearbyen, among mosses, 19 Aug. 1988, H. Knudsen [H471] (C-F-19329). – SWEDEN, Femsjö parish, Femsjö, N of Skatåker, 4 Oct. 1948, S. Lundell & G. Haglund [H407] (C-Fungi Exs. Suec. 2065 epitype).

Notes — The *H. lacunosa* morphospecies complex comprises at least four phylogenetic species with ± restricted distributions in Europe, i.e., *H. atra*, *H. nigra*, *H. sulcata* and *H. lacunosa* s.str. Pale (albino) forms may be mistaken for *H. crispa* but can be distinguished readily by the smooth outer surface and partial fusing of cap margin with the stipe in *H. lacunosa*. Morphologically, *H. lacunosa* resembles *H. atra* and *H. nigra*; however, *H. lacunosa* possesses a receptacle surface and stipe remaining light-coloured and strongly contrasting the hymenium colour when dried. Fries (1822) adopted Afzelius'

name for his broadly defined *H. lacunosa* and referred to Schaeffer's description and plate of *H. nigricans* (erroneously as '*mitra*' Schaeff.) as synonymous to *H. lacunosa* forma major (a.) in his sanctioning work (Fries 1822, 1832). *Helvella lacunosa* is here typified with Schaeffer's plate, supported with an epitype specimen from Sweden. The *rpb2* barcode sequence of *H. lacunosa* is identical among the sequenced specimens.

Helvella leucomelaena (Pers.) Nannf., in Lundell & Nannfeldt, Fungi Exsicc. Suecici Fasc. 19–20: 21, no. 952. 1941

Basionym. *Peziza leucomelas* Pers., Mycol. Eur. 1: 219. 1822.

Synonyms. *Aleuria leucomelaena* (Pers.) Gillet, Champ. France Discomyc.: 37. 1879 ('*leucomelas*').

Acetabula leucomelaena (Pers.) Sacc., Syll. Fung. 8: 61. 1889 ('*leucomelas*').

Paxina leucomelaena (Pers.) Kuntze, Revis. Gen. Pl. 2: 864. 1891 ('*leucomelas*').

Peziza sulcata Pers. b. (forma) Fr., Syst. Mycol. 2: 44. 1822.

Lectotype. NETHERLANDS, Herb. Persoon L 8945–6, (L), selected by Abbott & Currah (1997). *Epitype* designated here: SWEDEN, Gotland, Klintehamn parish, at the railway station, 7 May 1938, S. Lundell & E. Åberg (C-Fungi Exs. Suec. 952 '*Helvella leucomelas*' (Pers.) Nannf.). MycoBank MBT375407.

Acetabula calyx Sacc., Mycoth. Veneta: no. 168. 1873 (fide Landeros et al. 2015)

Paxina calyx (Sacc.) Kuntze, Revis. Gen. Pl. 2: 864. 1891.

Illustration — Dissing (1966b: f. 8).

Description of the species — Dissing (1966b: 36).

Specimens examined/sequenced. CHILE, Santiago, El Tabo, in pine wood, 11 July 1966, W. Lazo [H447] (C-F-92127). — DENMARK, Jutland, Nystrup Plantage 15 km NW Thisted, calcareous soil, 25 Nov. 1967, K. Toft [H267] (C-F-39492); Zealand, Hellerup Church Yard, in gravel under *Pinus*, 9 May 1998, T. Læssøe 4940 [H450] (C-F-38142). — SWEDEN, Gotland, Klintehamn parish, at the railway station, along sandy road in coniferous wood, almost covered by sand, 7 May 1938, S. Lundell & E. Åberg [H404] (C-Fungi Exs. Suec. 952, '*Helvella leucomelas*' (Pers.) Nannf. epitype). — USA, Massachusetts, Worcester Co., at Bolton Lime Quarry, 7 May 2006, K. Hansen & G. Lewis-Gentry KH.06.01 [H115] (FH).

Notes — We have selected an epitype specimen to support the lectotype in Weber (1972) and Landeros et al. (2012) observed that *H. leucomelaena* has aporhynchous asci, an observation we concur with. Landeros et al. (2015) compared LSU sequences from the type specimen of *A. calyx* with recent collections of *H. leucomelaena* and concluded they were the same. A specimen from Australia [KC012682] in Landeros et al. (2015) also matches our concept of *H. leucomelaena* (cf. Appendix 3).

Helvella leucophaea (Battarra) Pers., Observ. Mycol. 2: 19. 1799

Basionym. *Boletus leucophaea* Battarra, Fungorum Arimin.: 25. 1759.

Synonyms. *Helvella crispa* c. (forma) *lutescens*, *sicca subfulva* Fr., Syst. Mycol. 2: 14. 1822.

Lectotype designated here: Battarra, Fungorum Arimin.: t. III, f. B, 1759. MycoBank MBT375735.

Helvella pityophila Boud., J. Bot. 1: 218. 1887 ('*pityophila*').

Helvella crispa var. *pityophila* (Boud.) Donadini, Bull. Soc. Linn. Provence 28: 75. 1975.

Lectotype: FRANCE, Fontainebleau, Oct. 1885, Herb. Boudier (PC), not examined.

Illustrations — Trattinia (1809: pl. 28, as *H. leucophaea* Pers.), Boudier (1887: pl. 3; 1905–1910: pl. 227, as *H. pityophila*).

Description of the species — Boudier (1905–1910: 119, as *H. pityophila*).

Specimen examined/sequenced. FRANCE, Porquerelles, terrain sablonneux, 10 Dec. 1976, J.C. Donadini [H274] (C-F-45487).

Notes — This species resembles *H. crispa* in size and stature; however, the hymenium in fresh ascocarps is light brown, drying caramel brown and the receptacle and stipe are whitish. The paraphyses are thread-like and not significantly inflated at the clavate tips compared to the abruptly and subcapitately inflated paraphyses in *H. crispa*. Four *rpb2* and two *hsp* substitutions separate *H. leucophaea* and the sister species *H. crispa*. The LSU nrDNA sequences are insufficient to discriminate among the two. The selection of an epitype specimen is postponed until an extended study of the *H. crispa* morphospecies complex could be undertaken.

Helvella levis Bergeret, Phytanom. Univ. 1: t. 149. 1783 — Fig. 7c

Lectotype designated here: Bergeret, Phytanom. Univ. 1: t. 149. 1783. MycoBank MBT375700. *Epitype* designated here: DENMARK, M Zealand, Hejede Overdrev by Tjørnehus, 14 Sept. 2001, B.W. Pedersen (C-F-55188). MycoBank MBT375468.

Synonyms. *Helvella latispora* Boud., Bull. Soc. Mycol. France 14: 16. 1898.

Leptopodia latispora (Boud.) Boud., Icon. Mycol., liste prélim.: 2. 1904.

Lectotype. FRANCE, *Helvella* no. 480, '*H. latispora*' Boud. (PC-Herb. Boudier), selected by Dissing (1966b).

Illustrations — Bergeret (1783: pl. 149), Boudier (1898: pl. 3, f. 2; 1905–1910: pl. 233, as *Leptopodia latispora*), Van Vooren (2010: 43, photo 11, as *H. latispora*).

Description of the species — Dissing (1966b: 135, as *H. latispora*).

Specimens examined/sequenced. DENMARK, M Zealand, Hejede Overdrev by Tjørnehus, 14 Sept. 2001, B.W. Pedersen [H290] (C-F-55188 epitype); Lolland, Kristiansaede Forest, 6 km W Maribo, 5 Oct. 1968, P.M. Petersen [H264] (C-F-39370); Zealand, Copenhagen, Kongelunden, 25 Oct. 1974, H. Dissing [H266] (C-F-39367); Jutland, Pamhule Forest, on rich mouldy soil, 2 Sept. 1979, I. Weng [H265] (C-F-39366); East Jutland, W of Kongsted, Elbodalen, NW Fredericia, in mixed deciduous forest, 4 Oct. 2002, J. Vesterholt JV 660.02 [H393] (C-F-40830); NE Zealand, Gurre Sø, on soil under *Urtica*, 8 Oct. 1997, K. Hansen & T. Læssøe, KH 109.97 [H469] (C-F-52988); Konabbe Forest, 24 Sept. 2013, T. Kehlet [H458] (C). — GERMANY, Hamburg E, Sachsenwald, Friedrichsruh, under beech and oak, 12 Sept. 1973, I. Friedrichsen & Lorch [H480] (C-F-45517).

Notes — This species has commonly been treated under the younger, synonymous name *H. latispora* Boud. *Helvella levis* was placed in synonymy with *H. elastica* by Fries (1822). In our opinion, the description and figure of Bergeret's (1783) is not representative for *H. elastica*, but for the deflexed, saddle-shaped fungus commonly referred to as *H. latispora* in literature. Dissing's descriptions (1966a, b) of *H. latispora* fully cover Bergeret's fungus, which is lectotypified here with Bergeret's original plate (iconotype), supported with *hsp*, *rpb2* and LSU sequences from a newly selected epitype specimen from Denmark.

Helvella macropus (Pers.) P. Karst., Not. Sällsk. Fauna Fl. Fenn. Forh. 11: 224. 1870 — Fig. 9c

Basionym. *Peziza macropus* Pers., Ann. Bot. (Usteri) 15: 26. 1795; Fr., Syst. Mycol. 2: 57. 1822.

Synonyms. *Peziza macropus* Pers., Ann. Bot. (Usteri) 15: 26. 1795, var. *macropus*.

Peziza macropus var. *hirta* Pers., Ann. Bot. (Usteri) 15: 26. 1795.

Helvella macropus (Pers.) P. Karst., Not. Sällsk. Fauna Fl. Fenn. Forh. 11: 224. 1870, var. *macropus*.

Macroscyphus macropus (Pers.) Gray, Nat. Arr. Brit. Pl. 1: 672. 1821.

Macropodia macropus (Pers.) Fuckel, Jahrb. Nassauischen Vereins Naturk. 23–24: 331. 1870 ('1869–1870').

Aleuria macropus (Pers.) Gillet, Champ. France Discomyc.: 35. 1879.

Lachnea macropus (Pers.) W. Phillips, Man. Brit. Discomyc.: 207. 1887.

Cowlesia macropus (Pers.) Nieuwl., Amer. Midl. Naturalist 3: 300. 1916.

Cyathipodia macropus (Pers.) Dennis, British Cup Fungi: 7. 1960.

Lectotype designated here: Pers., *Observ. Mycol.* 1: pl. 1, f. 3. 1796. MycoBank MBT375701. *Epitype* designated here: SWEDEN, Uppland, Skogstibble parish, Rosenberg, 4 Sept. 1960, R. Santesson 13997 (C-Fungi Exs. Suec. 3266). MycoBank MBT375408.

Helvella hispida Schaeff., *Fung. Bavar. Palat. Nasc.* 4: 108. 1774.

Paxina hispida (Schaeff.) Seaver, *North Amer. Cup-fungi* (Operculates): 205. 1928.

Macropodia macropus var. *hispida* (Schaeff.) Killerm., *Kryptog. Forsch.* 2: 36. 1929.

Lectotype designated here: Schaeff., *Fung. Bavar. Palat. Nasc.* 2: pl. 167. 1763 ('*Elvela decima nona*'). MycoBank MBT375702.

Peziza hypocrateriformis Bergeret, *Phytonom. Univ.* 1: t. 169. 1783.

Lectotype designated here: Bergeret, *Phytonom. Univ.* 1: t. 169. 1783. MycoBank MBT375736.

Illustrations — Dissing & Nannfeldt (1966: f. 4, 5a–e, pl. III), Weber (1972: f. 23–24).

Descriptions of the species — Dissing & Nannfeldt (1966: 333), Dissing (1966b: 62), Weber (1972: 164, as *H. macropus* var. *macropus*).

Specimens examined/sequenced. CANADA, Alberta, Devonian Botanic Garden, Devon, 24 Aug. 1996, S.P. Abbott [H119] (FH); Quebec, 10 km NW Montreal at Biological Research Station, 2 Aug. 1997 [H120] (FH). – NORWAY, Østfold, Moss, Jeløya, Kjeldstadvik, humid deciduous forest, 18 Sept. 2013, T. Læssøe [H260] (O-253327); Oslo, Skullerud, on soil in deciduous forest, 3 Sept. 2009, M. Bjørnbækmo [H073] (O-253326); Akershus, Røyken, Nærnes, 10 Sept. 2009, K. Bjørum [H060] (O-253323); Akershus, Opppegård, Bestemorstranda, rich spruce forest, 19 Sept. 2009, C. Christiansen [H069] (O-292075); Akershus, Ski, N Busterud gård, in rich spruce forest, 16 Sept. 2006, A. Pedersen [H157] (O-370348); Oppland, Dovre, Grimsdalen, Buåi, in birch forest at the river, 23 July 1980, T. Schumacher [H228] (O-253324); Oppland, Dovre, Grimsdalen, Storberget, in birch forest, 8 Aug. 2009, T. Carlsen, I. Skrede & T. Schumacher TS 36.09 [H257] (O-253325); Hedmark, Åmot, Kvannbekken National Reserve, mixed rich coniferous forest, 30 Aug. 2002, P. Marstad [H158] (O-65347); Telemark, Drangedal, Henneseid, Trillingtjernåsen W, in mixed pine-oak forest, 15 July 2004, T.E. Brandrud TEB 95.04 [H142] (O-166155); Kragerø, Storkollen, valley between Storkollen and Lindvikskollen, in rich mixed forest, 5 Aug. 2000, T.E. Brandrud TEB 70.00 [H141] (O-168819); Rogaland, Vindafjord, Kvaløy, rich deciduous forest, 11 Sept. 2009, E. Dalen, L. Dalen, J.B. Jordal [H238] (O-291425); Sokndal, Skaråsen, rich soil under *Corylus*, 9 Sept. 2009, J.I. Johnsen & J.B. Jordal [H239] (O-291391); Hordaland, Ulvik, Veånerebekken, bare soil in *Fraxinus* dominated forest, 28 Aug. 2001, G. Flatabø [H159] (O-220323); Eidfjord, Hæreid, pasture land with *Betula*, 6 Oct. 2006, A. Oterhals [H160] (O-283072); Møre og Romsdal, Stordal, Stiggjeldet, deciduous forest, 5 Sept. 2003, D. Holtan & P. Larsen 78.2003 [H161] (O-223871); Sunndal, Sunndalsfjorden N Løvika, under *Corylus*, 11 Sept. 2001, J.B. Jordal [H165] (O-220225). – SWEDEN, Uppland, Skogstibble parish, Rosenberg, in forest, 4 Sept. 1960, R. Santesson 13997 [H412] (C-Fungi Exs. Suec. 3266 epitype). – USA, Alaska, Anchorage, between Anchorage and Denali National Park, among leaves of deciduous trees, 14 Aug. 1980, H. Dissing [H351] (C-F-56087); Massachusetts, Carlisle, Great Farm, 8 July 2006, L. Millman [H118] (FH); Massachusetts, Concord, Eastbrook Woods, 25 June 1998, D. Pfister [H124] (FH).

Notes — Persoon's and Fries' original concept of *Peziza macropus* included the European *H. macrospora* as well as *H. fibrosa* (= *Octospora villosa*). These two species are readily separable based on hymenium colour and microanatomical characters (see also *H. fibrosa* and artificial key). *Helvella macropus* is typified with Persoon's original plate in the 1796 issue of his work, which includes a coloured plate, and supported with a widely distributed epitype (exsiccate) specimen capturing specific barcode sequences to the species discrimination. Our molecular survey confirms the existence of at least three species of the *H. macropus* morphospecies complex, i.e., *H. macropus* s.str. with a mainly European and North American distribution, *Peziza subclavipes* (= *H. brevis*) in USA and Mexico (cf. Landeros et al. 2015: f. 3) (not included in our dataset) and *H. ephippioides* S. Imai reported from Japan (Imai 1932) (see extralimital *Helvella* species below).

Helvella macrosperma (J. Favre) R. Fellner & Landa, *Česka Mykol.* 45 (1–2): 35. 1991 — Fig. 4d

Basionym. *Helvella arctica* Nannf. var. *macrosperma* J. Favre, *Ergebn. Wiss. Untersuch. Schweiz. Nationalparkes* 5, 33: 199. 1955.

Synonym. *Helvella corium* var. *macrosperma* (J. Favre) Bizio, Franchi & M. Marchetti, *Riv. Micol.* 41: 232. 1998.

Holotype. SWITZERLAND, Val Nügliä 2550 m asl, leg. J. Favre, not examined.

Illustrations — Favre (1955: pl. 1, f. 2).

Apothecia short-stipitate, regularly cupulate, cap 0.5–1.8 cm diam, 0.5–1.5 cm high; stipe terete, solid, 0.4–1.5 cm high, 0.2–0.4 mm broad; hymenium and receptacle black (H1), receptaculum and stipe densely tomentose, hyphoid hairs mostly aggregated in conspicuous, pyramidal fascicles on the receptacle surface and stipe. *Medullary excipulum* of loosely interwoven *textura intricata*, hyphae 3–5 µm broad, short-celled; outer excipulum of brown-walled globose to angular cells, 10–20 µm diam, gradually arranged perpendicularly to the surface and forming a layer of closely packed cells that extend into dark brown-walled multicellular hyphoid hairs on the excipulum exterior, hairs generally 40–150 µm, at the margin to 300 µm in length, in some parts forming dense bundles, individual cells 10–15 µm broad, 10–40 µm long, constricted at septa with conspicuous deposits of incrustated pigments on the interior of the cell walls. *Asci* pleurorhynchous, 290–330 × 16–20 µm. *Ascospores* broadly ellipsoid, 18.5–22.5 × 11.5–13.8 µm. *Paraphyses* filiform, 2–2.5 µm broad, septate, with brownish pigments in their whole length, colour increasing in intensity towards the gnarled, clavate tips, 4.5–6.0 µm broad.

Specimens examined/sequenced. NORWAY, Dovre, Grimsdalen, Veslegrimsa, river bed, 2 Aug. 2007, T. Schumacher TS 54.07 [H029] (O-253328); Dovre, Tverrlibekken, 7 Aug. 2009, T. Carlsen, I. Skrede & T. Schumacher TS 21.09 [H047] (O-253329); *ibid.*, 7 Aug. 2009, T. Carlsen, I. Skrede & T. Schumacher TS 28.09 [H050] (O-253330); *ibid.*, 7 Aug. 2009, T. Carlsen, I. Skrede & T. Schumacher TS 31.09 [H053] (O-253331).

Notes — The species was originally described from the Swiss Alps (Favre 1955, as *H. arctica* Nannf. var. *macrosperma*). It is reported recently also from the French Alps (Van Vooren 2015). *Helvella macrosperma* is closely related to *H. alpestris*, from which it is distinguished by the prominent tufts of dark-pigmented hyphoid hairs on the receptacle surface and stipe. The microanatomy of ectal excipulum, ascospores and paraphyses also discriminate among the two. One *hsp*, one *rpb2*, four *tef*, and seven LSU substitutions separate *H. macrosperma* and *H. alpestris*.

Helvella monachella (Scop.) Fr., *Syst. Mycol.* 2: 18. 1822

Basionym. *Phallus monacella* Scop., *Fl. Carniol.*, ed. 2, 2: 476. 1772; Fr., *Syst. Mycol.* 2: 18. 1822 ('*monachella*' orth. mut.).

– non *Helvella monacella* Schaeff., *Fung. Bavar. Palat. Nasc.* 4: 106. 1774 ('*Elvela*'), nom. inval. (= *Helvella sulcata* Afzel.).

Lectotype designated here: Battarra, *Fungorum Arimin.*: t. 2, f. H, *sub* 'Boletus albus pileolo complicatus nigro', 1759. MycoBank MBT375704. *Epitype* designated here: HUNGARY, Széld, Bacs-Kiskun, in populeto-saliceto, 14 May 1979, M. Babos, L. Albert, J. Bükei & A. Friesz (C-F-92121 'Helvella leucopus Pers.' ex Herb. Musei Hist. Nat. Hung. Budapest, dupl.). MycoBank MBT375409.

Synonyms. *Helvella leucopus* Pers., *Mycol. Eur.* 1: 213. 1822.

Lectotype. FRANCE, Herb. Persoon no. 910.261-997 (L) selected by Dissing (1966a), not examined.

Helvella albipes Fuckel, *Jahrb. Nassauischen Vereins Naturk.* 23–24: 334. 1870. '1869–1870'.

Lectotype. AUSTRIA, *Fung. rhen.* 1240 '*H. albipes*' (BM), selected by Dissing (1966b), not examined.

Illustrations — Fuckel (1870: pl. 5, f. 2), Dissing (1966b: f. 38 (as *H. leucopus*), Moravec (1980: pl. 4, as *H. leucopus*), Van Vooren (2010: 43, photo 12).

Descriptions of the species — Fuckel (1870: 334, as *H. albipes*), Dissing (1966b: 138 as *H. leucopus*).

Specimens examined/sequenced. HUNGARY, Szelid, Bacs-Kiskun, in populeto-saliceto, 14 May 1979, M. Babos, L. Albert, J. Bükei & A. Friesz [H268] (C-F-92121 '*Helvella leucopus* Pers.' epitype); Örkeny, ad terram in populeto, 24 May 1965, I. Ferencz, E. Toth, E. Vessey & S. Vasadi [H269] (C-F-92120 ex Herb. Musei Hist. Nat. Hung. Budapest).

Notes — The *rpb2* and *hsp* sequences are identical among the sequenced specimens. *Helvella monachella* Scop. was sanctioned by Fries (1822), who listed *H. leucopus* as a presumable taxonomic synonym (Fries 1832). Fries (1822) misinterpreted Scopoli's species when he also included *H. spadicæ* as a forma b of *H. monachella* (Fries 1822), this latter fungus presumably representing a *Gyromitra* species, as also concluded by Dissing (1966b). We have selected Battarra's original illustration of 'Boletus albus pileolo complicatus nigro' (Battarra 1759) as lectotype ('iconotype') for the original fungus of Scopoli's (1772), since it was referred to in Fries' original description of the species. *Helvella albipes* Fuckel (1870) is a more recent heterotypic synonym. The lectotype of *H. monachella* is supported with an epitype from Hungary, supplying *rpb2*, *hsp* and LSU sequences for the purpose of a precise application of the name (ICN article 9.8).

Helvella nannfeldtii Skrede, T. Carlsen & T. Schumach. sp. nov. — MycoBank MB820326; *hsp* barcode GenBank KY784203; *rpb2* barcode GenBank KY772447; Fig. 4b

Etymology. Named in honour of the Swedish botanist and mycologist Jon Axel Nannfeldt.

Holotype. NORWAY, Oppland, Dovre, Grimsdalen, Veslegrimsa, 8 Aug. 2009, T. Carlsen, T. Schumacher & I. Skrede TS 22.09 (O-253338).

Apothecia short-stipitate-cupulate, black, 1–3 cm broad, 1–3 cm high; stipe terete, usually deeply buried in the soil, 0.2–0.3 cm broad, 0.5–2.0 cm long, greyish black above, whitish below, with or without grooves at base, receptacle surface pubescent, towards margin with long slender tufts of short-segmented, subhyaline to light brown-walled hyphoid hairs to 200 µm long staining in cotton blue, cells irregular in shape and generally much constricted at the septa. *Medullary excipulum* of loosely interwoven *textura intricata*, hyphae 3–5 µm broad. *Outermost excipulum* of *textura angularis*, cells dark brown, thick-walled, 15–30 µm diam, intermixed with broad short-segmented brownish hyphae forming a *textura intricata*. *Asci* pleurorhynchous, 230–270 × 15–19 µm. *Ascospores* ellipsoid, 18–21 × 11–13 µm. *Paraphyses* straight, dark brown along upper two thirds, 2–3 µm broad, septate, gradually enlarged to 5–6 µm at the subcapitate tips.

Specimens examined/sequenced. FRANCE, Savoie, Val d'Iserre, Gorges du Mal, 2400 m asl, 31 Aug. 1992, T. Schumacher F 83.92 [H212] (O-253332); Savoie, Bon Valle, Sur Arc, 2 Sept. 1992, T. Schumacher F 94.92 [H216] (O-253333). — NORWAY, Oppland, Dovre, Grimsdalen, Veslegrimsa, 8 Aug. 2009, T. Carlsen, T. Schumacher & I. Skrede TS 22.09 [H027] (O-253338 holotype); *ibid.*, 2 Aug. 2007, T. Schumacher TS 66.07 [H028] (O-253339); Grimsdalen, Tverrgjelet, on river bed, deeply immersed in sand, 6 Aug. 1996, A.H. Jensen & T. Schumacher [H254] (O-253341); *ibid.*, 2 Aug. 2007, T. Schumacher TS 60.07 [H017] (O-253337); Grimsdalen, Tverrà, 13 Aug. 1985, T. Schumacher [H367] (O-253343); Grimsdalen, Grimsa, on river terrace at the river, 25 Aug. 1996, T. Schumacher [H362] (O-253342); *ibid.*, 17 Aug. 2005, T. Schumacher [H188] (O-253340); Grimsdalen, Buài, at the river, 17 Sept. 1983, T. Schumacher & K. Østmo D 168.83 [H479] (O-253344); Hordaland, Ulvik, Finse, Blåisen, 27 July 2014, T. Schumacher [H452] (O-253334), [H454] (O-253335), 31 July 2014, K. Høiland [H457] (O-253336); Nordland, Rana, Virvassdalen, Beveråa, river bed, 30 July 1974, S. Sivertsen [H318] (C-92123 ex TRH).

Notes — *Helvella nannfeldtii* shows superficial resemblance to *H. corium* and *H. macrosperma*; however, the short cylindrical stipe, which is whitish below, helps discriminate the two latter

species in the field. *Helvella nannfeldtii* forms a well-supported lineage with *H. alpestris* and *H. macrosperma* in our phylogeny. Six *hsp*, two *rpb2*, four *tef* and 43 LSU substitutions, and two *hsp*, one *rpb2*, three *tef* and 41 LSU substitutions separate *H. alpestris* and *H. macrosperma*, respectively.

Helvella nigra Bergeret, *Phytonom. Univ.* 1: t. 147. 1783 — Fig. 6e

— non *Helvella nigra* Peck, *Bull. Torrey Bot. Club* 26: 70. 1899, nom. illeg. (homonym).

Lectotype designated here: Bergeret, *Phytonom. Univ.* 1: t. 147. 1783. MycoBank MBT375705. *Epitype* designated here: SWEDEN, Halland, Halmstad, Almeberget, 16 Sept. 2009, G. Holden (O-253345). MycoBank MBT375466.

Misapplied name

— *Helvella lacunosa* sensu Fr., *Syst. Mycol.* 2: 15. 1822.

Illustration — Bergeret (1783: pl. 147).

Apothecia stipitate-capitate, 2–6 cm across, cap saddle-shaped, bi- to trilobate, from 6–15 cm in height, apothecial margin adnate, firmly attached to the stipe at 4–6 points; hymenium wrinkled, dark grey (F1) to greyish black (G1) when fresh, drying darker; stipe concolorous or slightly paler, lacunose, receptacle surface concolorous or slightly paler, smooth, with distinct, branching ribs; stipe 2.0–4 cm broad, naked, ribbed, ash grey to almost black, longitudinal ribs high and prominent, sharp, partly anastomosing and double-edged, with deep 'holes' (lacunae) inbetween ribs, stipe chambered inside. *Medullary excipulum* of *textura intricata*, hyphae 3–5 µm broad. *Outer excipulum* thin, of intermixed broad-celled *textura intricata* and *textura globulosa-angularis*, the layer light brown, outermost cells club-shaped, hyaline, 10–30 × 5–15 µm, with loose few-celled outgrowths taking much colour in CB. *Asci* pleurorhynchous, 290–330 × 14–16 µm. *Ascospores* ellipsoid, 16.5–19 × 10.5–12 µm. *Paraphyses* straight, slightly bent at tips, light brown in the whole length, 3–4 µm broad below, enlarged to 6–8 µm at the tips.

Specimens examined/sequenced. SPAIN, La Rioja, Castroviejo, 9 Aug. 2014, A. Melendez, R. Martinez, C. Perez PIPE 0829 [H1029] (O-253404); Basque Country, Urkiola, 19 Oct. 2007, G. Munoz GM 1085 [H1030] (O-253405). — SWEDEN, Halland, Halmstad, Almeberget, beech forest, 16 Sept. 2009, G. Holden [H063] (O-253345 epitype); Halmstad, Holkåsen, 17 Sept. 2009, G. Stenström [H068] (O-253347); Halmstad, Biskopstorp, 17 Sept. 2009, K.-H. Larsson [H067] (O-253346).

Notes — We have resurrected the binomial *H. nigra* for this fungus, referring to a species placed in synonymy with *H. lacunosa* by Fries (1822). *Helvella nigra* can be distinguished by the large sized, reflexed and lobed apothecium with prominent ribs on the outer surface firmly adhered onto the stipe, and microscopically by apically bent paraphyses (like a 'golf-club'). The Swedish specimens studied by us occur on soil and deeply decayed wood. The selected lectotype of Bergeret's is supported here with an epitype from lowland Sweden supplying *hsp*, *rpb2*, *tef* and LSU sequences. Eight *hsp*, three *rpb2* and 25 LSU nrDNA characters distinguish *H. nigra* from *H. lacunosa*. An LSU sequence in GenBank (AJ 544211) from Germany labelled *H. lacunosa*, matches the specimens of *H. nigra* (cf. Appendix 3).

Helvella oblongispora Harmaja, *Karstenia* 18: 57. 1978

Holotype. GERMANY, Bavaria, Munich, Isar river, 23 July 1969, A. Einhelinger (C).

Illustration — Harmaja (1979: f. 7).

Description of the species — Harmaja (1979: 36).

Specimens examined/sequenced. GERMANY, Bavaria, Munich, Isar, 23 July 1969, A. *Einhellinger* (C holotype). – NORWAY, Oppland, Lunner, Mutta-gruvene naturminne, on calcareous gravel, 27 Aug. 2004, T.E. *Brandrud* & E. *Bendiksen* TEB 278.04 [H132] (O-166316). – SWITZERLAND, Graubünden, Mota Jüda, Val Plavna, on path with small stones, 30 Aug. 1979, H. *Dissing* [H332] (C-F-56844); Graubünden, Ofenpass, near bridge under Raitschana, at P-place N National Park, 5 Sept. 1979, H. *Dissing* [H448] (C-F-56914).

Notes — *Helvella oblongispora* is morphologically similar to *H. costifera* and *H. calycina*; however, the aporhynchous ascus base and species specific DNA sequences confirm its affiliation to the leucomelaena lineage together with *H. leucomelaena*, *H. confusa* and *H. crassitunicata*. We have examined the holotype specimen under the lens, but were unsuccessful in extracting amplifiable DNA from this specimen.

Helvella pallescens Schaeff., Fung. Bavar. Palat. Nasc. 4: 114. 1774 ('*Elvela*') — Fig. 8b

Synonym. *Helvella sulcata* β (var.) *pallescens* (Schaeff.) Fr., Syst. Mycol. 2: 16. 1822.

Lectotype designated here: Schaeff., Fung. Bavar. Palat. Nasc. 4: t. 322. 1774 ('*Elvela tricésima quinta*'). MycoBank MBT375713. *Epitype* designated here: NORWAY, Møre og Romsdal, Norddal, Stiggjelet, 29 Aug. 2003, D. *Holtan* (O-66205). MycoBank MBT375410.

Illustrations — Schaeffer (1774: pl. 322), ? Boudier (1905–1910: pl. 226, as *H. lactea*).

Apothecia bilobate to campanulate to irregularly saddle-shaped, cap 0.6–2 cm broad, by 2–3 cm high, underside glabrous, edge of cap adnate (reflexed) and fused with the stipe at 3–4 points; hymenium and stipe white to pale greyish, hymenium white to pale grey (3-5A-B1-2), drying brownish yellow (5B-C7-8); receptacle surface and stipe pale yellowish to brown, drying brown; stipe long and slender, 0.5–1.5 cm broad, 4–6 cm high, hollow, with 4–5 longitudinal ribs and a few lacunae inbetween. *Medullary excipulum* of an interwoven *textura intricata*, hyphae of variable thickness, 4–10 μm broad. *Outer excipulum* of *textura globulosa-angularis*, cells 20–40 μm diam, outermost cells more elongated and prismatic giving rise to a cover of densely packed club-shaped cells on receptacular surface. *Asci* pleurorhynchous, 280–310 × 14–15 μm. Young asci with numerous cyanophilic ascospores with large pustules adhered to the spore wall. *Ascospores* broadly ellipsoid, 15.0–18.2 × 10.2–13.2 μm. *Paraphyses* hyaline, 2–3 μm broad, septate, gradually enlarged into irregular clavate tips, 6–10 μm broad.

Specimens examined/sequenced. NORWAY, Møre og Romsdal, Norddal, Stiggjeldet, rich moldy soil under *Corylus avellana*, 29 Aug. 2003, D. *Holtan* [H138] (O-66205 epitype); *ibid.*, [H070] (O-289039); Østfold, Hvaler, Asmaløy, Fonten, on soil in rich deciduous forest, 29 Aug. 1992, Roy *Kristiansen* RK 49784 [H373] (O-253355); Rogaland, Hjelmeland, Hetlandsbygda W Kvitefjell, on soil under *Corylus*, 27 Sept. 2009, O. *Førland* & J.B. *Jordal* [H236] (O-291458); Hordaland, Ulvik, Veånesbekken, on soil in deciduous forest under *Betula*, 28 Aug. 2001, G. *Flatabø* [H136] (O-220306).

Notes — This small and slender, whitish to greyish species has apparently been confused with *H. lactea*, which shares a similar colour and micromorphological characters; however, *H. pallescens* has a more slender and narrow stipe and sharper ribs that extend onto the proximal parts of the receptacle keeping the margin firmly attached to the stipe. Microanatomical features that distinguish it from *H. lactea* are longer asci (280–310 μm in *H. pallescens* vs 240–260 μm in *H. lactea*) and differently shaped paraphyses. The species is nested with *H. atra* and *H. sulcata* as the closest species (sisters) in the lacunosa clade (clade C). Eight *rpb2* and nine *hsp* substitutions separate *H. pallescens* and *H. lactea*. We have selected Schaeffer's plate 322 as lectotype (Schaeffer 1774) and supported it with sequences of *rpb2*, *tef*, and LSU from an epitype specimen from Norway.

Helvella palustris Peck, Ann. Rep. N. Y. State Mus. Nat. Hist. 33: 31. 1880 — Fig. 6c

Holotype. USA, New York, Manlius Center, Aug., C.H. *Peck* (NYS), not examined.

Illustration — Weber (1972: f. 40).

Description of the species — Weber (1972: 189).

Specimens examined/sequenced. FINLAND, Kuusamo, Juuma, The Vuomas, in gravel pit, 25 Aug. 1978, H. *Dissing* [H350] (C-55330). – JAPAN, Honshu, Gumma Prefecture, Tone-gum, Katashima-mura, Jujo Seishi Co. Forest, on soil, 26 Aug. 1983, T. *Schumacher* [H195] (O-253356). – NORWAY, Oppland, Dovre, Grimsdalen, Buådalen, in spring horizon in the subalpine birch forest, 11 Sept. 1982, T. *Schumacher* & K. *Østmo* 479.82 [H468] (O-253362); Grimsdalen, at Grimsdalshytta, 16 Aug. 2001, T. *Schumacher* [H001] (O-253357); Grimsdalen, Tverrådalen, moist slope along river, 25 Aug. 1996, T. *Schumacher* [H184] (O-253361); *ibid.*, 7 Aug. 2009, T. *Carlsen*, I. *Skrede* & T. *Schumacher* TS 12.09 [H019] (O-253358); *ibid.*, TS 13.09 [H043] (O-253359); Grimsdalen, at margin of minerotrophic fen, 23 Aug. 1996, S. *Landvik* & T. *Schumacher* TS 204.96 [H181] (O-253360).

Notes — This characteristic species of the lacunosa clade is a medium-sized, bi- to trilobate black *Helvella* species in which the cap is reflexed towards a slender and longitudinally ribbed stipe. The typical habitat is along rivulets and in deep moss carpets of rich, minerotrophic fens in subalpine areas. Weber (1972) compared the type specimens of *H. palustris* and *H. philonotis* and concluded they were conspecific. Based on morphology and DNA barcode sequences we have found good reasons to distinguish these two species (see *H. philonotis*). Landeros et al. (2015) collected a specimen from the USA under the name of *H. aff. sulcata* [JX993082] that seems to belong here (cf. Appendix 3).

Helvella panormitana Inzenga, Funghi Siciliani 1: 41. 1865 — Fig. 7a

Synonym. *Leptopodia panormitana* (Inzenga) Boud., Hist. Classif. Disco-myc. Europe: 37. 1907.

Lectotype designated here: Inzenga, Funghi Siciliani 1: pl. 4, f. 1₁₋₄. 1865. MycoBank MBT375706. *Epitype* designated here: SWEDEN, Halland, Laholm, Hallandsåsen N, on soil in beech forest, 16 Sept. 2009, C.C. *Mellberg* (O-253363). MycoBank MBT375469.

Illustrations — Inzenga (1865: pl. 4, f. 1₁₋₄).

Apothecia stipitate-capitate, cap campanulate to bilobate, 1–2.5 cm broad, 1.5–3 cm high, long-stipitate, margin free, reflexed towards stipe, hymenium pale greyish brown (5-8D-E3, receptacle smooth, white or pale yellow (3A4), concolorous with stipe, drying brownish orange (5C4-6); stipe 0.4–1 cm broad, by 3–15 cm high, solid to hollow, occasionally with grooves towards the base. *Subhymenium* and *medullary excipulum* of highly gelatinous hyphae, 3–4 μm broad, embedded in an amorphous gelatinous matrix. *Outer excipulum* a mixture of *textura intricata* and *textura angularis*, hyphae to 8 μm broad, angular cells generally 25–40 μm diam, partly inflated to 60–70 μm diam, outermost cells giving rise to densely packed rows of prismatic to club-shaped cells 10–20 μm broad, 10–30 μm long, outermost cell club-shaped and heavily staining in CB. *Asci* pleurorhynchous, 290–310 × 14–16 μm. *Ascospores* ellipsoid, 19–24 × 11.5–13.5 μm. *Paraphyses* c. 3 μm broad below, septate, light brown in colour, gradually enlarging towards the 6–8 μm broad clavate tips.

Specimens examined/sequenced. NORWAY, Hordaland, Bømlø, Grønås-vågen, under *Corylus*, 1 Sept. 2002, A. *Knutsen* [H143] (O-65394); Bømlø, Hildeneset, pasture land in deciduous forest, 17 Sept. 2007, A. *Knutsen* [H137] (O-284515); Granvin, Kvanndal E, boreonemoral rich broad-leaved deciduous forest, 25 Sept. 2005, E. *Bendiksen* EB 290.05 [H154] (O-167560); Møre og Romsdal, Alesund, Magerholm, under *Corylus*, 8 Oct. 2006, P.G. *Larsen* [H237] (O-360894); Møre og Romsdal, Stordal, Seljeneset, rich de-

ciduous forest with *Corylus*, *Betula* and *Populus*, 18 Sept. 2005, P.G. Larsen [H145] (O-203499); Møre og Romsdal, Sykkylven, Klungregylet, rich soil in hazel wood, 18 Sept. 2001, D. Holtan [H130] (O-171669); Møre og Romsdal, Midsund, Otrøya, Trelvika, in SW exposed *Corylus* forest, 10 Sept. 2003, J.B. Jordal [H144] (O-178718). – SWEDEN, Halland, Laholm, Hallandsåsen N, on soil in beech forest, 16 Sept. 2009, C.C. Mellberg [H064] (O-253363 epitype).

Notes — We have adopted the name *H. panormitana* for this species of the *elastica* clade (clade E). The species was originally described from Sicilia, Italy, by Inzenga (1865), but was later referred to as a synonym of *H. elastica* (Inzenga 1869). Two *rpb2*, one *hsp* and seven LSU substitutions separate the Swedish and Norwegian specimens. *Helvella panormitana* deviates from the morphologically similar *H. elastica* in five *hsp*, 11 *rpb2* and 10 LSU substitutions.

Helvella paraphysitorquata I. Arroyo & Calonge, in Calonge & Arroyo, Mycotaxon 39: 210. 1990

Holotype. SPAIN, Teruel, Albarracin, 3 June 1988, I. Arroyo & F.D. Calonge (MA-Fungi 24512). *Isotype* (C-F-45305).

Illustrations — Calonge & Arroyo (1990: f. 2), Landeros et al. (2012: f. 30).

Descriptions of the species — Calonge & Arroyo (1990: 210), Landeros et al. (2012: 54).

Specimen examined/sequenced. SPAIN, Teruel, Albarracin, 3 June 1988, I. Arroyo & F.D. Calonge [H271] (C-F-45305 isotype).

Notes — A molecularly and morphologically unique species, separated from its sister species *H. pubescens* by 11 *rpb2* and 11 *hsp* and from *H. rivularis* by eight *rpb2* and 10 *hsp* substitutions, respectively. Landeros et al. (2015) published an LSU nrDNA sequence of a specimen referred to as *H. ephippium* [JN 048874] that shows sequence similarity to *H. paraphysitorquata* (cf. Appendix 3).

Helvella pezizoides Afzel., Kongl. Vetensk. Acad. Nya Handl. 4: 308. 1783

Basionym. *Helvella pezizoides* Afzel., Kongl. Vetensk. Acad. Nya Handl. 4: 308. 1783; Fr., Syst. Mycol. 2: 20. 1822.

Synonym. *Leptopodia pezizoides* (Afzel.) Boud., Icon. Mycol., liste prélim.: 2. 1904.

Lectotype. Afzel., Kongl. Vetensk. Acad. Nya Handl. 4: t. 10, f. 2, 1783, designated by Dissing (1966b). *Epitype* designated here: SWEDEN, Halland, Halmstad, Almeberget, moist beech forest, 16 Sept. 2009, S. Lund (O-253366). MycoBank MBT375411.

Illustrations — Afzelius (1783: pl.10, f. 2), Dissing (1966b: f. 32b).

Description of the species — Dissing (1966b: 117).

Specimens examined/sequenced. DENMARK, Jutland, Oksbøl Plantage, 13 km W Varde, 27 Oct. 1968, P.M. Petersen [H418] (C-F-45301); North Jutland, Fosdalen, Vor Frues kilde, soil on slope, 6 Oct. 1997, M. Christensen & K. Hansen KH-97-96 [H431] (C-F-52986). – JAPAN, Honshu, Tochigi Prefecture, Okunikko, Kotoku Bokujo, 26 Aug. 1983, T. Schumacher J119.83 [H204] (O-253364). – NEPAL, Langtang Area, N Kyangjin, moraines of Langtang Lirung Glacier, 4000 m asl, 9 Sept. 1986, J. Poelt [H230] (C ex Herb. GZU 109.86). – NORWAY, Vestfold, Horten, Karljohansvern, 21 July 1981, P. Marstad & S. Aase [H196] (O-253365); Vestfold, Tønsberg, along road near lawn with *Quercus*, 21 July 1981, P. Marstad & R. Kristiansen [H420] (C-F-45505). – SWEDEN, Halland, Halmstad, Almeberget, moist beech forest, 16 Sept. 2009, S. Lund [H061] (O-253366 epitype); *ibid.*, [H065] (O-253367).

Notes — The excellent description by Afzelius (1783), including a lot of details about apothecial ontogeny, leaves no doubt about the identity of this small to medium-sized, brownish black species of the fallax-pezizoides lineage. *Helvella pezizoides* resembles *H. pulla* in microanatomical features; however, the hymenium is dark brownish black to black in *H. pezizoides* and

grey to greyish brown in *H. pulla*. We have selected a specimen from the collecting ground of Afzelius' in Sweden as an epitype, highlighting the original concept of *H. pezizoides*.

Helvella philonotis Dissing, Bot. Tidsskr. 60: 117. 1964 — Fig. 6d

Holotype. ICELAND, Hveragerdi, Mt Tindar, in moss in a seeping spring, 31 July 1959, M. Lange 130 (C-F-45481).

Synonyms. *Helvella dovrensis* T. Schumach., Mycotaxon 43: 34. 1992. *Holotype*. NORWAY, Oppland, Dovre, Grimsdalen, Tverrliseter, 5 Aug. 1989, T. Schumacher 54.89 (O-253305)
? *H. queletii* Bres. var. *alpina* R. Heim & L. Rémy, Bull. Soc. Mycol. France 48: 53. 1932.

Misapplied names

– *Helvella alpestris* sensu Häffner, Beih. Z. Mykol. 7: 60. 1987.
– *Helvella corium* forma *alpestris* sensu J. Favre, Ergebn. Wiss. Untersuch. Schweiz. Nationalparkes 5, 33: 27. 1955.

Illustrations — Dissing (1964: f. 8), Schumacher & Mohn Jensen (1992: 19, as *H. dovrensis*).

Descriptions of the species — Dissing (1964: 117; 1966b: 112), Schumacher (1992: 34, as *H. dovrensis*), Schumacher & Mohn Jensen (1992: 19, as *H. dovrensis*).

Specimens examined/sequenced. AUSTRIA, Tirol, Obergurgl, Rotmoostal, 2300–2460 m asl, 19 Aug. 1990, T. Schumacher [H475] (O-253290); *ibid.*, 23 Aug. 1990, T. Schumacher [H381] (O-253289). – FRANCE, Savoie, Les Vallions, Vanoise National Park, 2600 m asl, on calcareous soil, 28 Aug. 1992, T. Schumacher F 28.92 [H220] (O-253293); Savoie, Val d'Isère, Gorges du Mal, on river terraces, 31 Aug. 1992, T. Schumacher F 75.92 [H214] (O253291); *ibid.*, F 82.92 [H218] (O-253292). – ICELAND, Hveragerdi, Mt Tindar, in moss in a seeping spring, 31 July 1959, M. Lange 130 [H492] (C-F-45481 holotype); Grøndalur, near Kloarfjell, on mosses in a seeping spring, 30 July 1959, M. Lange 90 [H272] (C-F-45486 paratype). – NORWAY, Oppland, Dovre, Grimsdalen, Tverrliseter, on sandy soil, 5 Aug. 1989, T. Schumacher G 54.89 [H193] (O-253305 holotype of *H. dovrensis*); Grimsdalen, Veslegrimsa, on river terrace, 2 Aug. 2007, T. Schumacher TS 57.07 [H038] (O-253299); *ibid.*, 8 Aug. 2009, T. Carlsen, I. Skrede, T. Schumacher TS 32.09 [H023] (O-253297); Grimsdalen, Tverrådalen, on slopes towards the river Tverråi, 7 Aug. 1989, T. Schumacher G 71.89 [H200] (O-253304); *ibid.*, 31 July 2007, T. Schumacher TS 7.07 [H037] (O-253298); Grimsdalen at Storberget, 8 Aug. 2009, T. Carlsen, I. Skrede, T. Schumacher TS 26.09 [H048] (O-253300); Grimsdalen, Buåi, in the valley at the Buåi estuary, on calcareous soil, 5 Aug. 1989, T. Schumacher G 49.89 [H198] (O); Grimsdalen, Tverrgjelet, 2 Aug. 2007, T. Schumacher TS 64.07 [H015] (O-253296); 8 Aug. 2009, T. Carlsen, I. Skrede, T. Schumacher TS 29.09 [H051] (O-253301); Grimsdalen, Grimsdalshytta, 5 Aug. 1989, T. Schumacher G 15.89 [H199] (O-253303); *ibid.*, 16 Aug. 2001, T. Schumacher [H005] (O-253294); *ibid.*, 31 July 2007, T. Schumacher TS 06.07 [H006] (O-253295). – SWITZERLAND, Graubünden, Albula Pass, N of the road near Crap Alv, 30 Aug. 1984, T. Schumacher Sch 42.84 [H361] (C-F-57376).

Notes — *Helvella philonotis* may have been described from the French Alps as a variety (var. *alpina*) of *H. queletii* (= *H. solitaria*) by Heim & Rémy (1932). There are no authentic specimens left to support this assumption (Dissing 1964, Heim in litt.). The synonymy of *H. dovrensis* with *H. philonotis* is established here based on *hsp*, *rpb2* and LSU sequence similarity of holotype specimens of the two taxa. *Helvella philonotis* differs from *H. palustris* by three *rpb2*, one *hsp* and no LSU substitutions. Although genetically uniform, the two species are easily separated based on macromorphology and ecology, i.e., in *H. philonotis* the apothecia are short-stipitate and cupulate to laterally compressed to irregular saddle-shaped with a recurved margin and with a greyish black stipe with irregular grooves and blunt ribs scarcely continuing onto the receptacle surface. The Icelandic material represents a long-stalked form of the species; in *H. palustris* the apothecia are bi- to trilobately saddle-shaped with an adnate reflexed margin and a stipe with distinct, longitudinal, parallel ribs. *Helvella philonotis* seems restricted to the arctic-alpine biome of Europe while *H. palustris*

seems confined to rich minerotrophic fens (mires) in boreal and boreo-nemoral forest biomes. The Norwegian specimens of *H. alpestris* in Landeros et al. (2012, 2015) represent *H. philo-notis*. Recent records of *H. dovrensis* from *Quercus* root tips at high altitudes in Southwest China may represent another species (Hwang et al. 2015).

Helvella phlebophora Pat. & Doass. in Pat., Tab. Analyt. Fung. Ser. 1, 5: 208. 1886

Synonyms. *Globopilea phlebophora* (Pat. & Doass.) Beauseign., Contr. Etude Fl. Mycol. Landes: 205. 1926.

Lectotype designated here: Patouillard, Tab. Analyt. Fung. Ser. 1, 5: f. 468. 1886. MycoBank MBT375707. *Epitype* designated here: ICELAND, Austur-Skaftafellsysla, Skaftafell, 20 Aug. 1981, H.F. Gøtzsche HFG 84-31 (C-F-45405 epitype). MycoBank MBT375412.

Illustrations — Dissing (1966a: f. 8b, f; 1966b: f. 30), Weber (1972: f. 34).

Descriptions of the species — Dissing (1966b: 110), Weber (1972: 182).

Specimens examined/sequenced. ICELAND, Austur-Skaftafellsysla, Skaftafell, 20 Aug. 1981, H.F. Gøtzsche HFG 84-31 [H273] (C-F-45405). — JAPAN, Honshu, Tochigi, Asegata, Chuzenjikhon, Okunikko, 22 Aug. 1983, T. Schumacher J 28.83 [H197] (O-253368).

Notes — No authentic material of this characteristic species was located by Dissing (1966b). One substitution in *rpb2* distinguishes the two collections from Japan and Iceland.

Helvella pubescens Skrede, T. Carlsen & T. Schumach., *sp. nov.* — MycoBank MB820328; *hsp* barcode GenBank KY784257; *rpb2* barcode GenBank KY772506

Etymology. From Latin 'downy with short soft hairs'; pertaining to hairy stipe and receptacle.

Holotype. CANADA, Alberta, Wagner Natural Area near Spruce Grove, on the ground under *Picea*, 6 July 1994, S.P. Abbott (FH).

Apothecia stipitate-cupulate to disc-shaped, cap 2–3.5 cm broad, 0.5–1 cm high, slightly compressed; hymenium greyish yellow (3-4B-C4-8) when fresh, drying dark yellowish brown (5F5); receptacle pale grey (B1-2), delicately pubescent; stipe slender, terete, towards base with inconspicuous grooves, pubescent, 1.5–3 cm long, 0.3–0.6 cm broad, light grey to whitish, drying greyish, densely covered by pyramidal 'warts', i.e., bundles of hyphoid hairs. *Medullary excipulum* of *textura intricata*, individual hyphae hyaline, 3–4 µm broad. *Outer excipulum* of *textura angularis*; outermost layer with cells densely packed in rows consisting of drumshaped to clubshaped cells, 15–40 µm diam, outermost cells giving rise to short-segmented hyaline, hyphoid hairs to 200 µm long, partly arranged in fascicled tufts, hairs with drum-shaped cells constricted at septae and heavily staining in CB. *Asci* pleurorhynchous, 270–290 × 13–15 µm. *Ascospores* ellipsoid, 17.0–20.8 × 10–11.8 µm. *Paraphyses* subhyaline, septate, 3–4 µm broad below, enlarged to 6–8 µm at the tips.

Specimens examined/sequenced. CANADA, Alberta, Wagner Natural Area near Spruce Grove, on the ground under *Picea*, 6 July 1994, S.P. Abbott [H121] (FH holotype). — NORWAY, Østfold, Skjeberg, Hafslundsparken, among mosses on rich soil under *Corylus*, 16 Aug. 1986, R. Kristiansen RK 45.86 [H251] (O-253369). — USA, Oregon, Benton Co., National Forest Lane CO., McKenzie District, on soil in moist ditch along road, 5 July 1991, H. Dissing Oregon 36.91 [H333] (C-56499); Oregon, Benton Co., National Forest Lane CO., MacDonald Forest, on moss grown trunk, along stream, 6 July 1991, H. Dissing Oregon 39.91 [H334] (C-56502).

Notes — Specimens of *H. pubescens* form a lineage of its own in our phylogeny. The American specimen is separated from the European (Norwegian) and Canadian specimens by

two *rpb2* and two *hsp* substitutions. A specimen from Mexico (JX 993064) referred to as *H. aff. ephippium* in Landeros et al. (2015) belongs here (cf. Appendix 3). The material from Alberta, Canada, and from Østfold, Norway, which was referred to as *H. rivularis* by Abbott & Currah (1997) also belongs here. *Helvella pubescens* may be confused with *H. scyphoides*, but the hymenium and stipe have more contrasting colours compared to the latter. Moreover, they belong in different lineages (cf. Fig. 2).

Helvella pulla Holmsk., Beata Ruris Otia Fung. Dan. 2: 49. 1799 — Fig. 9d

Basionym. *Helvella pulla* Holmsk., Beata Ruris Otia Fung. Dan. 2: 49. 1799; Fr., Syst. Mycol. 2: 20. 1822.

Synonyms. *Leptopodia pulla* (Holmsk.) Boud., Icon. Mycol., liste prélim.: 2. 1904.

Lectotype designated here: Holmsk., Beata Ruris Otia Fung. Dan. 2: t. 26. 1799. MycoBank MBT375708. *Epitype* designated here: NORWAY, Møre og Romsdal, Nesset, Eikesdalen, beneath Rangåfjellet, 26 Sept. 2008, T. Læssøe (O-69282). MycoBank MBT375413.

Helvella fuliginosa Schaeff., Fung. Bavar. Palat. Nasc. 4: 113. 1774. ('Evela')

Helvella elastica Bull. b. (forma); Fr., Syst. Mycol. 2: 21. 1822.

Lectotype designated here: Schaeff., Fung. Bavar. Palat. Nasc. 4, t. 320. 1774. ('Evela tricesima tertia'). MycoBank MBT375709.

Illustrations — Schaeffer (1774: pl. 320), Holmskjold (1799: pl. 26).

Apothecia stipitate-capitate, cap 0.5–1.5 cm broad, 0.5–1.5 cm high, saddle-shaped, bilobate and involute (reflexed) throughout development; hymenium pale grey to medium grey (C-E1), receptacle concolorous, subpubescent; stipe grey, terete or slightly compressed, subpubescent, greyish, 3–6 cm long, 0.3–0.5 cm broad, firmly attached to deeply decayed wood. *Medullary excipulum* of loosely interwoven *textura intricata*, hyphae c. 2–4 µm broad, subhyaline, intermixed with some broader, brown-walled hyphae. *Outer excipulum* of a dense *textura intricata* to *prismatica*, hyphae 5–15 µm broad, partly brown-walled, short-segmented, turning out perpendicular to receptacle surface singly or in loose bundles, outermost cells inflated and club-shaped, 15–30 × 10–20 µm, heavily staining in CB. *Asci* pleurorhynchous, 275–310 × 13–15 µm. *Ascospores* ellipsoidal, 17.6–19.0 × 10.6–12.0 µm. *Paraphyses* subhyaline, relatively broad below, 3–4 µm, gradually enlarged along upper half to 8–12 µm at the tips.

Specimens examined/sequenced. NORWAY, Møre og Romsdal, Nesset, Eikesdalen, beneath Rangåfjellet, 26 Sept. 2008, T. Læssøe [H149] (O-69282 epitype); Østfold, Moss, Jeløya, Kjelstadvik, deciduous forest, under tree trunk, 18 Sept. 2013, K. Varenius [H259] (O-253370).

Notes — We have found good reasons to resurrect Holmskjold's name for this characteristic greyish species of the fallaxpezizoides lineage. The species was thoroughly described and illustrated by Holmskjold (1799) and the name sanctioned by Fries (1822). No authentic specimen of Holmskjold's remains at the Botanical Museum in Copenhagen. We also refer *H. fuliginosa* to this species, typified with Schaeffer's original plate. *Helvella pulla* resembles *H. sublicia* in colours; however, ascocarp ontogeny and microanatomical details discriminate among the two.

Helvella queletiana Sacc. & Traverso in Sacc., Syll. Fung. 19: 850. 1910

Synonyms. *Helvella venosa* Quél., Compt. Rend. Assoc. Franc. Avancem. Sci. 9: 672. 1881, nom. illegit. (homonym).

= *Helvella phlebophora* Sacc., Syll. Fung. 8: 20. 1889, nom. illegit. (homonym).

Neotype designated here: DENMARK, Zealand, Boserup, 29 Apr. 1995, B.T. Olsen (C-F-45303). MycoBank MBT375414.

Illustration — Dissing (1966a: f. 8d–e).

Description of the species — Dissing (1966b: 95).

Specimen examined/sequenced. DENMARK, Zealand, Boserup, under *Fagus*, 29 April 1995, B. T. Olsen [H403] (C-F-45303 neotype).

Notes — *Helvella queletiana* is a spring fungus similar to *H. phlebophora* in colours and folding of the apothecium; however, there are morphological details as well as eight *rpb2* substitutions that distinguish the two species.

Helvella rivularis Dissing & Sivertsen, Bot. Tidsskr. 75: 101. 1980 — Fig. 5d

Holotype. NORWAY, Nordland, Rana, Krokstrand, Tørrbekken, 7 Sept. 1972, H. Dissing & S. Sivertsen MO 95.72 (C-F-59447).

Illustration — Dissing & Sivertsen (1980: f. 2).

Description of the species — Dissing & Sivertsen (1980: 101).

Specimens examined/sequenced. NORWAY, Nordland, Rana, Krokstrand, Tørrbekken, 7 Sept. 1972, H. Dissing & S. Sivertsen MO 95.72 [H276] (C-F-59447 holotype); *ibid.*, 7 Sept. 1975, H. Dissing & S. Sivertsen [H312] (C-F-86705); Oppland, Dovre, Grimsdalen, at Tverråi, on calcareous soil on river terraces and slopes along the river, 6 Aug. 1984, T. Schumacher & K. Østmoe D 128.84 [H368] (O-253385); *ibid.*, 25 Aug. 1996, T. Schumacher [H245] (O-253381); Grimsdalen, Veslegrimsa, on gravel on river bed, 15 Aug. 2001, T. Schumacher [H363] (O-253382); Grimsdalen, Tverrgjelbekken, on river terrace, 8 Aug. 2009, T. Carlsen, T. Schumacher & I. Skrede TS 25.09 [H025] (O-253380); Grimsdalen, Buåi, in rivulet running into Buøi, 17 Sept. 1983, T. Schumacher & K. Østmoe D 167.83 [H365] (O-253383); Buådalen, on rich, moldy soil in subalpine birch forest under *Aconitum septentrionale*, 8 Aug. 1982, T. Schumacher & K. Østmoe 149.82 [H424] (O-253386); Grimsdalen, Grimsa at Storberget, dry fen vegetation under *Salix* in subalpine birch forest, 18 Sept. 1983, T. Schumacher & K. Østmoe D 226.83 [H366] (O-253384); Nordland, Rana, Dunderland, Messingåa, 8 Sept. 1972, S. Sivertsen & H. Dissing [H319] (C-F-92124).

Notes — *Helvella rivularis* has a bicentric subalpine to alpine distribution in Norway. Records of the species from other areas and countries need to be re-assessed based on a DNA barcoding approach. Some specimens referred to as *H. rivularis* in Abbott & Currah (1997), including specimens from Canada and the lowlands of Norway, are shown here to belong elsewhere.

Helvella scyphoides Skrede, T. Carlsen & T. Schumacher, *sp. nov.* — MycoBank MB820329; *hsp* barcode GenBank KY784273; *rpb2* barcode GenBank KY772523; Fig. 5b

Etymology. From Latin ‘cup-shaped’ apothecium.

Holotype. NORWAY, Hedmark, Åmot, Kvannbekken, 30 Aug. 2002, T. Poussi (O-65348).

Apothecia regularly stipitate-cupulate, cup 1.5–3 cm broad, 1–2 cm high; hymenium greyish brown (5-6D3), drying dark brown (5-6F5-8), receptacle surface paler, drying greyish (E1), densely pubescent; stipe slender, terete, towards base with inconspicuous grooves, whitish to yellowish, 0.4–0.5 cm broad, 2–3.5 cm high, densely covered by pyramidal ‘warts’ (bundles of hyphoid hairs). *Medullary excipulum* of *textura intricata*, individual hyphae hyaline, 3–4 µm broad. *Outer excipulum* of *textura angularis* to *textura prismatica*, interspaced with broad, thick-walled hyaline hyphae; outermost layer with cells densely packed in rows, cells 15–30 µm diam, outermost cells giving rise to short-segmented hyaline, hyphoid hairs, 100–150 µm long, consisting of drum-shaped to club-shaped cells, partly arranged in fascicled tufts, heavily staining in CB. *Asci* pleuro-rhynchous, 270–295 × 13–15 µm. *Ascospores* ellipsoid, 19.8–21.6 × 11.7–12.8 µm. *Paraphyses* subhyaline to light brown, 3–4 µm broad below, septate, enlarged to 6–8 µm at the clavate tips.

Specimen examined/sequenced. NORWAY, Hedmark, Åmot, Kvannbekken, 30 Aug. 2002, T. Poussi [H140] (O-65348 holotype).

Notes — This new species, recorded on the basis of a single specimen from Norway, forms a distinct lineage in our phylogeny. *Helvella scyphoides* resembles the sister species *H. hypocrateriformis* in shape and colour, but the stipe is longer and stipe and receptacle more densely pubescent. Five *rpb2* and six *hsp* substitutions distinguish *H. scyphoides* and *H. hypocrateriformis*. A specimen from Estonia, recorded as *H. aff. cupuliformis* in Landeros et al. (2015), is concluded to belong here based on the published LSU nrDNA sequence (cf. Appendix 3).

Helvella semiobruta Donadini & Berthet, Bull. Soc. Mycol. France 91: 555. 1975

Holotype. FRANCE, Rhone, D’Aubagne, 15 Dec. 1972, J.C. Donadini (LY P.B. 949). *Isotype.* (C-F-45507).

Illustrations — Donadini & Berthet (1975: f. 1–8).

Description of the species — Donadini & Berthet (1975: 553).

Specimens examined/sequenced. FRANCE, Rhone, D’Aubagne, 15 Dec. 1972, J.C. Donadini [H277] (C-F-45507 isotype). — SPAIN, Valdepenas, Ciudad Real, 25 Mar. 1975, F. Calonge [H307] (C-F-45467).

Notes — This Mediterranean species has a convex cap and a short greyish stipe with a few longitudinal blunt ridges and grooves. It is nested with *H. helvellula* and *H. juniperi* in a highly divergent lineage of the lacunosa clade (clade C).

Helvella silvicola (Beck) Harmaja, Karstenia 14: 103. 1974

Basionym. *Otidea silvicola* Beck, in Sacc., Syll. Fung. 8: 97. 1889.

Synonyms. *Wynnella silvicola* (Beck) Nannf., Ann. Bot. Fenn. 3: 309. 1966.

Peziza atrofusca Beck, Fl. Hernstein: 131. 1884, nom. illeg. (homonym). *Otidea atrofusca* Beck ex Rehm, in Winter, Rabenh. Krypt.-Fl., ed. 2, 1.3 (lief 43): 1027. 1894, nom. inval. (Art. 36.1(c)).

Wynnea atrofusca R. Heim, Bull. Soc. Mycol. France 41: 442. 1926 (‘1925’), nom. illeg. (Art. 52.1).

Wynnella atrofusca Svrček, Česka Mykol. 17: 45. 1963, nom. illeg. (Art. 52.1).

Holotype. AUSTRIA, Niederösterreich, Schwarza, in silvis abietinis, June 1883, Beck (PRC-1372 ex Herb. Beck (‘*Peziza atrofusca* n. sp.’), not examined.

Otidea neglecta Masee, Grevillea 22: 66. 1894.

Misapplied name

– *Wynnella auricula* (Schaeff.) Boud. sensu Boud., Icon. Mycol., liste prélim.: 2. 1904.

Illustrations — Boudier (1905–1910: pl. 250, as *Wynnella auricula*), Svrček (1963: pl. 48), Van Vooren (2013: photos).

Descriptions of the species — Boudier (1905–1910, vol. 4: 134, as *Wynnella auricula*), Parslow & Spooner (2009: 102), Van Vooren (2013: 172).

Specimens examined/sequenced. KIRGHISIA, Tianshan Interior, Montes Naryntau, 22 July 1967, A. Raitviir [H281] (C-F-60841). — SWITZERLAND, Graubünden, Las Paluda, on the ground under *Pinus*, 1750 m asl, 29 Aug. 1984, H. Dissing [H489] (O); Graubünden, Mota Jüda, Val Plavna, along path, 1600 m asl, 30 Aug. 1979, E. Horak & H. Dissing [H283] (C-F-56847); Graubünden, along the river E of Suras, Mats da Nossa Donna, 31 Aug. 1984, H. Dissing [H282] (C-F-57385).

Notes — The species has previously been accommodated in the genus *Wynnella*, which, except for the ear-shaped apothecium, is morphologically similar to *Helvella*. Dissing (1972) concluded that the ear-shape and the horny consistency of the dried apothecium were the only differences to separate *Wynnella* from *Helvella*. Previous data also suggested a grouping

of *Wynnella* with *Helvella* (O'Donnell et al. 1997, Landvik et al. 1999). *Wynnella* occupies an isolated position outside the rest of the helvellas in our phylogenetic trees, which may support its generic status within the *Helvellaceae*.

Helvella solitaria P. Karst., Bidrag Kannedom Finlands Natur Folk 19: 37. 1871 — Fig. 3b

Synonyms. *Peziza solitaria* P. Karst., Not. Salsk. Fauna Fl. Fenn. Forh. 10: 111. 1869, nom. illeg. (homonym).

Lachnea solitaria (P. Karst.) Bizz. & Sacc., Mycoth. Veneta no. 323. 1876.

Holotype. FINLAND. Mustiala, in horto ad marg. Rivula, 21 Sept. 1866, P. Karsten PAK 3288 (H), not examined. *Epitype* designated here: SWEDEN, Uppland, Uppsala, Stadsskogen, W of Skogshall, 13 July 1942, R. Gustafsson & S. Lundell (C-Fungi Exs. Suec. 3267 '*Helvella queletii* Bres.'). MycoBank MBT375415.

Helvella queletii Bres., Rev. Mycol. 4: 211. 1882.

Acetabula queletii (Bres.) Benedix, Kulturpfl. 10: 365. 1962.

Holotype. ITALY, Boses di lance sopra Terzolaj, May 1882, Bresadola (S), not examined.

Helvella ulvinenii Harmaja, Karstenia 19: 42. 1979, fide Landeros et al. (2015).

Illustrations — Dissing (1964: f. 9, 1966b: f. 18), Dissing & Nannfeldt (1966: pl. 2, 2), Weber (1972: f. 27–28), Harmaja (1977a: f. 1, 1979: f. 8, as *H. ulvinenii*), Schumacher & Mohn Jenssen (1992: 21).

Descriptions of the species — Dissing (1964: 118, 1966b: 73), Weber (1972: 169), Harmaja (1979: 42), Schumacher & Mohn Jenssen (1992: 21).

Specimens examined/sequenced. CANADA, Alberta, Gregoire Lake, Provincial Park near Fort McMurray, on the ground at roadside under *Populus tremuloides*, 26 July 1996, S.P. Abbott [H122] (FH). — FRANCE, Savoie, Gorge du Mal, 2400 m asl, on sandy soil, 31 Aug. 1992, R. Fellner F 64.92 [H090] (O-253371). — GEORGIA, Kaukasus, Kasberghi, Gvethi valley, on sandy soil rich in herbs along trail, 2000 m asl, 13 July 1988, E. Johannessen [H252] (O-253372). — ICELAND, Sudur-Mulasysla, Hallormsstadur, Mörkin nursery and arboretum, on soil, 4 Aug. 1993, H. Knudsen [H340] (C-F-34316); Nordur-Mulasysla, Holl in Hjaltastadarthingha, on sandy soil, 5 Aug. 1993, O. Aas [H341] (C-F-34321). — NORWAY, Akershus, Nesodden, Flaskebekk, Bellevue, on grass in garden, 26 June 1987, A.E. Torkelsen 80.87 [H171] (O-129536); Oslo, Hovedøya, under detritus, 9 June 1996, L. Winter [H176] (O-58891); Oppland, Dovre, Grimsdalen, Tverråi, on silt among mosses underneath *Salix* shrubs, 7 Aug. 1989, T. Schumacher G66.89 [H080] (O-253376); *ibid.*, 16 Aug. 2001, T. Schumacher [H004] (O-253374); *ibid.*, 21 Aug. 2005, T. Schumacher [H186] (O-253377); *ibid.*, 21 Aug. 2005, T. Schumacher [H187] (O-253378); Oppland, Dovre, Grimsdalen, Storberget, 8 Aug. 2009, T. Carlsen, I. Skrede & T. Schumacher TS 15.09 [H021] (O-253375); Oppland, Lom, Høyrokampen, 1400 m asl, in *Dryas* association, 29 Aug. 1957, F.-E. Eckblad [H353] (O-129541); Hedmark, Folldal, Råtåsjøhøi, 6 Aug. 1980, on soil, E. Johannessen [H358] (O-253373); Sør-Trøndelag, Oppdal, Vårstigen to Mt Knutshø, north-western slopes in birch forest on rich, calcareous soil, 14 Aug. 1985, T. Schumacher [H215] (O-253379); *ibid.*, N. Knutshø, 14 Aug. 1987, A.-E. Torkelsen 148.87 [H174] (O-129533); Nordland, Rana, Sdr. Bjøllåvatn 20 km W of Lønsdal, on soil in *Dryas* association, 17 Aug. 1981, H. Dissing Rana 81.012 [H315] (C-F-54680); *ibid.*, Rana 81.014 [H316] (C-F-54682); *ibid.*, Rana 81.015 [H314] (C-F-54683). — RUSSIA, Lukunskij forest reserve, NE Khatanga, on silty soil with mosses on lake embankment, 23 Aug. 1993, H. Knudsen [H326] (C-F-34410). — SWEDEN, Uppland, Uppsala, Stadsskogen, W of Skogshall, on clayey soil in coniferous plantation, 13 July 1942, R. Gustafsson & S. Lundell; *ibid.*, 6 July 1948, S. Lundell & R. Morander [H370] (C-Fungi Exs. Suec. 3267 epitype). — SWITZERLAND, Graubünden, S – Charl, Val Sesvanna, 2300–2400 m asl, under *Pinus*, 31 Aug. 1984, S. Redhead [H330] (C-F-57390).

Notes — Dissing (1966b) adopted Bresadola's name (*H. queletii*) for this fungus. Harmaja (1977a) and Landeros et al. (2012), after a re-study of the holotype specimen of *Peziza solitaria*, concluded that the name *H. solitaria* was the older and correct name for this fungus. Since the holotype specimen is old and presumably cannot be critically identified by a barcode

sequence, we have selected an epitype specimen from Sweden to support the typification. The morphology and LSU nrDNA sequence of the holotype specimen of *H. ulvinenii* [JX 993085], which was examined by Landeros et al. (2012, 2015), matches *H. solitaria* in all details and represents the high altitude form of *H. solitaria* (cf. Appendix 2). This alpine morphotype has also been observed in our sample from alpine areas in Europe. A specimen from the USA designated *H. acetabulum* [KC122805], and two specimens from Spain and one from Germany recorded by Landeros et al. (2015), also belong here (cf. Appendix 2). The world-wide distributed collections of *H. solitaria* studied by us vary in only one *rpb2* character. *Helvella solitaria* is nested in an unsupported acetabulum-solitaria lineage in our phylogeny. It differs from its sister species *H. dryadophila* in 16 *rpb2*, 12 *hsp*, 14 *tef* and 35 LSU substitutions.

Helvella sublicia Holmsk., Beata Ruris Otia Fung. Dan. 2: 51. 1799 — Fig. 9e

— non *Peziza sublicia* Holmsk., Beata Ruris Otia Fung. Dan. 2: 26, pl. 10. 1799 (= *H. fibrosa* (Wallr.) Korf).

Lectotype designated here: Holmsk., Beata Ruris Otia Fung. Dan. 2: pl. 27. 1799. MycoBank MBT375710. *Epitype* designated here: DENMARK, Zealand, Sorø Sønderkov, 2 Oct. 1993, K. Hansen (C-F-39823). MycoBank MBT375416.

Synonyms. *Helvella ephippium* Lév., Ann. Sci. Nat., Bot., sér. 2, 16: 240. 1841.

Leptopodia ephippium (Lév.) Boud., Hist. Classif. Discomyc. Europe: 37. 1907.

Lectotype. Lév., Ann. Sci. Nat., Bot., sér. 2, 16, t. 15, f. 7. 1841.

?*Peziza helvelloides* Fr., Summa Veg. Scand. 2: 348. 1849, nom. illeg. (homonym).

Illustrations — Holmskjold (1799: pl. 27), Lévillé (1841: pl. 15, f. 7, as *H. ephippium*), Dissing & Lange (1967: f. 1a, 7d, as *H. ephippium*).

Descriptions of the species — Holmskjold (1799: 51), Dissing (1966b: 114, as *H. ephippium*), Dissing & Lange (1967: 355).

Specimens examined/sequenced. DENMARK, Zealand, Sorø Sønderkov, 2 Oct. 1993, K. Hansen [H417] (C-F-39823 epitype); Hareskoven, 29 Sept. 1993, K. Hansen & S.K. Sandal [H422] (C-F-39826); Møn, Klinteskoven at Nælderenden, soil in roadside, 30 Oct. 1999, K. Hansen KH-99-25 [H423] (C-F-53175). — NORWAY, Akershus, Asker, Rabben, moldy soil in deciduous forest, 2 Oct. 1994, G. Gulden 88.94 [H148] (O-70080); Bærum, Kalvøya, on calcareous soil, 28 Aug. 1988, T. Schumacher [H229] (O-253312).

Notes — *Helvella sublicia* has commonly been treated under the younger synonymous name of *H. ephippium*. Holmskjold's fungus was apparently overlooked in Fries' sanctioning works (Fries 1822, 1828, 1832), but was probably recognized later by him under the new name *Peziza helvelloides* (Fries 1849). *Helvella sublicia* differs from the other European saddle-shaped *Helvella* species in its greyish colours and pubescent receptacle surface. Dissing & Nannfeldt (1966) compared *H. sublicia* (as *H. ephippium*) with *H. fibrosa* (as *H. villosa*) and concluded they were probably closely related, a conclusion which gains no support by our molecular phylogeny (cf. Fig. 2). We observed that the *hsp* and *rpb2* sequences were identical among the Norwegian and Danish specimens.

Helvella sulcata Afzel., Kongl. Vetensk. Acad. Nya Handl. 4: 305. 1783

Basionym. *Helvella sulcata* Afzel., Kongl. Vetensk. Acad. Nya Handl. 4: 305. 1783; Fr., Syst. Mycol. 2: 15. 1822.

Lectotype designated here: Afzel., Kongl. Vetensk. Acad. Nya Handl. 4: t. 10, f. 1, 1783. MycoBank MBT375711. *Epitype* designated here: NORWAY, Oslo, Malmøykalven, in grass field on calcareous soil, 13 Oct. 2006, O. Smith & A.-S. Karlsson (O-68095). MycoBank MBT375417.

Synonyms. *Helvella monacella* Schaeff., Fung. Bavar. Palat. Nasc. 4: 106. 1774. ('*Elvela*'), nom. inval.

Helvella lacunosa Afzel. b. (forma) minor, stipites nigricante Fr., Syst. Mycol. 2: 15. 1822.

Lectotype designated here: Schaeff., Fung. Bavar. Palat. Nasc. 2: t. 162. 1763, '*Elvela decima quarta*' (= *Helvella monacella* Schaeff.). MycoBank MBT375712.

Illustration — Schaeffer (1763: pl. 162, as '*Elvela decima quarta*').

Apothecia stipitate-capitate, cap 1–4 cm broad, 3–6 cm high, saddle-shaped, bi- to trilobate, adnate, margin attached to stipe at 3–4 points; hymenium black, even or slightly wrinkled; receptacle surface greyish brown (5DE4-7), smooth, without ribs on receptacle surface; stipe 2–5 cm high, 0.5–3 cm broad, (apothecial height : stipe height = 1 : 1), naked, prominently ribbed, ribs sharp and deep, partly double-edged and anastomosing, with deep 'holes' (lacunae) inbetween, 4–6 along the circumference, almost no stipe flesh. *Medullary excipulum* of loose *textura intricata*, hyphae c. 4–5 µm broad. *Outer excipulum* of more broad-celled *textura intricata*, the hyphae turning out parallel and arranged in dense, prismatic, hyaline cell rows perpendicular to apothecial surface, cells 8–15 µm broad, outermost cells club-shaped, 10–30 × 5–15 µm, loosely arranged, dense colouring in CB. *Asci* pleurorhynchous, 290–320 × 13–16 µm. *Ascospores* broadly ellipsoid, 14.8–16.8 × 10.5–13.2 µm. *Paraphyses* straight, light brown below, increasingly brown-coloured above, 3–4 µm broad, clavately enlarged to 6.5 µm at the tips.

Specimens examined/sequenced. NORWAY, Oslo, Malmøykalven, in grass field on calcareous soil, 13 Oct. 2006, O. Smith & A.-S. Karlsson [H152] (O-68095 epitype). — SPAIN, La Rioja, Clavijo, 22 Nov. 2013, R. Martínez RM 2238 [H1027] (O-253406).

Notes — The species is apparently rare in Northern Europe, but may have been confused with *H. lacunosa* (cf. Dissing 1964, 1966b). Afzelius (1783) was uncertain whether *H. sulcata* deserved specific rank when he described *H. sulcata* and recorded seven additional species of *Helvella* from Sweden. He also regretted not having had access to Schaeffer's monumental work during his investigations (Afzelius 1783). Schaeffer's illustration (1763) and description (1774) of *Elvela monacella* appear to match *H. sulcata* in all details. As *H. monacella* was sanctioned by Fries for another fungus (Fries 1822), the name is unavailable for Afzelius' fungus. We have found good reasons to retain *H. sulcata* as a specific taxon, clearly distinguishable from *H. lacunosa* and other representatives of the *H. lacunosa* morphospecies complex in morphological and molecular details. We have selected Afzelius' original illustration as a lectotype (iconotype) and supported it with a newly collected epitype from Norway. Nine *rpb2*, five *hsp* and 15 LSU substitutions distinguish *H. sulcata* and *H. lacunosa*. A specimen from the USA named *H. lacunosa* in Nguyen et al. (2013) has identical LSU sequence [KC-122796] with our specimen of *H. sulcata* from Norway (cf. Appendix 3).

Helvella terrestris (Velen.) Landvik, Mycologia 91: 283. 1999

Basionym. *Pindara terrestris* Velen., Monogr. Discom. Bohemiae: 341. 1934.

Lectotype selected by Van Vooren (2014): CZECH REPUBLIC, Mnichovice, at the river in summer, (PRM-147368), not examined.

Illustration — Van Vooren (2014: 43).

Description of the species — Landvik et al. (1999: 283).

Specimen examined/sequenced. NORWAY, Nord-Trøndelag, Verdal, Ramsås, along rivulet with *Trichophaea* sp., 28 Aug. 1983, S. Sivertsen 83-138 [H284] (C).

Notes — This morphologically and molecularly highly diverged species was discussed in detail in Landvik et al. (1999) (cf. Fig. 2).

EXTRALIMITAL SPECIES

In addition to the 55 European *Helvella* species treated above, we discovered 27 extralimital, non-European species lineages among the sequenced specimens that are shortly commented upon.

Helvella capucinoides Peck, Bull. New York State Mus. Nat. Hist. 157: 27. 1912

Holotype. USA, Massachusetts, North River, Warren Co., 27 Sept. 1911, Peck (NYS), not examined.

Specimens examined/sequenced. USA, Michigan, Washtenaw Co., Stinchfield Woods, 13 Oct. 1968, N.J. Smith 2147 [H398] (C-F-92116); Maine, Pratt Island, W. Southport, on mossy garden soil, 21 Sept. 1997, D. Pfister [H113] (FH).

Notes — *Helvella capucinoides* may represent an available name for this American taxon. The species is apparently also known from Mexico (Landeros et al. 2015; as *H. albella* (JX 993063)). The two North American collections share identical *rpb2* and *hsp* sequences. Peck described three American species of the *H. elastica*-group, i.e., *H. gracilis* (1872), *H. adhaerens* (1902) and *H. capucinoides* (1912). These taxa were reconsidered by Dissing & Lange (1967), who merged them into their broad concept of *H. elastica*. Authentic specimens of *H. capucinoides* were illustrated in Dissing (1966b: 129, f. 35). Two *rpb2*, three *hsp* and three LSU bp characters distinguish *H. capucinoides* and *H. panormitana*.

Helvella compressa (Snyder) N.S. Weber, Beih. Nova Hedwigia 51: 35. 1975

Basionym. *Paxina compressa* Snyder, Mycologia 28: 486. 1936.

Holotype. USA, Washington, Eaton, 5 May 1934, L.C. Snyder (WTU). *Isotype* (NY), not examined.

Illustration — Weber (1975: pl. 8).

Description of the species — Weber (1975: 35).

Specimen examined/sequenced. USA, California, Fort Oro, leaf duff of deciduous wood (oak), 14 Feb. 1998, K. Richmond [H112] (FH).

Notes — The specimen in FH supplied partial sequences from *hsp*, *rpb2* and LSU. A morphologically similar but molecularly divergent species was recently reported from the American continent under this name (Landeros et al. 2015); however, the published LSU sequences [JX 993052, AY544655] are suggestive of *H. corbierei* (cf. Appendix 3).

Helvella costata Schwein., Syn. Fung. Carolinae Sup. Sec. Obs.: 88. 1822

Specimen examined/sequenced. USA, California, Berkley, off RTE24, Fish Ranch Road, 18 Feb. 1998, B. Neill [H100] (FH).

Notes — The cited specimen located in FH is tentatively referred to *H. costata*. It may eventually serve as a neotype for this American taxon. It is distinguishable from the European *H. acetabulum* by three *rpb2*, seven *hsp* and seven LSU characters. Two specimens from USA [KC 122798, KC 122799], recorded as *H. leucomelaena* in Landeros et al. (2015), belong here (cf. Appendix 3). *Helvella unicolor* sensu Abbot & Currah (1997) may represent this species as well.

Helvella crassitunicata N.S. Weber, Beih. Nova Hedwigia 51: 30. 1975

Holotype. USA, Washington, Mount Rainier, Narada Falls, 10 Aug. 1948, A.H. Smith 30052 (MICH-11561), not examined.

Illustration — Landeros et al. (2012: f. 24).

Descriptions of the species — Weber (1975: 30), Landeros et al. (2012: 47).

Specimens examined/sequenced. CANADA, British Columbia, Whistler Nat. Park, on soil in subalpine spruce forest, 13 Aug. 1994, T. Schumacher [H222] (O-253286). — USA, Washington, Pierce Co., Mount Rainier Nat. Park, Goble's Knob, 12 Oct. 1952, A.H. Smith 40875 [H299] (C-F-92106 paratype).

Notes — Landeros et al. (2012) examined the morphology of the holotype specimen in MICH. We have supplied a partial *rpb2* sequence from a paratype specimen (Smith 40875) of *H. crassitunicata* located in C.

Helvella ephippioides S. Imai, Bot. Mag. Tokyo 46: 172. 1932

Isotype. JAPAN, Hokkaido, Nopporo, Ishikari, ad terram in silvis, 7 Aug. 1927, S. Imai (UPS), not examined.

Specimen examined/sequenced. JAPAN, Honshu, Tochigi Pref., Okunikko, S Yonoko lake, 23 Aug. 1983, T. Schumacher J 71.83 [H085] (O-253267).

Notes — Among the *Helvella* collections from Japan studied by us, we discovered this morphologically and molecularly well-characterised species, which should be compared with authentic specimens of *H. ephippioides* (Imai 1932). *Helvella ephippioides* shares macromorphological and ascospore characteristics (acuminate spores) with *H. macropus* and was placed in synonymy with *H. macropus* by Dissing (1966b). We have supplied *hsp*, *tef*, *rpb2* and LSU sequences from the above cited specimen. *Helvella subfusispora* in Liu et al. (1985) should also be compared with *H. ephippioides*.

Helvella griseoalba N.S. Weber, Michigan Bot. 11: 162. 1972

Holotype. USA, Michigan, Cheboygan Co., Univ. of Michigan Biological Station, Douglas Lake, 10 June 1968, N.J. Smith (MICH), not examined.

Illustrations — Weber (1972: f. 22), Landeros et al. (2012: f. 26).

Descriptions of the species — Weber (1972: 162), Landeros et al. (2012: 49).

Specimen examined/sequenced. USA, Michigan, Washtenaw Co., Crooked Lake, 9 June 1973, under *Quercus*, C. Nimke 347 [H306] (C-F-92112).

Notes — Landeros et al. (2012) compared the type specimens of *H. costifera* and *H. griseoalba* and found several morphological features that separated the two. We have studied material of *H. griseoalba* from Washtenow Co., Michigan (9 June 1973 C. Nimke 347), determined by Nancy Smith Weber and deposited in C. This specimen deviates from *H. costifera* in five *hsp* and nine *rpb2* characters. Landeros et al. (2015) supplied an LSU sequence from the holotype of *H. griseoalba* deposited in MICH. A few European collections assigned to *H. griseoalba* in the fungarium of C have been re-examined by us and are referred to either *H. costifera*, *H. calycina* or *H. confusa*.

Helvella maculata N.S. Weber, Beih. Nova Hedwigia 51: 27. 1975

Holotype. USA, Michigan, Idaho Bonner Co., Hoodoo Mountain, 5 Oct. 1968, H.V. Smith & N.J. Smith 2124 (MICH), not examined.

Illustrations — Weber (1975: pl. 7, f. 1–2), Landeros et al. (2012: f. 29).

Description of the species — Weber (1975: 27).

Specimen examined/sequenced. USA, Alaska, at Eklutna Lake, 24 Aug. 1973, V.L. Wells & P.E. Kempton 1577 [H303] (C-F-45400).

Notes — The cited specimen forms a single specimen lineage in our phylogeny (cfr. Fig. 2).

Helvella stevensii Peck, Bull. Torrey Bot. Club. 31: 182. 1904

Synonyms. *Leptopodia stevensii* (Peck) Le Gal, Rev. Mycol. 2: 9. 1937.

Holotype. USA, Michigan, Detroit, June 1903, R.H. Stevens (NYS), not examined.

Helvella connivens Dissing & M. Lange, Mycologia 59: 351. 1967.

Holotype. USA, Michigan, Cross Village, along roadside, 21 July 1947, Brooks, Lange & A.H. Smith (MICH). *Isotype.* *ibid.*, (C-F-45350).

Illustrations — Weber (1972: f. 43–46).

Descriptions of the species — Weber (1972: 193, 1975: 35).

Specimens examined/sequenced. USA, Michigan, Cross Village, along roadside, 21 July 1947, Brooks, Lange & A.H. Smith [H297] (C-F-45350 isotype of *H. connivens*); Michigan, Cross Village area, Wycamp Lake Road, Cheboygan Co., 8 July 1969, N.J. Smith 2209 [H394] (C-F-92117).

Notes — Dissing & Lange (1967) and Dissing (2000) included North American as well as European specimens in their broad concept of *H. stevensii*. The European specimens of *H. stevensii* sensu Dissing & Lange (1967) are here referred to *H. corbierei*. Weber (1972) and Landeros et al. (2015) compared authentic material of *H. stevensii* and *H. connivens* and concluded they were the same, a disposition concurred by us.

Helvella subglabra N.S. Weber, Michigan Bot. 11: 179. 1972

Holotype. USA, Michigan, Wahtenaw Co., Stinchfield Woods, near Dexter, 13 Oct. 1968, N.J. Smith 2145 (MICH), not examined.

Illustrations — Weber (1972: f. 32–33), Landeros et al. (2012: f. 35).

Descriptions of the species — Weber (1972: 179), Landeros et al. (2012: 58).

Specimen examined/sequenced. USA, Michigan, Washtenaw Co., Pick-erel Lake, under white pine, 4 Oct. 1972, N.J. Smith [H280] (C-F-65405 topotype).

Notes — *Helvella subglabra* is nested in the fallax-pezizoides lineage. Abbott & Currah (1997) and Landeros et al. (2012) examined the holotype specimen of *H. subglabra* and placed it in synonymy with *H. pezizoides*. This is contradicted by our results. Although similar to *H. pezizoides* in shape, *H. subglabra* is greyish brown in colour and distinguished molecularly from *H. pezizoides* by three *rpb2* and two *hsp* substitutions.

Helvella vespertina N.H. Nguyen & Vellinga, Mycologia 105: 1281. 2013

Holotype. USA, California, Sonoma, Salt Point State Park, 15 Jan. 2012, T.W. Osmundson (UC-1999204), not examined.

Illustration — Nguyen et al. (2013: f. 1D–J).

Description of the species — Nguyen et al. (2013: 1281).

Specimens examined/sequenced. USA, California, San Francisco, Land's End, 4 Nov. 1981, R. Trial [H102] (FH); Maine, Washington Co., at Humbolt Research Institute, on station ground, 1 July 2000, S. LaGreca [H116] (FH).

Notes — This species of the *H. lacunosa* morphospecies complex was recently described from North America. The species has not been recorded from Europe.

***Helvella* sp. 'INDIA'**

Specimen examined/sequenced. INDIA, Udampur, Sanasar, on humid soil in *Pinus excelsa* forest, 10 Aug. 1967, K.S. Thind [H421] (C-F-45704).

Notes — This distinctive Asian specimen belongs in the *elastica* clade (clade E) (cf. Fig. 2).

***Helvella* sp. 'JAPAN 1'**

Specimen examined/sequenced. JAPAN, Honshu, Tochigi Pref., Okunikko, Chuzenjikhohan, Asegata, forest floor, 22 Aug. 1983, T. Schumacher J 35.83 [H206] (O-253388).

Notes — Morphologically, the Japanese specimen resembles *H. fibrosa*, which is the sister species to 'Japan 1' and 'Japan 2' in our molecular phylogeny.

***Helvella* sp. 'JAPAN 2'**

Specimen examined/sequenced. JAPAN, Honshu, Tochigi Pref., Okunikko, Chuzenjikhohan, 22 Aug. 1983, T. Schumacher J 33.83 [H093] (O-253389).

Notes — The specimen is morphologically similar to *H. fibrosa* from which it is distinguished by 16 *hsp* and 12 *rpb2* substitutions.

***Helvella* sp. 'JAPAN 3'**

Specimen examined/sequenced. JAPAN, Fokushima Prefecture, Tadami, Mt Asakusa, on rotten trunk of *Fagus crenulata*, 30 Oct. 1991, L. Ryvarde 30206 [H213] (O-253390).

Notes — The specimen is sister to *H. pallescens* in our phylogeny.

***Helvella* sp. 'JAPAN 4'**

Specimens examined/sequenced. JAPAN, Honshu, Tochigi Pref., Okunikko, Chuzenjikhohan, Asegata, forest floor, 25 Aug. 1983, T. Schumacher J 105.83 [H461] (O-253391); *ibid.*, T. Schumacher J 104.83 [H478] (O-253392).

Notes — This species belongs in the *H. lacunosa* morpho-species complex. It possesses a greyish black hymenium and greyish stipe when fresh. It is distinguished from its sister *H. atra* by four *hsp* and two *rpb2* substitutions.

***Helvella* sp. 'JAPAN 5'**

Specimen examined/sequenced. JAPAN, Honshu, Tochigi Pref., Okunikko, Karikami, along inlet creek S lake, 23 Aug. 1983, T. Schumacher J 70.83 [H466] (O-253393).

Notes — This specimen belongs in the *H. lacunosa* morpho-species complex. It possesses a greyish hymenium and stipe when fresh.

***Helvella* sp. 'JAPAN 6'**

Specimen examined/sequenced. JAPAN, Honshu, Tochigi Pref., Okunikko, Chuzenjikhohan, Asegata, forest floor, 25 Aug. 1983, T. Schumacher J 103.83 [H482] (O-253394).

Notes — This specimen is morphologically similar to *H. sublicia*, but clusters in another lineage, i.e., the *fallax-peizoides* lineage.

***Helvella* sp. 'PAPUA 1'**

Specimen examined/sequenced. PAPUA NEW GUINEA, Manki, W Bulolo, Morobo District, on soil in *Castanopsis* forest, 24 Apr. 1972, E. Horak [H432] (C-F-45531).

Notes — This specimen was recorded as *Helvella* sp. (aff. *H. pezizoides*?) by Dissing (1979). It differs from *H. pezizoides* in two *rpb2* and four *hsp* substitutions.

***Helvella* sp. 'PAPUA 2'**

Specimen examined/sequenced. PAPUA NEW GUINEA, Manki, W Bulolo, Morobo District, among litter under *Lithocarpus* and *Castanopsis*, 13 Oct. 1971, E. Horak [H400] (C-F-45434).

Notes — This specimen was referred to *H. lacunosa* by Dissing (1979) from which it diverges in seven *rpb2* and six *hsp* characters. The stipe is whitish.

***Helvella* sp. 'USA 1'**

Specimen examined/sequenced. USA, New York, Ithaca, Six mile creek, among leaves and soil in deciduous wood, 24 Aug. 1989, H. Dissing, Cornell 28.89 [H416] (C-F-58799).

Notes — This specimen is nested in the *fallax-peizoides* lineage. It shows morphological resemblance to *H. fallax*, but can be distinguished by a conspicuously long and narrow stipe. Five *rpb2* bp and eleven *hsp* substitutions discriminate against the latter.

***Helvella* sp. 'USA 2'**

Specimen examined/sequenced. USA, California, Yolo Co., Stebbins Reserve, Cold Canyon, in duff under *Laurus*, Jan.–Feb. 1988, D. Pfister [H103] (FH).

Notes — This specimen of the *H. lacunosa* morphospecies complex is molecularly nested in the *lacunosa* clade (clade C).

***Helvella* sp. 'USA 3'**

Specimen examined/sequenced. USA, Idaho, Bonner Co., across the river from Priest River, 29 June 1972, N.S. Weber 3629 [H376] (C-F-92118).

Notes — This specimen belongs in the *elastica* clade (clade E). It resembles *H. monachella* in morphology from which it differs in 15 *hsp* characters. We were unsuccessful in obtaining an *rpb2* sequence from this specimen.

***Helvella* sp. 'USA 4'**

Specimen examined/sequenced. USA, Massachusetts, Concord, Eastbrook, on calcareous soil, 25 June 1998, D. Pfister [H104] (FH).

Notes — Molecularly, the specimen represents an American relative of *H. pallescens*.

***Helvella* sp. 'USA 5'**

Specimen examined/sequenced. USA, Iowa, White Rock Conservancy, on soil in oak – hickory woods, 22 July 2008, R. Healy [H110] (FH).

Notes — This specimen belongs in the *corbierei-stevensii* lineage of the *elastica* clade (clade E). It differs from *Helvella* 'USA 6' in four *rpb2* and three *hsp* substitutions and from *H. levis* in three *rpb2* and one *hsp* substitutions.

***Helvella* sp. 'USA 6'**

Specimen examined/sequenced. USA, Michigan, Oakland Co., Highland State Recreation Area, Goose Pond, on dirt along path, 27 Aug. 1979, N.S. Weber 4784 [H291] (C-F-92104).

Notes — This specimen belongs in the *corbierei-stevensii* lineage of the *elastica* clade (clade E). Morphologically, the specimen resembles *H. levis* from which it is distinguished by four *hsp* and no *rpb2* substitutions. It differs from *H. stevensii* in seven *hsp* and seven *rpb2* substitutions and from *H. corbierei* in three *hsp* and four *rpb2* substitutions.

***Helvella* sp. ‘USA 7’**

Specimen examined/sequenced. USA, Michigan, Washtenaw Co., Ann Arbor, Saginaw Forest, under conifers, 11 July 1940, A.H. Smith 15183 [H377] (C-F-92119).

Notes — The above cited specimen from USA, Michigan, has been referred to as *H. sulcata* by Nancy Weber (annotation on herbarium specimen). It differs from European collections of *H. fusca* in three *rpb2* characters and five *hsp* characters, from *Helvella* ‘USA 4’ in five *rpb2* bp and five *hsp* characters, from *Helvella* ‘PAPUA 2’ in four *rpb2* and 4 *hsp* characters, and from *H. lactea* in three *rpb2* and four *hsp* characters.

***Helvella* sp. ‘USA 8’**

Specimen examined/sequenced. USA, Michigan, Luce Co., Tahquamenon Falls State Park, Upper Falls, in humus in dense mixed woods, 14 Aug. 1956, H.D. Thiers 4093 [H429] (C-F-92105).

Notes — This specimen is nested in the fallax-pezizoides lineage. It differs from its sister taxon *H. pezizoides* in seven *rpb2* and six *hsp* characters.

DISCUSSION

We discovered 83 genetically distinct species lineages based on sequence data from 432 *Helvella* specimens from Europe and some scattered localities on other continents. When we combined our molecular data with morphology and biogeography, our results suggest that there are at least 55 *Helvella* species in Europe. Our data are also suggestive of a fair number of undescribed species occurring on the American and Asian continents (Fig. 1). Formal recognition of American and Asian species is deferred, pending additional material from these regions.

Phylogenetic informative loci in Helvella

More than one molecular marker is needed in order to discriminate species when using a GCPSR approach. How many loci that are needed is widely discussed (Rokas et al. 2003, Aguilera et al. 2008, Balasundaram et al. 2015). Recent studies have shown that which molecular markers you choose to use is as important as how many (Aguilera et al. 2008, Balasundaram et al. 2015). The choice of partial sequences from a few genes with high phylogenetic informativeness can allow the construction of robust phylogenies and minimize the amount of sequences needed (Townsend 2007, Aguilera et al. 2008, Schmitt et al. 2009, Balasundaram et al. 2015). Development of new markers that are informative at different phylogenetic levels may thus be useful for inferring phylogenetic relationships and resolving species lineages.

In our study we analysed four loci, one of these – *hsp* – was not previously used for species delimitation in the *Pezizales*. However, *hsp* has proven useful at the intraspecific level in the pyrenomycete *Daldinia locata* (Johannesson et al. 2000) and in recognising cryptic species in the basidiomycete genera *Heterobasidion* and *Serpula* (Johannesson & Stenlid 2003, Kauserud et al. 2006, Balasundaram et al. 2015). The *hsp* marker was successfully amplified from most strains in our dataset, possessed high phylogenetic informativeness and was useful in delimiting species in *Helvella*. The partial *hsp* sequence amplified was only 270 bp, which may explain the success in obtaining sequences from old specimens.

The three other molecular markers (*tef*, *rpb2* and LSU) of our dataset are widely used in fungal phylogenies, inclusive of the *Pezizales*. Recently, *tef* was suggested as a secondary barcode for fungi because of its ability to resolve closely related species (Hansen & Olariaga 2015, Stielow et al. 2015). However,

while we experienced that the *tef* primers worked well on DNA extracted from fresh specimens, it usually failed to amplify DNA from even recently dried *Helvella* specimens. For this reason, *tef* was excluded from our final phylogenetic analyses, since we wanted to construct a phylogeny that contained a broad sample of taxonomically important (type) specimens of *Helvella*. *Rpb2* has also been a successful inclusion in multilocus datasets to delimitate species in genera of the *Pezizales*, e.g., in *Peziza* (Hansen et al. 2005), *Morchella* (Taskin et al. 2010, 2012, O’Donnell et al. 2011, Du et al. 2012a), *Tuber* (Bonito et al. 2013) and *Otidea* (Hansen & Olariaga 2015). This marker also worked well across the breadth of the genus *Helvella*.

In fungi the LSU marker, or parts of LSU (D1/D2 region) combined with the ITS from the nuclear ribosomal DNA, has long been used to discriminate species on its own (Kurtzman & Robnett 1998, Fell et al. 2000, Schoch et al. 2012). It has recently also been employed as the sole locus to infer phylogenies and discriminate species of *helvellas* from the American continents (Nguyen et al. 2013, Landeros et al. 2015). The LSU marker proved useful in resolving some species relationships in our study as well and had the highest phylogenetic informativeness of the markers in our dataset (Appendix 2). However, the level of LSU divergence across the inferred lineages was not homogenous compared to the *rpb2* and *hsp* data (Table 3). In the alpestris-nannfeldtii lineage the LSU diversity was very high, and the branch of *H. nannfeldtii* was exceptionally long compared to most lineages in our LSU tree. In this respect it differed from the other loci where the diversity in this lineage was comparable to the other lineages. Thus, by adding information from the diversity analyses to our understanding of the different loci we concluded that *rpb2* and *hsp* outperformed the LSU nrDNA locus in species discrimination power.

The unsuitability of ITS in isolation to infer phylogeny and delimit species in *Helvella* was already demonstrated by Landvik et al. (1999). They reported that *Helvella* differed remarkably from other molecular studies of pezizomycete genera at that time in that the ITS nrDNA region was too divergent to align across the breadth of the genus and that even the usually highly conserved *ssu* and 5.8S nrDNA gene varied among the species. Nevertheless, later studies have shown that ITS may be a useful nrDNA region to include in a multilocus dataset in smaller genera and lineages and subgroups of highly divergent pezizomycete genera as well, e.g., in *Morchella* (Taskin et al. 2010, 2012, Du et al. 2012a, b), *Otidea* (Olariaga et al. 2015), and *Helvella* (Zhao et al. 2015, 2017).

Our results add to a number of studies within the *Ascomycota* that have shown that sequence data from single copy protein-coding genes are more informative than the nuclear ribosomal DNA in resolving species (Hansen et al. 2005, Hofstetter et al. 2007, Taskin et al. 2012, Hansen & Olariaga 2015). We therefore advocate for using the combined information from single copy genes such as *hsp*, *tef* and *rpb2*, and LSU in combination, for phylogenetic and systematic studies in *Helvella*.

Inference of species and lineages in Helvella

Historically, species recognition in *Helvella*, as in most groups of *Pezizomycetes*, has relied on a morphological species concept mostly drawing on macroscopic characters of the apothecium, including the hymenium, excipulum and stipe. The shape, colours and outer surface characters of the cap and stipe have been especially important characters for the discrimination of species. The research by Dissing (1964, 1966a, b) and Dissing & Nannfeldt (1966) emphasized the importance of paraphysis pigmentation, reflected in the colour of the hymenium and concluded that in most species hymenium colour is a constant feature, e.g., in *H. crispa* and *H. lactea* the colour is always whitish,

in *H. sublicia* and *H. pulla* greyish, and in *H. corium* and *H. helvellula* blackish. According to Dissing (1966b), a larger variation in colour of the hymenium was allowed in some species ranging from pale greyish brown to brown to nearly black, e.g., in *H. solitaria* (as *H. queletii*), *H. lacunosa* and *H. elastica*. From field observations on fresh *Helvella* specimens and in working on dried fungarium samples, we observed that colours of fresh apothecia can change drastically even when specimens were gently dried. In general, we have adopted a more restricted set of colour range of hymenium and receptacle surface for some species guided by observations of fresh specimens of the pertinent species.

There are few distinctive microanatomical characters useful in species delimitation in *Helvella*. As already pointed out in the introduction, most species and species groups are described by a suite of graded characters shared by restricted or more extended groups of species. Dissing (1972) concluded that the (only) distinctive characters on species level were type of fruitbody, colour, and glabrous or pubescent outer surface of the receptacle and stipe. Except for *H. macropus*, the spores were of minor diagnostic value. We found the microanatomy of the ectal excipulum and specifically the shape, colour, and distribution of the outermost hyphoid hairs, whether fascicled or scatteredly distributed – or both – on the receptacle surface, to be of particular diagnostic value in morphologically similar groups, e.g., in the fallax-peizoides, alpestris-nannfeldtii and the alpina-corium lineages. The pigmentation and shape of the apical portion of the paraphyses also helped in species identification in some species groups, e.g., in the crispa and the alpestris-nannfeldtii lineages. As already pointed out by Häffner (1987) and Landeros et al. (2015), a major two-division of *Helvella* species is observed in the shape of the ascus base, whether aporhynchous (no crozier) or pleurorhynchous (forked, with crozier). The leucomelaena lineage has species with an aporhynchous ascus base, which is also gained or retained in the alpina-corium lineage, that separates against the rest of the helvellas with a pleurorhynchous ascus base. For a detailed discussion on micromorphological features valued and used in species discrimination of helvellas, we refer to Dissing (1966b), Eckblad (1968), Weber (1972, 1975) and Landeros et al. (2012, 2015).

Our phylogenetic analyses revealed several *Helvella* morpho-species complexes that harboured pseudocryptic variation, i.e., species that can be recognized morphologically only after molecular systematic data unveiled their existence (Knowlton 1993, 2000). For instance, the morphologically similar species pairs of *H. corium*/*H. macrosperma*, *H. lactea*/*H. pallascens* and *H. elastica*/*H. panormitana*, which were initially indiscernible due to the lack of discriminating morphological characters, could be resolved as genealogically exclusive using sequence data. Our results indicate that these species pairs are genetically divergent and located in distantly related *Helvella* lineages.

Furthermore, our study showed that in *Helvella*, DNA sequence information contributed valuable diagnostic characters and could even serve as the backbone of taxonomic descriptions for many species. Nevertheless, it is assumed that a re-evaluation of macromorphological characters such as ascocarp ontogeny and shape and colour of the apothecia based on fresh specimens of the pertinent species may reduce the number of morphologically indistinguishable species and thus support the molecularly discernible phylogenetic *Helvella* species.

In the same way as morphology is not a good predictor of phylogeny, we observed that our sequence data was sometimes insufficient to fully resolve morphologically and ecologically dissimilar species pairs, e.g., *H. juniperi* and *H. semiobruta* of the helvellula lineage, and *H. philonotis* and *H. palustris* of the

palustris-philonotis lineage. Thus, additional phylogenetically informative markers are needed to improve the resolution within these lineages.

The origin and evolution of the large and complex ascomata of *Helvella* have inspired several evolutionary hypotheses and proposals for infrageneric subdivisions of *Helvella* (Le Gal 1947, Dissing 1966b, Weber 1972, Abbott & Currah 1997, Landeros et al. 2015). These infrageneric classifications mostly rest on differences in ascocarp ontogeny and outer surface characters of receptacle and stipe in different species groups and have been reviewed recently by Landeros et al. (2015). Our phylogenies do not provide a robust framework for evaluating these morphology-based infrageneric classification schemes proposed by earlier workers, as we gave priority to include a few ribosomal and protein coding loci of short length (269–700 bp) to be successful in amplifying old as well as newly collected fungarium specimens, providing high levels of informativeness at the tips of the phylograms, at the expense of longer segments of genes necessary to develop a robust hypothesis of evolutionary relationships within the genus. To infer infrageneric groups that reflect evolutionary relationships it will be necessary to identify combinations of genes that produce a fully resolved backbone and describe a complete set of highly supported lineages within this large genus of the *Pezizomycetes*.

A few patterns worth mentioning, however, is the substipitate and externally ribbed and internally chambered or hollow inflated stipitate species groups nested in the early diverging branches of our trees, opposed to the later diverging branches, e.g., the alpestris-nannfeldtii, the alpina-corium lineages and clades C, D and E constituting species groups with cylindrical (terete), hollow or solid stipes. The hairiness of the outer receptacle surface and stipe that were given heavy weight in the infrageneric classifications proposed by Dissing (1966b), Weber (1972) and Abbott & Currah (1997), i.e., transitions from hairless to pubescent to villose apothecia, or reverse, seem to have occurred in many lineages, implying that these character states are not useful in delimiting monophyletic groups in *Helvella*.

DNA barcodes in *Helvella*

The molecular-based methods now provide an accessory approach for species identification. Once species are well established under a robust phylogenetic framework, it becomes possible to identify specimens to species by DNA barcoding of only one or a few loci. Our study repeatedly reminded us that a 100 % conclusive identification had to rely on barcode sequences in addition to morphological examination of the specimens under study.

ITS is accepted as the universal barcode for fungi by the Consortium for the Barcode of Life (Schoch et al. 2012). Using a universal barcode is advantageous, as was shown by Du et al. (2012b) in the comparably large genus *Morchella*. They determined the species identity of GenBank sequences of *Morchella* using the ITS barcode for species already delimited by a multilocus phylogeny and concluded that ITS sequences were useful in identifying 77 % of the known phylopecies and that at least 66 % of the named *Morchella* sequences in GenBank are misidentified. We assume that comparable results will be found for *Helvella*, thus it would be advantageous to provide ITS sequences for all *Helvella* species as well. ITS sequences for selected *Helvella* species have been obtained in some studies (Landvik et al. 1999, Nguyen et al. 2013, Ariyawansa et al. 2015, Landeros et al. 2015, Zhao et al. 2015, 2017). However, we only managed to amplify ITS for a few species in our initial trials. The difficulties in amplifying the ITS for some *Helvella* species when using universal primers were first documented by Weideman (1998), who found it profitable

to produce selective ITS primers to amplify targeted *Helvella* groups from ectomycorrhizal root tips.

We observed the inter- and intraspecific barcode gaps of *rpb2* and *hsp* in combination allowed for a conclusive identification of all European *Helvella* species of our sample. Nevertheless, it would be profitable also to obtain species-specific ITS sequences for barcoding purposes. Bearing in mind the difficulties in obtaining ITS amplicons for many *Helvella* species, which may possibly be caused by primer mismatch using the currently available ITS primers, it would be useful in the near future to develop *Helvella* specific ITS primers for barcoding purposes. Such primers would probably also improve the possibility of detecting *Helvella* ITS sequences from soil amplicon studies using ITS as the target sequence.

Consequently, at present we advocate using partial *rpb2* and *hsp* gene sequences, which have a high PCR and sequencing success rate, as the primary DNA barcodes to molecularly identify old and fresh specimens of *Helvella*.

Biogeography and ecology

In their overviews of European and North American *Helvella* species, Dissing (1964, 1966a, b, Dissing & Lange 1967), Weber (1972, 1975) and Abbott & Currah (1997) included samples from different regions and continents that encompass many morphologically similar but distinct phylogenetic species of *Helvella*. This implies that biogeographic and ecological hypotheses of *Helvella* spp. are problematic because most reports in the literature include specimens with misapplied binomials. The level of disjunct intercontinental distribution of species in our dataset is limited; from the many species included from Europe and North America, most are endemic to one continent (Fig. 1). However, some species were found on more than one continent, e.g., *H. alpestris*, *H. capucina* and *H. solitaria* were all found in Europe and North America, *H. phlebopora* in Greenland and East Asia, and *H. fistulosa* in Europe, North America and East Asia. Our sampling efforts have been on Europe, thus, there are too few collections from other continents to confidently draw conclusions regarding the distribution of species. Nevertheless, because of the large proportion of endemism seen from our sample we suspect that more species are to be found on other continents, as also reflected by the many new published species from, e.g., China over the last few decades (Liu et al. 1985, Liu & Cao 1988, Cao & Liu 1990, Cao et al. 1990, Zhuang 2004, Zhao et al. 2015, 2017, Wang et al. 2016). High levels of endemisms have also been demonstrated in other comparably large Pezizalean genera. In *Morchella* only two out of 18 species from Eurasia were present in both Europe and Asia (O'Donnell et al. 2011), while in *Otidea* only 6 of 29 species in Europe were also present in North America (Hansen & Olariaga 2015).

Our results show that many closely related species are sympatric throughout their range, while others are partially sympatric or allopatric. For instance, the morphologically similar parasympatrically occurring *H. corium*, *H. alpina*, *H. nannfeldtii* and *H. alpestris* occupy overlapping habitats of the alpine biome of northern Europe. Further sampling on other continents and a re-examination of herbarium collections, including DNA sequences for species identification, will be necessary to re-assess the biogeography and ecology of *Helvella* worldwide.

Molecular ecological studies have documented the presence of *Helvella* spp. as part of the mycorrhizal fungal community of a broad spectrum of trees and shrubs (Weidemann 1998, Tedersoo et al. 2006, Hwang et al. 2015). In an LSU nrDNA phylogenetic study of potential pezizalean ectomycorrhizae, Tedersoo et al. (2006) obtained four unknown ectomycorrhizal sequences nested within *Helvella*. Two newly described species

in North America, i.e., *H. vespertina* and *H. dryophila* were reported as ectomycorrhizal with gymnosperms and *Quercus*, respectively (Nguyen et al. 2013). More recently, ITS sequences representing three clades within *Helvella* were obtained from ectomycorrhizal root tips in addition to a local sample; however, members of two of the *Helvella* clades were not recovered from uncultured root tips (Hwang et al. 2015). Moreover, Hobbie et al. (2001) investigated isotopes of five *Helvella* samples that exhibited diverse levels of enrichment and depletion of γ ^{13}C and γ ^{15}N , and concluded that it was unclear whether *Helvella* has a mycorrhizal life style. We observed that some *Helvella* species are always found in close association with the same plants, e.g., *H. dryadophila* and *H. arctoalpina* with *Dryas* and *H. fusca* with *Populus*. Nevertheless, further investigation of these relationships, by sampling and sequencing ectomycorrhizal root tips, is needed to confirm ectomycorrhizal relationships among *Helvella* species.

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INDEX TO SPECIES AND VARIETIES

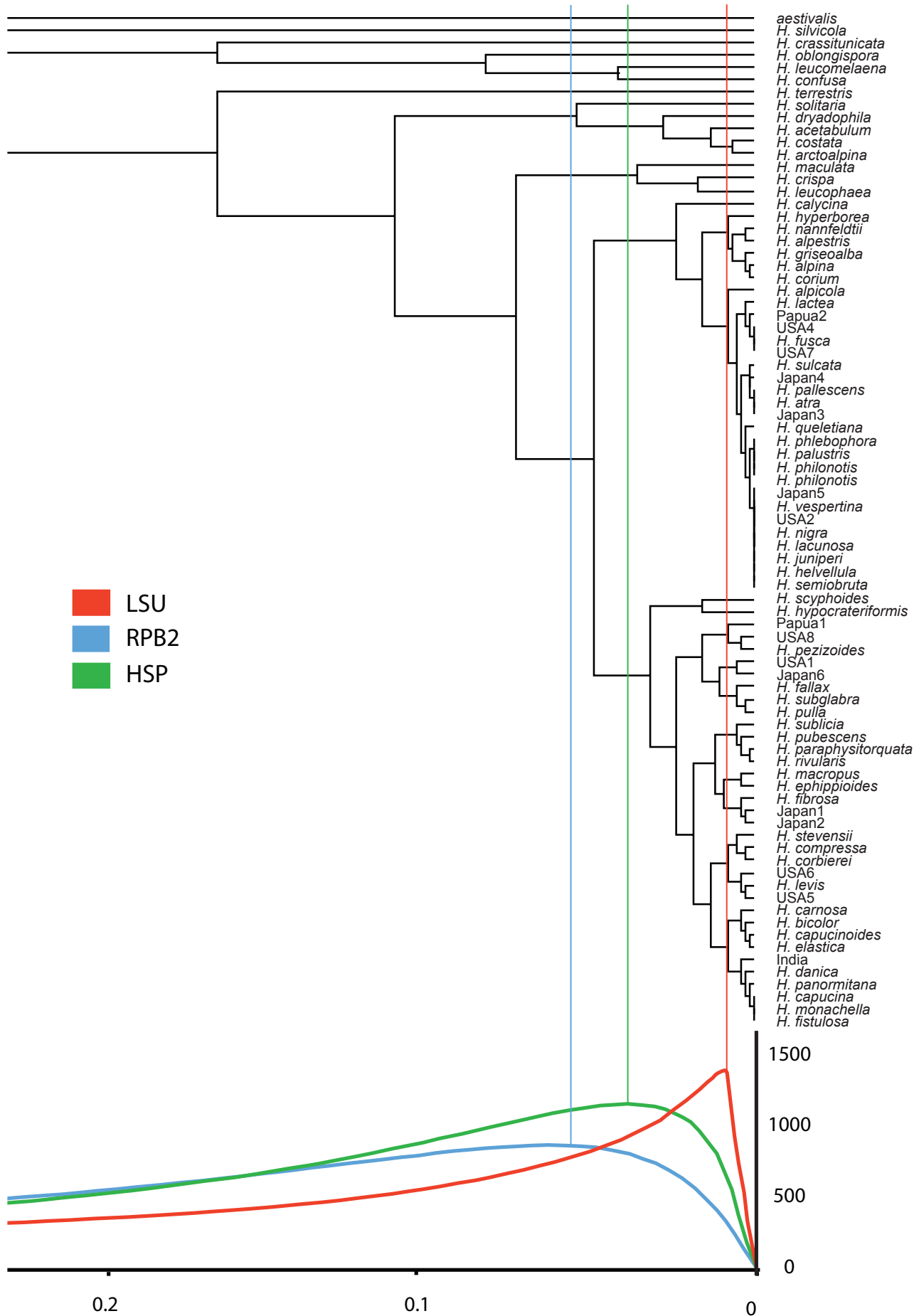
Accepted names treated in this work are in **bold-italic**. The number refers to the pagenummer.

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|--|------------------------------|---|------------------------|
| acetabulum 217 | costata 239 | juniperi 230 | pedunculata 223 |
| aestivalis 214 | costifera 224 | lactea 230 | pezizoides 235 |
| alba 225 | crassitunicata 240 | lacunosa 230 | philonotis 235 |
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| albida 225 | cupuliformis 229 | leucomelaena 231 | pithyophila 231 |
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| alpestris 217 | danica 225 | leucophaea 231 | pulchra 229 |
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| alpina 219 | dovrensis 235 | levis 231 | queletiana 236 |
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| arctoalpina 220 | ephippioides 240 | maculata 240 | scyphoides 237 |
| atra 220 | ephippium 238 | monachella 232 | semiobruta 237 |
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| calyciformis 221 | fallax 226 | nannfeldtii 233 | solitaria 238 |
| calycina 221 | fibrosa 228 | nigra 233 | stevensii 240 |
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| corbierei 224 | hyperborea 229 | panormitana 234 | vespertina 240 |
| corium 224 | hypocrateriformis 229 | paraphysitorquata 235 | villosa 228 |

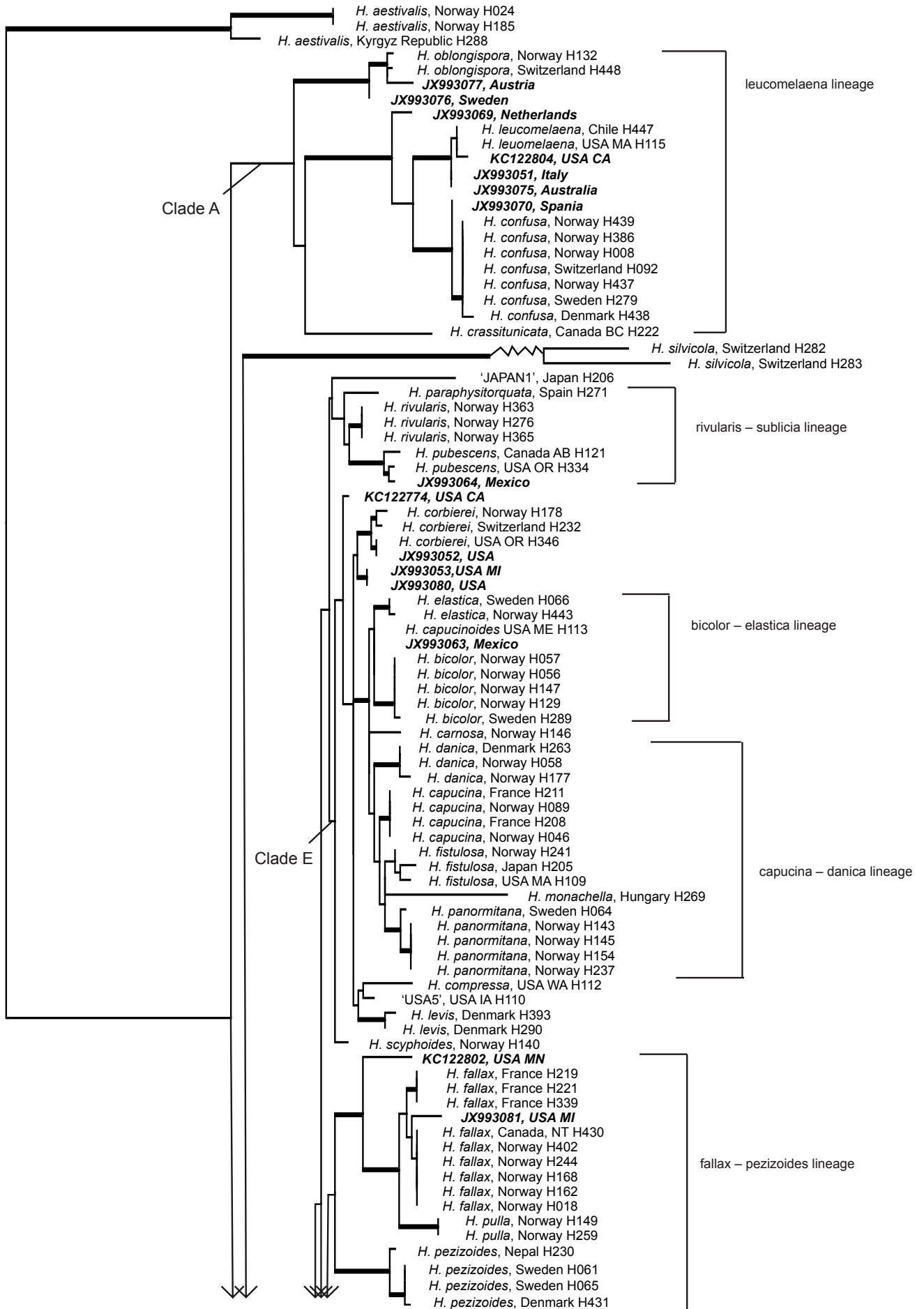
Appendix 1 Extralimital *Helvella* taxa not treated in the present synopsis. Altogether 470 *Helvella* names, representing taxa originally described as *Helvella* or later referred to or excluded from *Helvella* for taxonomic or nomenclatural reasons, are summarized in Index Fungorum (<http://www.indexfungorum.org>). In addition to the currently accepted names for the various *Helvella* species, which are to be found in Species Fungorum (<http://www.speciesfungorum.org>), the Index includes all accepted or suspected synonymous, homonymous and unpriorable names of the accepted species of *Helvella* and its former segregate genera. We have compiled a list of names suspected by us to represent synonymous or applicable names to extant *Helvella* species, but not treated in our synopsis or not yet fully accounted for in the Index Fungorum. Many of these will have to be typified and eventually re-assessed in a future monograph of the genus. * = accepted species in Species Fungorum; # = uncertain species affinity in Index Fungorum.

- **Helvella adhaerens* Peck, Ann. Rep. N. Y. State Mus. Nat. Hist. 54: 956. 1902.
Dissing 1966b: 131 = *H. elastica*.
- **Helvella aestivalis* (R. Heim & L. Rémy) Dissing & Raitv., Eesti NSV Tead. Akad. Toim. Biol. Ser. 23: 105. 1974.
- **Helvella affinis* Velen., Ceske Houby 4–5: 890. 1922.
Dissing 1966b: 64 = *H. macropus*.
- **Helvella agaricoides* Kreh, Pflz- Kräuterfreund: 205. 1922.
- Peziza amphora* Quéll., Bull. Soc. Bot. France 23: 331. 1877 '1876'.
Index Fungorum = *H. solitaria*; Dissing 1966b: 37 = *H. leucomelaena*.
- **Helvella astieri* Korf & Donadini, Rep. Tottori Mycol. Inst. 10: 397. 1973.
- **Helvella aterrima* Velen., Monogr. Discom. Bohemiae: 388. 1934.
Dissing 1966b: 102 = *H. lacunosa*.
- **Helvella bachu* Q. Zhao, Zhu L. Yang & K.D. Hyde, in Zhao Q, Sulayman M, Zhu X-t, et al., Mycologia 108: 830. 2017 '2016'.
- #*Helvella badia* Saut., Flora, Regensburg 24 (20): 319. 1841.
Sauter 1841: 319 = *H. affinis lacunosa*.
- Helvella barlae* Boud. & Pat., J. Bot., Paris 2: 445. 1888.
Index Fungorum = *H. crispa*; Dissing 1966b: 88 = *H. crispa*.
- **Helvella beatonii* (Rifai) Harmaja, Karstenia 14: 103. 1974.
- **Helvella branzeiana* Svrček & J. Moravec, Česka Mykol. 22: 87. 1968.
- #*Helvella brevipes* DC apud de Candolle & Lamarck, Fl. France, ed. 3 (Paris) 6: 28. 1815.
Dissing 1966b: 140 = *H. leucopus*.
- Helvella brevipes* Gillet, Champ. France Discomyc. 1: 11. 1879, nom. illeg. (Art. 53.1) (homonym).
- **Helvella brevis* (Peck) Harmaja, Karstenia 14: 104. 1974.
Abbott & Currah 1997: 75 = *H. macropus*.
- **Helvella brevissima* Peck, Bull. Torrey Bot. Club 30: 100. 1903.
- **Helvella bulbosa* Font Quer, Cavanillesia 3: 173. 1931.
- Helvella bulbosa* (Hedw.) Kriese, Boletus, Schr.Reihe 1: 29. 1984, nom. illeg. (Art. 53.1) (homonym)
Index fungorum = *H. macropus*.
- **Helvella chinensis* (Velen.) Nannf. & L. Holm, in Lundell, Nannfeldt & Holm, Publ. Herb. Univ. Uppsala 18: 5. 1985.
- #*Helvella cinerea* Vill., Hist. Pl. Dauphiné 3, 2: 1045. 1789.
Fries 1822: 20, 1832: 95 = *H. pulla*.
- **Helvella cinerella* Velen., Monogr. Discom. Bohemiae: 386. 1934.
Dissing 1966b: 115 = *H. ephippium*.
- #*Helvella cinereocandida* Hazsl., Ertek. Természettud. Köréb. Magyar Tud. Akad. Ertek 11 (19): 14. 1882 '1881'.
- **Paxina clypeata* (Pers.) Linder, in Polunin, Bull. Natl. Mus. Canada, Biol. Ser. 26, 97: 257. 1947.
- #*Helvella conformis* Pers., Mycol. Eur. 1: 216. 1822.
Fries 1822: 25, 1832: 95 = *Verpa patula* Fr. (?).
- **Helvella constricta* Boud., Hist. Classif. Discomyc. Europe: 36. 1907.
Dissing 1966b: 102 = *H. lacunosa*.
- Helvella cookeana* (Boud.) Sacc. & Traverso, in Sacc., Syll. Fung. 19: 844. 1910.
Index Fungorum = *H. pezizoides*; Dissing 1966b: 119 = *H. pezizoides*.
- **Helvella cornuta* Velen., Monogr. Discom. Bohemiae: 385. 1934.
- Phallus costatus* Batsch, Elench. Fung. (Halle): 129. 1783.
Index Fungorum = *H. crispa*.
- #*Helvella craterella* (Hedw.) Quéll., Enchir. Fung.: 274. 1886 ('*Helvela*')
Dissing 1966b: 64 = *H. macropus*.
- **Helvella dissingii* Korf, Mycotaxon 31: 381. 1988.
Korf 2008: 307 = *H. fibrosa*.
- **Helvella dryophila* Vellinga & N.H. Nguyen, in Nguyen NH, Landeros F, Garibay-Orijel, et al., Mycologia 105: 1278. 2013.
- **Macropodia dubaleni* (Boud.) Sacc. & Trotter, Syll. Fung. 22: 628. 1913.
Dissing 1966b: 131 = *H. elastica*.
- **Paxina dupainii* (Boud.) Seaver, North Amer. Cup-fungi (Operculates) (New York): 207. 1928.
Dissing 1966b: 75 = *H. queletii*.
- **Helvella dura* Velen., Monogr. Discom. Bohemiae: 386. 1934.
Dissing 1966b: 131 = *H. elastica*.
- **Helvella engleriana* Henn., Bot. Jahrb. Syst. 18 (4 (Beibl. 44)): 40. 1894.
- #*Helvella exarata* Gillet, Champ. France Discomyc. 1: 9. 1879.
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Notes — According to Dissing (1979) the species belongs in the *H. crispa* group. We were unsuccessful in obtaining any barcode sequences from the isotype specimen (C-F-45480) in C.

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- **Helvella solida* Velen., Monogr. Discom. Bohemiae: 387. 1934.
Dissing 1966b: 131 = *H. elastica*.
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- **Paxina subclavipes* (W. Phillips & Ellis) Seaver, North Amer. Cup-fungi (Operculates): 206. 1928.
Dissing 1966b: 64 = *H. macropus*.
- Helvella subcostata* Cooke, Mycographia 1: 90. 1879.
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- #*Helvella tabacina* Mont., Fl. Chil. 1: 396. 1854.
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Notes — In the description of *H. unicolor*, Dissing (1966a, b) reported that the species is vernal, which is in accordance with the neotype specimen selected by Dissing from France, and collected in April. Dissing's description and drawings of the species are, however, based on a specimen in F. Petraks Flora Bohemiae et Moraviae exsiccata no. 2326 (as '*Acetabula sulcata*' (Pers.) Fuckel) from Czechia, collected in September 1930. This specimen has been re-examined by us, but we were unsuccessful in obtaining any barcode sequences from this specimen. The immature specimens of Petrak's are morphologically similar to *H. costifera*. According to Dissing (1966b), *H. unicolor* is distinguished from *H. acetabulum* and *H. costifera* by excipulum anatomy and exceptionally broad spores, 17–(19.2)–21 × 13–(14.6)–16 µm. The hymenium, as well as the upper portion of the receptacle surface and ribs are cacao-brown to leather-brown (tan), gradually becoming ochreous towards the base (Dissing 1966b). These latter observations could not be reconfirmed by us and the possibility of a mix up of two morphologically similar taxa under the name *H. unicolor* seems likely. The identity of *H. unicolor*, as well as the collections referred to as *H. unicolor* by Dissing (1966a, b) and by Abbott & Currah (1997) from North America, need to be reassessed based on a molecular approach.
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Dissing 1966b: 64 = *H. macropus*.
- **Helvella vacini* Velen., Nov. Mycol. Noviss.: 156. 1947.
Dissing 1966b: 68 = *H. villosa*.
- #*Helvella venosa* Fr., Syst. Mycol. 2: 22. 1822.
- #*Helvella verpoides* Fr., Summa Veg. Scand. 2, sectio Post.: 346. 1849.
- **Helvella verruculosa* (Berk. & M.A. Curtis) Harmaja, Karstenia 18: 57. 1978.
Notes — Abbott & Currah (1997) compared the type specimens of *H. verruculosa*, *H. arctoalpina* and *H. dryadophila* and concluded they were conspecific. Later, Landeros et al. (2012) compared the holotype specimens of *H. verruculosa* and *H. dryadophila* and placed them in synonymy for the following reasons: "We did not observe chambers in the stipe and neither the ribs on the sterile surface of the apothecium. In fact, for the last reason, *H. verruculosa* can be confused with *H. solitaria* and *H. ulvinenii*, which do not have ribs on the sterile surface". The status of *H. verruculosa* needs to be re-assessed based on molecular data.
- Acetabula vulgaris* Fuckel, Jahrb. Nassauischen Vereins Naturk. 23–24: 330. 1870 '1869–1870'.
Dissing 1966b: 52 = *H. acetabulum*.
- **Helvella xinjiangensis* J.Z. Cao, L. Fan & B. Liu, Acta Mycol. Sin. 9: 186. 1990.
- **Helvella zhongtiaensis* J.Z. Cao & B. Liu, Mycologia 82: 642.

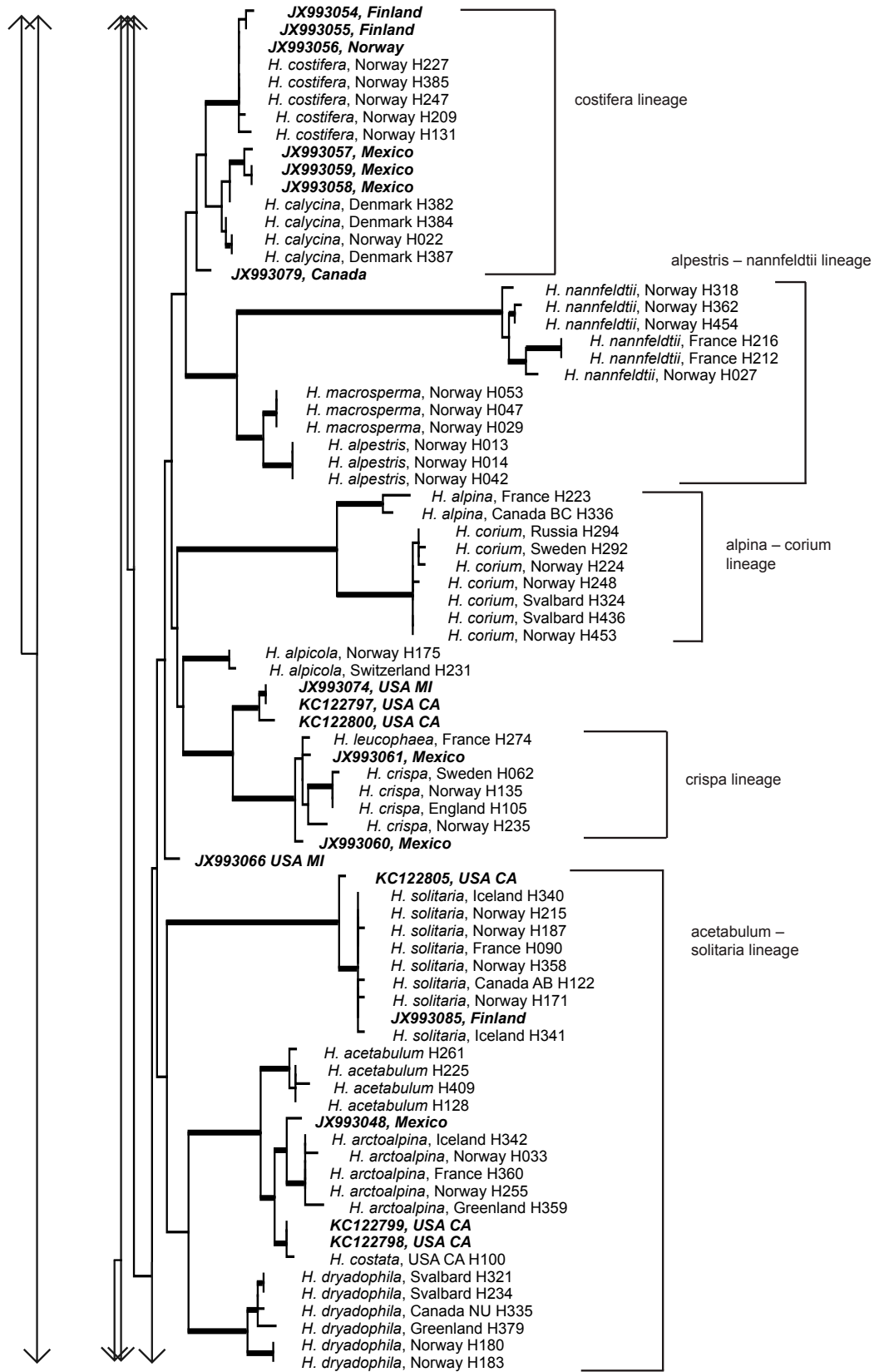


Appendix 2 Phylogenetic Informativeness graph of the three molecular markers: partial 28S large ribosomal sub unit (LSU), heat shock protein 90 (*hsp*) and RNA polymerase II (*rpb2*) based on an ultrametric tree of one individual per species.



Appendix 3 Maximum Likelihood tree of an alignment of partial 28S large ribosomal sub unit (LSU) based on specimens included in the present study, in addition to selected LSU sequences available in GenBank. Sequences downloaded from GenBank are in *italics*. Bootstrap values > 70 are indicated with **bold** branches.

Appendix 3 (cont.)



Appendix 3 (cont.)

