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Additions to the knowledge of the genus *Helvella* in Europe. New records and *de novo* description of five species from the Nordic region

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Abstract: *Helvella* is a species-rich genus, forming a large variation of astounding ascocarps in many different habitats. During the last decade, molecular markers and morphological characters have been combined to delimit and identify cryptic species in this genus. We report on a list of 54 species of *Helvella s.s.* in the Nordic region and describe five new species, *i.e. H. bresadolae*, *H. convexa*, *H. japonica*, *H. nordlandica* and *H. oroarctica*. The morphological and molecular characteristics of the new species and the emended / hypocrateriformis, / fibrosa-macropus, and / fallax-pezizoides lineages of *Helvella s.s.* are shortly commented upon. Further we include a discussion of the distribution of species in the Nordic region based on a large set of studied collections. The ecological versatility and variable geographic patterns of these species indicate that cryptic species may have contrasting ecology in their local habitats.

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INTRODUCTION

Helvella is a speciose genus of the order *Pezizales* of the *Pezizomycetes* (*Ascomycota*) that comprises a polymorphic group of larger apothecial fungi. Species of the genus range in shape from subsessile to stipitate, with a cupulate or lobed capitate apothecium, seated on a cylindrical, ribbed and/or furrowed stipe.

In a series of biosystematic studies of the genus *Helvella* in Europe, we used multiple gene genealogies, single gene sequences and morphological characters to clarify species limits and assess species-level relationships in this group of ascomycetous fungi (Skrede *et al*. 2017, 2020, Hansen *et al*. 2019, Løken *et al*. 2020). Species names and distribution maps of *Helvella* spp. in literature and on the internet reflects an outdated taxonomy that does not represent current knowledge of biodiversity and biogeography of the genus, and at best represents an underestimate of the true diversity of recognisable *Helvella* species in Europe.

The ignorance of species diversity also distorts the impression of how widespread these species are and which ecological needs they may have. Species that seem widespread may instead be species complexes of many species with very specific niches.

The current study is a follow-up of the biodiversity and biogeography of this species-rich group of fungi in the Nordic region (Skrede *et al*. 2017, Hansen *et al*. 2019, Løken *et al*. 2020), with emphasis on collections from Denmark, Norway and Sweden. We provide a list of species including information about the countries where fresh and dried specimens of the pertinent species have been barcoded and determined, followed by descriptions and phylogenetic placement of five newly described species in Norway and Sweden. We also include a discussion about the distribution patterns and possible ecological role of *Helvella* spp.

MATERIALS AND METHODS

We have investigated most collections of *Helvella* in the fungaria C, S, UPS, TRH, TROM and O. All collections we have investigated from the Nordic region and obtained a sequence from are summarised in Supplementary Table S1. As we have worked in the fungaria in Norway, Sweden and Denmark, collections from these countries are overrepresented in our data.

In order to understand the biogeographical pattern of a well-resolved species complex we made detailed maps of all collections of the *Helvella corium* species aggregate, including the species *H. corium, H. alpina, H. pseudoalpina, H. nannfeldtii, H. alpestris, H. macrosperma* and *H. alpicola* (Løken *et al*. 2020). For this group a high number of collections were available, increasing the probability that the species are collected from most of their distribution areas. Distribution maps were produced using ArcMap v. 10.8.1 (http://www.esri.com). The elevation raster was downloaded via NOAA (NOAA National Geophysical Data Center 2009; Amante & Eakins 2009) and the Arctic Circle via Natural Earth.

A subset of all collections was carefully examined morphologically, using the methodology below. Microscopic examinations of fresh specimens, when available, and from squash mounts of fresh and rehydrated (dried) specimens

mounted in water and methylene blue in lactic acid (Cotton blue) were undertaken. In addition, a selection of fresh apothecia was fixed in formalin-aceto-alcohol (5 mL formalin, 5 mL glacial acetic acid, 90 mL 70 % ethyl-alcohol pr 100 mL solution), then dehydrated in a graded butyl alcohol series, embedded in paraffin, sectioned at 8–10 µm thickness, and stained in safranin-fast-green, following the protocol of Johansen (1940). Photomicrographs were taken with a Cannon 35 mm camera mounted on a Zeiss WL microscope. Microanatomical terms follow Starbäck (1895) and Korf (1973).

For most collections we have produced at least one DNA sequence as a barcode. For new species and closely related species included in the phylogenetic analyses we have amplified and sequenced several genetic markers. For all samples we have followed the same protocols. DNA from individual specimens was extracted using the E.Z.N.A.®HP Fungal DNA Kit (Omega Biotek D3195), following the slightly modified procedure from Skrede *et al*. (2017). The three genetic markers, heat shock protein 90 (*hsp*), RNA polymerase II second largest subunit (*rpb2*) and nuclear ribosomal large subunit DNA (LSU) were amplified using PuReTaq Ready-To-Go PCR Beads (GEhealthcare, Waukesha, WI), and purified with 10 % ExoSAP-IT (GEhealthcare, Waukesha, WI). For primer sequences, detailed PCR conditions, and sequencing techniques, see the procedures in Skrede *et al*. (2017). In addition to sequences produced in the present study, sequences from a representative selection of *Helvella* species were downloaded from GenBank and included for reference. The sequences were automatically aligned using the MUSCLE v. 3.8.425 (Edgar 2004) plugin in Geneious Prime v. 2019.2.3 (Biomatters, Auckland), followed by manual inspection. Alignments of each marker are available in the Dryad data repository (https://doi.org/10.5061/dryad.h44j0zpqm).

The collection information and Genebank accession numbers of specimens included in the phylogeny are summarised in Table 1. Alignments of each marker were analysed individually by the Maximum Likelihood (ML) method implemented in RAxML v. 8.2.11 (Stamatakis 2006), using the GTRCAT approximation. A concatenated alignment was made, allowing for the inclusing of some missing data, we allowed for the inclusion of some missing data by permitting individuals lacking one or two of the markers (one individual lack *hsp*, five lack *rpb2* and 20 lack LSU). Bootstrap analyses using 1 000 pseudo-replications were included in all ML analyses. The concatenated alignment is available in Dryad data repository (https://doi.org/10.5061/dryad.h44j0zpqm). The ML analyses were the basis for species delimitation, using a simplified genealogical concordance phylogenetic species recognition (Avise & Ball 1990, Taylor *et al*. 2000, Dettman *et al*. 2003).

RESULTS

Distribution of species in Norden

Specimens collected in the Nordic region are summarised in Table2. Detailed information about origin, collection data, collector and available DNA sequences of each collection are found in Supplementary Table S1. Some species are found in many countries in the Nordic region, *e.g. Helvella acetabulum*, *H. corium* and *H. fallax* are found in Denmark, Norway, Sweden, Svalbard and Greenland, and others have a more restricted distribution, *e.g. H. semiobruta, H. retinervis and H. ephippioides* found only in Sweden, *H. queletiana* and *H. platypodia* only in Denmark and *H. macrosperma* only in Norway. This indicates that there is a large diversity in biogeographical distribution patterns in *Helvella*.

For the more detailed distribution of the *H. corium* species aggregate, it can be observed that *H. corium* has a wide distribution in both the lowland and high mountain areas (Fig. 1). This contrasts the other species of this aggregate, with alpine/arctic distributions. However, also among these, there are large variations, *e.g*. *H. nannfeldtii* is found widespread in alpine and arctic areas, while *H. alpicola* is only found in a restricted calcareous mountain area close to the arctic circle in Norway (but also recorded from a single mountain locality in Graubünden, Switzerland, see Skrede *et al*. 2017).

Phylogenetic placement of five new species from Norden

For the phylogenetic analyses, 45 individuals of the new species and their close relatives were included. A total of 19 *hsp*, 17 *rpb2* and six LSU sequences were newly produced for this study and were submitted to GenBank. All GenBank accession codes of included sequences can be found in Table 1. A concatenated 3-gene alignment of 1 361 bp, including 347 bp of *rpb2*, 294 bp of *hsp*, and 720 bp of LSU, submitted to ML analysis identified three major evolutionary lineages and a number of clades and subclades, all with a bootstrap support above 90 % (Fig. 2). Five independent clades/ subclades were discerned as new species to science. Two of these, *i.e.* the stipitate-cupulate *H. oroarctica* and *H. nordlandica*, are nested in the / hypocrateriformis lineage, where *H. oroarctica* is a sister species to *H. scyphoides*, *H. platypodia* and *H. nordlandica,* and *H. nordlandica* a sister to *H. scyphoides* and *H. platypodia*. All species of this lineage have stipitate-cupulate apothecia. Two new species with a convex (capitate) apothecium, *i.e. H. convexa* and *H. japonica,* are circumscribed and phylogenetically assembled to the / fibrosa-macropus lineage, which now consists of five species. This lineage exhibits a broad spectrum of apothecial shapes, from regularly stipitae-cupulate to bi- to tri-lobed stipitate-capitate. *Helvella convexa*, *H. macropus* and *H. ephippioides* constitute one clade, and *H. fibrosa* and *H. japonica* a sister clade. The fifth new species, *i.e. H. bresadolae,* is nested in the / fallax-pezizoides lineage, in which four stipitate-capitate European species now are accommodated in two clades: one clade with *H. pulla* and *H. fallax*, and the other with *H. pezizoides* and *H. bresadolae* (*cf*. Fig. 2).

Taxonomy

Hypocrateriformis lineage *sensu* Skrede *et al*. (2017):

Helvella nordlandica Skrede & T. Schumach., ***sp. nov.*** – MycoBank MB 848109. Fig. 3A, B.

Etymology: Pertaining to its discovery and restricted distribution in Nordland County of Norway.

Typus: **Norway**, Nordland, Rana, Store Alteren, 7 Sep. 1972, *S. Sivertsen & H. Dissing* (**holotype** C-F-102977).

Table 1. Locality, identification, type and sequence information for *Helvella* and *Dissingia* specimens included in the phylogeny in Figure 2. The ID column contains type information and sequencing and fungaria identification numbers. The columns LSU, *hsp*, *rpb2* and ITS are GenBank accession numbers. Accession numbers in italics are new accessions from this study.

Species	ID	LSU	*hsp*	*rpb2*	ITS	Locality	Coll. date	Collector – Collector ID
D. confusa	H092 (O-F-253272)	KY772960	KY784242	KY772489	–	Switzerland, Graubünden, Las Palüds	29.8.1984	H. Dissing
H. bresadolae	H990 (S-F-126512)	–	*OQ633417*	–	–	France, Nice	61.889	J.-B. Barla
	H992. (S-F-126515)	–	*OQ680208*	*OQ631109*	–	Austria, Südtyrol	1883	ex Herb. Rehm: *Helvella Bresadolae nom. prov*.
	Holotype, H1038 (TROM-F-610068)	*OQ626668*	*OQ633402*	*OQ631094*	–	Norway, Nordland, Saltdal, Junkerdalen	10.08.2016	S. Bua Løken, T. Schumacher
H. convexa	H746 (UPS-F-145717)	*OQ626669*	*OQ633414*	*OQ631107*	*OQ641537*	Sweden, Hälsingland, Gnarp	27.08.1983	C. Eriksson, J.-O. Ewimo
	Holotype, H761 (UPS-F-145677)	*OQ626670*	*OQ633415*	*OQ631108*	–	Sweden, Gästrikland, Valbo	10.08.1957	J.Ax. Nannfeldt
	H1504 (C-F-45532)	–	*OQ633406*	*OQ631100*	–	Finland, Kevo, Útsjok	20.08.1965	M. Lange
H. ephippioides	H085 (O-F-253267)	KY772957	KY784237	KY772484	–	Japan, Honshu, Tochigi	26.08.1983	T. Schumacher
	H899 (S-F-123286)	–	–	*OQ631106*	–	Sweden, Dalarna, Åsledsberget	12.08.1981	L. E. Kers
	H2297 (O-F-)	–	*OQ680209*	*OQ631110*	–	Japan, Honshu, Tochigi	25.08.1983	T. Schumacher
H. fallax	H018 (O-F-253351)	KY772913	KY784195	KY772439	–	Norway, Innlandet, Dovre	08.08.2009	T. Carlsen, I. Skrede, T. Schumacher
	H162 (O-F-280610)	KY773009	KY784292	KY772543	–	Norway, Innlandet, Løten	17.10.2006	R. Haugan
	Epitype, H339 (C-F-84621)	KY773117	KY784442	KY772693	–	France, Savoie, Bonnsval-sur-Arc	02.09.1992	E. Horak
H. fibrosa	H164 (O-F-088570)	KY773011	KY784294	KY772544	–	Norway, Viken, Bærum	28.08.1988	T. Schumacher
	H166 (O-F-185923)	KY773013	KY784296	KY772546	–	Norway, Vestfold og Telemark, Sande	12.09.1985	P. Marstad
	H167 (O-F-185919)	KY773014	KY784297	KY772547	–	Norway, Vestfold og Telemark, Tønsberg	11.09.1985	P. Marstad
H. hypocrateriformis	H275 (C-F-57126)	–	KY784390	KY772638	–	Switzerland, Graubünden, Ramosch	07.09.1982	H. Dissing
	H300 (C-F-92131)	–	KY784410	KY772659	–	Sweden, Uppland, Uppsala	30.07.1936	K. G. Ridelius
	Epitype, H301 (C-F-85205)	–	KY784411	KY772660	–	Sweden, Uppland, Uppsala	21.07.1948	R. Molander
H. japonica	**Holotype**, H093 (O-F-253389)	KY772961	KY784243	KY772490	*OQ645455*	Japan, Honshu, Tochigi	22.08.1983	T. Schumacher
	H636 (UPS-F-646633)	–	–	*OQ631104*	*OQ645456*	Sweden, Värmland, Forshaga	19.08.1992	C. Svensson
	H736 (UPS-F-145658)	–	*OQ680210*	–	–	Sweden, Umeå, Håkmark	06.09.1953	L. Hjortsberg
	H995 (S-F-126523)	*OQ626667*	*OQ633413*	*OQ631105*	–	Sweden, Södermanland, Salem	08.09.1992	K. Jaederfeld
	H2147 (O-F-93944)	–	*OQ680211*	*OQ631099*	*OQ645454*	Norway, Innlandet, Nordre Land	26.08.1998	G. Gaarder, G. Høitomt
H. macropus	H073 (O-F-253326)	KY772954	KY784233	KY772480	–	Norway, Oslo, Skullerud	03.09.2009	M. F. M. Bjorbaekmo
	H119 (FH)	KY772973	KY784255	KY772504	–	Canada, Alberta, Devon	24.08.1996	S.P. Abbott
	H165 (O-F-220225)	KY773012	KY784295	KY772545	–	Norway, Møre og Romsdal, Sunndal	11.09.2001	J.B. Jordal
H. nordlandica	**Holotype,** H1338 (C-F-102977)	–	*OQ633416*	–	–	Norway, Nordland, Rana	07.09.1972	H. Dissing, S. Sivertsen

Table 1. (Continued).

Species	ID	LSU	*hsp*	*rpb2*	ITS	Locality	Coll. date	Collector – Collector ID
	H1340 (C-F-53795)	–	*OQ633404*	*OQ631096*	–	Norway, Nordland, Rana	07.09.1972	H. Dissing
	H1341 (C-F-53798)	–	*OQ633405*	*OQ631097*	–	Norway, Nordland, Rana	07.09.1972	H. Dissing
	H2536 (TRH-09644)	*OQ626672*	*OQ633409*	*OQ631101*	–	Norway, Nordland, Saltdal	09.08.1983	U. Söchting
H. oroarctica	H1983 (TROM-F-610003)	*OQ626671*	*OQ633408*	*OQ631098*	MN656177	Norway, Troms og Finnmark, Målselv	16.08.2017	S. Bua Løken, T. Schumacher
	Holotype, H2586 (TRH-07436)	–	*OQ633411*	*OQ631103*	–	Norway, Troms og Finnmark, Storfjord	29.07.1979	S. Sivertsen
H. pezizoides	**Epitype**, H061 (O-F-253366)	KY772945	KY784225	KY772471	–	Sweden, Halland, Halmstad	16.09.2009	S. Lund
	H204 (O-F-253364)	KY773038	KY784328	KY772579	–	Japan, Honshu, Tochigi	26.08.1983	T. Schumacher
	H431 (C-F-52986)	KY773161	KY784525	KY772768	–	Denmark, N Jutland, Fossdalen	06.10.1997	M. Christensen, K. Hansen
H. platypodia	H1795 (C-F-39482)	–	MN598121	–	–	Denmark, Zealand, Lellinge	30.08.1961	L. Hansen, M. Lange, H. Dissing
	H1796 (C-F-64490)	–	MN598122	–	–	Denmark, East Jutland, Tudsedamsmosen	13.10.1981	S. A. Elborne
	Epitype, H1939 (O-F-256566)	–	MN598139	MN626790	–	Spain, Rioja, Sorzano	11.06.2013	L. Ballester
H. pulla	**Epitype**, H149 (O-F-253370)	KY772623	KY784282	–	–	Norway, Møre og Romsdal, Nesset	26.09.2008	T. Læssøe
	H259 (O-F-253370)	KY773080	KY784374	–	–	Norway, Viken, Moss	18.09.2013	K. Varenius
	H2629 (O-F-256569)	–	MN598156	MN626758	–	Spain, Rioja, Sorzano	11.06.2013	Luis Ballester
H. scyphoides	**Holotype**, H140 (O-F-65348)	KY772989	KY784273	KY772523	–	Norway, Innlandet, Åmot	30.08.2002	T. Pousi
	H1336 (C-F-102975)	–	*OQ633403*	*OQ631095*	–	Norway, Nordland, Rana	20.09.1974	S. Sivertsen
	H2545 (TRH-09321)	–	*OQ633410*	*OQ631102*	–	Norway, Trøndelag, Snåsa	12.09.1985	K. Kolaas, S. Sivertsen

Table 2. List of molecularly identified *Helvella* specimens from the Nordic countries. Total number of sequenced specimens are shown in parenthesis; number of new, fresh specimens from field work in 2015–2018 is given as (- fx).

Species	Author	Geographic origin of collections in Norden
Helvella acetabulum	(L.) Quel.	Norway (25), Denmark (8), Greenland (3), Sweden (31), Iceland (2)
Helvella alpestris	Boud.	Norway (48-f12), Greenland (7), Sweden (1)
Helvella alpicola	Skrede, T. Carlsen & T. Schumach.	Norway (14-f5)
Helvella alpina	Skrede, T. Carlsen & T. Schumach.	Norway (5-f1), Greenland (8), Sweden (1|)
Helvella arctoalpina	Harmaja	Norway (46-f3), Svalbard (4), Greenland (12), Sweden (4), Iceland (1)
Helvella atra	Oeder	Norway (41-f9), Denmark (24), Sweden (10), Iceland (1)
Helvella bicolor	Raddi	Norway (23-f2), Denmark (1), Sweden (2), Finland (1)
Helvella bresadolae	Skrede & T. Schumach.	Norway (1-f1)
Helvella calycina	Skrede, T. Carlsen & T. Schumach.	Norway (5-f1), Denmark (4), Greenland (1)
Helvella capucina	Quel.	Norway (29-f6), Greenland (2)
Helvella carnosa	Skrede, T. Carlsen & T. Schumach.	Norway (2), Sweden (7)
Helvella convexa	Skrede & T. Schumach.	Sweden (2), Finland (1)
Helvella corbierei	(Malencon) Van Vooren & Frund	Norway (10)
Helvella corium	(O. Weberb.) Massee	Norway (139-f14), Svalbard (17), Denmark (17), Greenland (38), Sweden (97), Finland (3)
Helvella costifera	Nannf.	Norway (27-f1), Denmark (7), Greenland (1), Sweden (23), Finland (1), Iceland (1)
Helvella crispa	(Scop.) Fr.	Norway (12-f1), Denmark (2), Sweden (9)
Helvella danica	Skrede, T. Carlsen & T. Schumach.	Norway (4), Denmark (16)
Helvella dryadophila	Harmaja	Norway (10-f5), Svalbard (13), Greenland (23), Sweden (3)
Helvella elastica	Bull.	Norway (7), Denmark (17), Sweden (6), Finland (2)
Helvella ephippioides	S. Imai	Sweden (1)
Helvella fallax	Quel.	Norway (73-f23), Denmark (5), Greenland (2), Sweden (16), Finland (1), Iceland (1)
Helvella fibrosa	(Wallr.) Korf	Norway (41-f2), Denmark (5), Sweden (19), Finland (2), Iceland (2)
Helvella fistulosa	Alb. & Schw.	Norway (11-f1), Iceland (3)
Helvella hyperborea	Harmaja	Norway (8), Finland (1)
Helvella hypocrateriformis	Schaeff.	Sweden (3)
Helvella japonica	Skrede, S.B. Løken & T. Schumach.	Norway (1), Sweden (3)
Helvella lactea	Boud.	Denmark (2), Sweden (3)
Helvella lacunosa	Afz.	Norway (101-f4), Svalbard (9-f6), Denmark (10), Greenland (13), Sweden (9), Iceland (10)
Helvella levis	Berg.	Norway (1), Denmark (42), Sweden (11)
Helvella macropus	(Pers.) P. Karst.	Norway (33), Denmark (6), Sweden (9), Finland (2)
Helvella macrosperma	(J. Favre) R. Fellner & Landa	Norway (9-f4)
Helvella nannfeldtii	Skrede, T. Carlsen & T. Schumach.	Norway (73-f24), Greenland (7), Sweden (7), Iceland (1)
Helvella nigra	Berg.	Denmark (27), Sweden (3)
Helvella nordlandica	Skrede & T. Schumach.	Norway (4)
Helvella oroarctica	S.B. Løken & T. Schumach.	Norway (2-f1)
Helvella pallescens	Schaeff.	Norway (5), Denmark (4), Sweden (4)
Helvella palustris	Peck	Norway (25-f4), Greenland (18), Sweden (3), Finland (2), Iceland (1)
Helvella panormitana	Inzenga	Norway (8), Denmark (13), Sweden (1)
Helvella pezizoides	Afz.	Norway (5), Denmark (5), Sweden (3)
Helvella philonotis	Dissing	Norway (32-f9), Sweden (2), Iceland (4)
Helvella phlebophora	Pat. & Doass.	Iceland (3), Norway (1)
Helvella phlebophoroides	Skrede & T. Schumach.	Denmark (16)
Helvella platypodia	(Boud.) Donadini	Denmark (3)
Helvella pseudoalpina	S.B. Løken, Skrede & T. Schumach.	Norway (7-f4), Greenland (3), Svalbard (1)

Table 2. (Continued).

Species	Author	Geographic origin of collections in Norden
Helvella pubescens	Skrede, T. Carlsen & T. Schumach.	Norway (1), Denmark (6), Sweden (1)
Helvella pulla	Holmsk.	Norway (3), Denmark (19)
Helvella queletiana	Sacc. & Trav.	Denmark (3)
Helvella retinervis	Skrede & T. Schumach.	Sweden (2)
Helvella rivularis	Dissing & Sivertsen	Norway (47-f3), Sweden (4), Finland (3), Iceland (1)
Helvella scyphoides	Skrede, T. Carlsen & T. Schumach.	Norway (10)
Helvella semiobruta	Donadini & Berthet	Sweden (1)
Helvella solitaria	P. Karst.	Norway (46-f4), Svalbard (2-f1), Denmark (3), Greenland (16), Sweden (11), Iceland (3)
Helvella sublicia	Holmsk.	Norway (4), Denmark (48), Sweden (19)
Helvella sulcata	Afz.	Norway (1), Denmark (6)
Balsamia aestivalis	(R. Heim & L. Remy) K. Hansen, Skrede & T. Schumach.	Norway (14-f1), Svalbard (8), Greenland (9), Sweden (1)
Dissingia confusa	K. Hansen & X.H. Wang	Norway (25), Denmark (6), Sweden (16)
Dissingia leucomelaena	(Pers.) K. Hansen & X.H. Wang	Norway (1), Denmark (4), Sweden (13)
Dissingia oblongispora	(Harmaja) T. Schumach. & Skrede	Norway (3), Sweden (3)

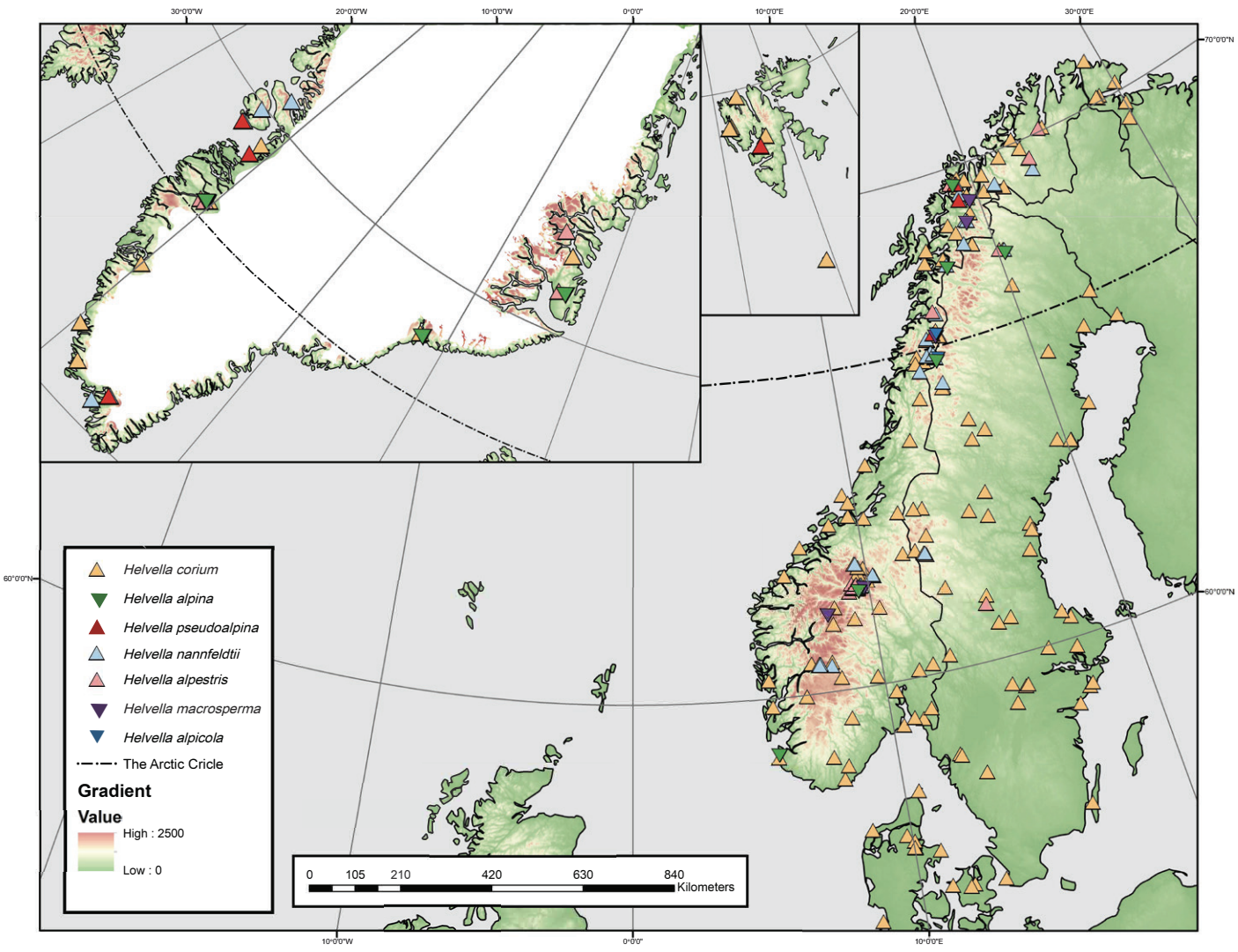

Fig. 1. Map of the distribution of the species of the *Helvella corium* species aggregate (species defined according to Løken *et al.* 2020) from Sweden, Norway, Denmark, Svalbard and Greenland based on the collections in the fungaria C, O, S, TRH, TROM and UPS.

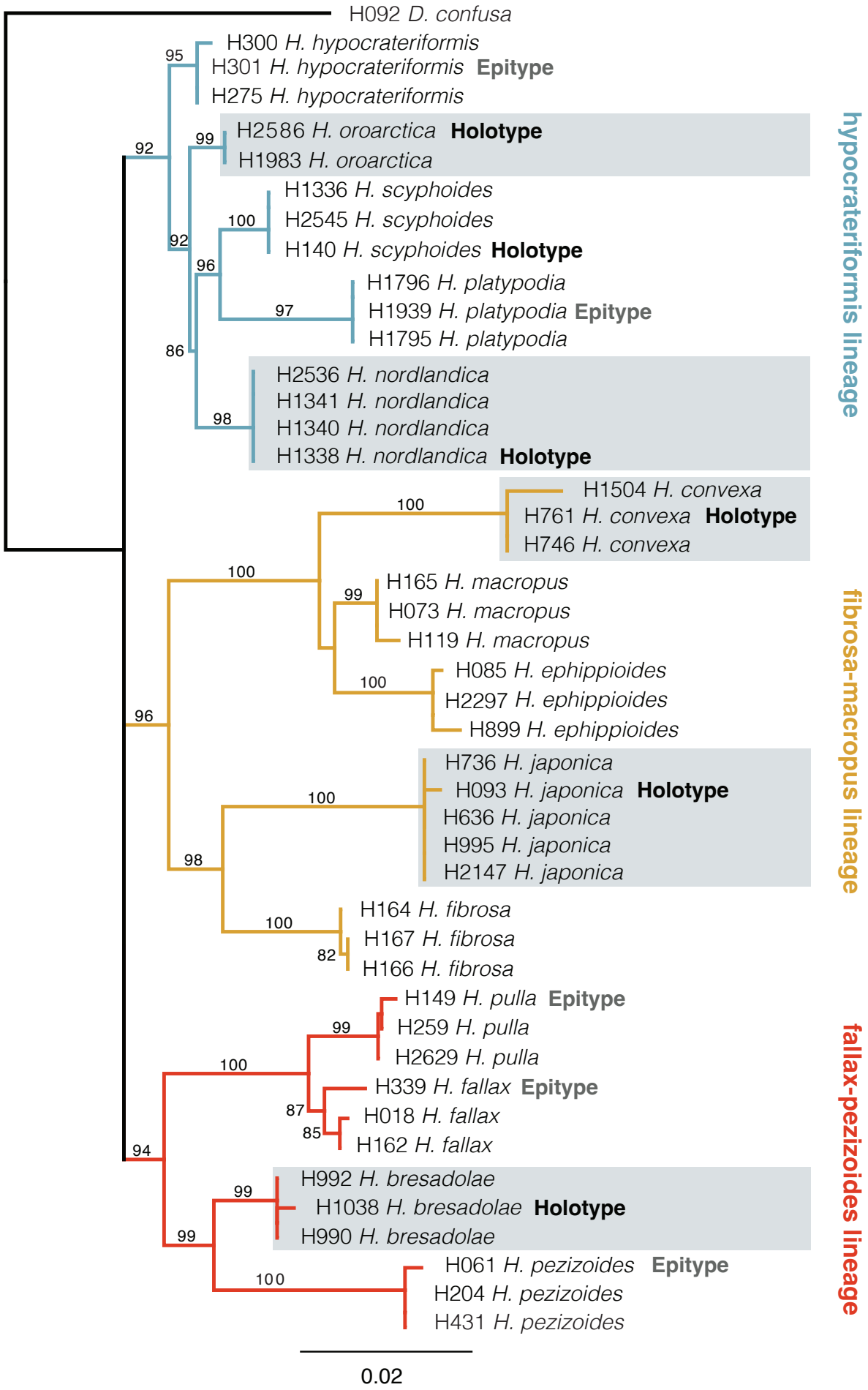

Fig. 2. Maximum likelihood tree made using the GTRCAT approximation in RAxML of new and representative species of *Helvella*. *Dissingia confusa* is used as outgroup. The tree is based on a partitioned alignment of the three molecular markers *hsp*, *rpb2* and LSU.

Fig. 3. *Helvella nordlandica*, coll. C-F-102977 – **holotype**; Norway, Nordland, Rana, Store Alteren, 7 Sep. 1972 *leg*. S. Sivertsen & H. Dissing. **A.** Dried specimens. **B.** Envelope, originally labelled *Helvella cupuliformis*.

Apothecium regularly stipitate-cupulate, 0.4–1.2 cm broad, stipe 1.5–2.6 cm tall, 0.1–0.3 cm wide; *hymenium* brown, drying dark chocolate brown; receptacle paler, greyish, densely pubescent, with conspicuous tufts of fascicled hyphae deeply staining in Cotton blue; stipe terete, solid, sub-pubescent, yellowish white along the whole length, thus contrasting the greyish receptacle and brownish hymenium above. *Medullary excipulum* of densely interwoven *textura intricata*, hyphae short-celled, 3–6 µm broad. *Outer excipulum* of *textura angularis*, single cells 10–20 µm diam, towards the outer surface drum-shaped to club-shaped, forming densely packed cell rows extending into tufts of fascicled hyphoid hairs, 70–150 µm long, by 6–12 µm broad. *Asci* pleurorhynchous, 245–270 × 13–15 µm, 8-spored. *Ascospores* ellipsoid, 16.2–16.8–17.8 × 10.5–11.2–12.2 µm, with one large internal oil drop (when mature). *Paraphyses* straight, unbranched, cell walls brownish along the whole length, 3.0–4.2 µm broad below, gradually enlarged to 6–7 µm at the clavate tips.

Specimens examined/sequenced: See Table 1.

Notes: *Helvella nordlandica* belongs in the / hypocrateriformis lineage, as delineated by Skrede *et al*. (2017). We have selected a specimen in C (ex TRH), collected and labelled *H. cupuliformis,* as the holotype specimen of this new species (Fig. 3). *Helvella nordlandica* resembles *H. scyphoides* in size, shape and colours. However, the two species are separated based on larger asci and ascospores in the latter (*cf.* Skrede *et al.* 2017).

Helvella oroarctica S.B. Løken & T. Schumach., ***sp. nov.*** MycoBank MB 848112. Fig. 4A–C.

Etymology: Refers to its preference of mountainous areas of the Arctic (oroarctic).

Typus: **Norway**, Troms, Storfjord, Stordalen at Dalheim, 29 Jul. 1979, *S. Sivertsen* (**holotype** TRH-7436).

Apothecia short-stipitate-cupulate, brownish, 0.5–1.5 cm broad, first slightly compressed with margin enrolled, then regularly cupulate, hymenium milk-chocolate brown, receptacle densely villose, brown, with conspicuous brownish tufts of hyphae forming conspicuous "warts"; stipe terete, solid, pubescent, 0.5–1.2 cm tall, 0.2–0.3 cm wide, yellowish to whitish. *Medullary excipulum* of densely interwoven *textura intricata*, hyphae short-celled, 3–7 µm broad. *Outer excipulum* of *textura globulosa-angularis*, cells brownish, 10–20 µm diam, towards surface arranged in rows forming a layer of closely packed cells that extend into dark brown-walled multicellular hyphoid hairs on the excipulum exterior, hairs 40–250 µm long, by 8–15 µm broad, outermost cells cylindrical to irregularly club-shaped, variable in shape and size, ± constricted at septa. *Asci* pleurorhynchous, 260–290 × 13–19 µm, 8-spored. *Ascospores* ellipsoid, 16.4–17.6–20.4 × 10.7–11.6–12.8 µm, with one large internal oil drop. *Paraphyses* straight, light brown in the whole length, 3.5–5.5 µm below, gradually enlarged to 8–10 µm at the subcapitate tips.

Specimens examined/sequenced: See Table 1.

Notes: *Helvella oroarctica* belongs in the / hypocrateriformis lineage, as delineated by Skrede *et al*. (2017). We have selected a specimen in TRH, collected and labelled *H. rivularis,* as the holotype specimen of this new species (Fig. 4). *Helvella oroarctica* is a short-stalked, minute, chocolate brown, densely hairy species with no similar sibling species of this lineage. Moreover, the species apparently has rather specific "demands", having so far been recorded in two localities of high mountain vegetation on calcareous ground at a distance of 8 km apart in a restricted area of Troms County in Northern Norway. Five *hsp* and two *rpb2* substitutions discriminate *H. oroarctica* from *H. hypocrateriformis*, and five *hsp* and five *rpb2* substitutions from *H. nordlandica*.

Fig. 4. *Helvella oroarctica, coll*. TRH-F-7436 – **holotype**; Norway, Troms, Storfjord, 29 Jul. 1979, *leg. & det. S. Sivertsen*. **A.** Dried specimens. **B.** Envelope, originally labelled *Helvella rivularis.* **C.** Coll. TROM-F-610003 – Norway, Troms og Finnmark, Målselv, Iselvdalen, Håkåfjell, 16 Aug. 2017, *leg*. *S. Bua Løken & T. Schumacher*, photo of fresh specimens *in situ*.

Fibrosa – macropus lineage *sensu* Skrede *et al*. (2017):

Helvella convexa Skrede & T. Schumach., ***sp. nov.*** MycoBank MB 848113. Fig. 5A, B.

Etymology: Pertaining to its convex stipitate-capitate apothecia.

Typus: **Sweden**, Gästrikland, Valbo, Lindesnäs, 10 Aug. 1957, *J.A. Nannfeldt* 153233 (**holotype** UPS-F-145677).

Illustration: Dissing (1966: fig. 32.b, as *H. pezizoides*).

Apothecia stipitate-capitate, involute, 1.0–2.0 cm broad, solitary, brownish black, with edge permanently deflexed; hymenium black, receptacle surface densely pubescent, brownish black stipe slender, terete, solid, pubescent, 3.8–6.4 cm tall, 0.3–0.7 cm wide. *Medullary excipulum* of a loosely interwoven *textura intricata*; hyphae multiseptate, light brown-walled, 3.5–5 µm broad. *Outer excipulum* of *textura angularis – globosa*, cells 15–30 µm diam, brown-walled, towards surface cells in rows turning out perpendicularly to receptacle surface, outermost cells giving rise to brown-walled, multiseptate, short-segmented hyphoid hairs in dense fascicles, hairs 60–180 µm long, individual hair cells 12–25 µm long, by 8–15 µm broad, cells constricted at septa. *Asci* pleurorhynchous, 260–295 × 10.2–13.0 µm, 8-spored. *Ascospores* ellipsoid, smooth, slightly pointed towards the poles, 17.0–19.3–20.8 × 8.4–9.0–9.6 µm, with one large internal oil drop. *Paraphyses* straight, brown-coloured along the whole length, 2.5–3.2 µm broad below, enlarged to 4–5 µm broad in upper third, clavately enlarged to 8–13 µm at the tips.

Specimens examined/sequenced: See Table 1.

Notes: *Helvella convexa* is sister species to *H. macropus* and *H. ephippioides* in our phylogeny (Fig. 2). The sequenced specimen from Gästrikland, Sweden, selected as the holotype specimen by us (Fig. 5), was photographed and identified as *H. pezizoides* by Dissing (1966: 117, fig. 32.b.). This specimen, with a long and slender stipe, is probably representative of Dissing's misconception of *H. pezizoides* when stating "*one more detail to illustrate H. pezizoides absolute precise: sometimes the stipe is longer and more slender than shown by Afzelius and Boudier"* (Dissing 1966: 119). The long and slender stipe typically accords to *H. convexa* and may probably be helpful in the field in discriminating against the look-alike species *H. pezizoides*.

Fig. 5. *Helvella convexa, coll*. UPS-F-14567 – **holotype**; Sweden, Gästrikland, Valbo, Lindesnäs, 10 Aug. 1957, *leg. J. A. Nannfeldt*. **A.** Dried specimens. **B.** Envelope, originally labelled *H. atra*, later annotated *H. pezizoides*.

Helvella japonica Skrede, S.B. Løken & T. Schumach., ***sp. nov.*** MycoBank MB 848114. Fig. 6A, B.

Etymology: Pertaining to Japan; *i.e.* the place of its first discovery by the senior author in Nikko National Park, Honshu.

Typus: **Japan**, Honshu, Tochigi Prefecture, Okunikko, Chuzenjikohan, 22 Aug. 1983, *T. Schumacher*, J33/83 (**holotype** O-F-253389).

Apothecia stipitate-capitate, saddle-shaped, at first cupulate, then expanding to bi-to tri-lobate with a recurved margin, 1.2–2.8 cm broad, hymenium brownish grey, receptacle greyish, densely pubescent to villose; stipe 3.0–10.5 cm tall, 0.35–0.60 cm wide, terete, solid, villose, concolourous with receptacle. *Medullary excipulum* of dense *textura intricata*, hyphae 3–7 µm broad. *Outer excipulum* of *textura angularis*, cells unordered (not in parallel rows), individual cells to 20–30 µm long, by 10–20 µm broad, outermost cells smaller, building tufts of hyphoid hairs to 150 µm in length. *Asci* cylindrical, with a stout base, 200–240 × 14–17 µm, 8-spored. *Ascospores* broadly ellipsoid, 16.8–18.1–19.5 × 10.3–11.0–11.8 µm, with one large internal oil drop. *Paraphyses* straight, 3–4.5 µm broad below, gradually enlarged to 6.5–8 µm at the tips.

Specimens examined/sequenced: See Table 1.

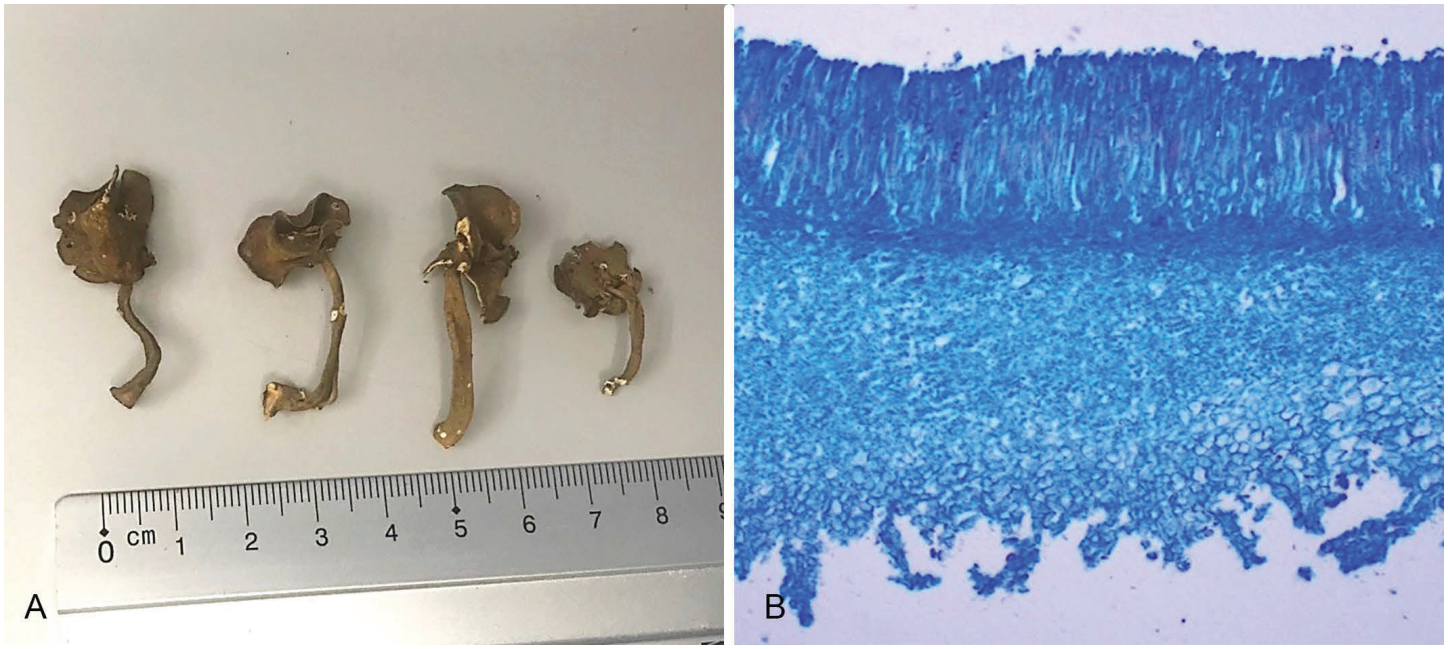

Fig. 6. *Helvella japonica*, *coll*. O-F-253389 – **holotype**; Japan, Honshu, Tochigi, Okunikko, Chuzenjikohan, 22 Aug. 1983, *leg. T. Schumacher* J33/83. **A.** Dried specimens. **B.** Vertical median section of apothecium stained in safranin – fast green.

Notes: *Helvella japonica* is sister species to *H. fibrosa* in our phylogeny (Fig. 2). The species was included as *Helvella* sp. "JAPAN 2" in Skrede *et al*. (2017). We have selected a specimen from Japan in the fungarium of Oslo as the holotype specimen (Fig. 6). Additional specimens of *H. japonica* have also turned up in recent sequenced material from Sweden and Norway. Gross morphology resembles *H. pezizoides* and *H. sublicia* of the / fallax-pezizoides and the / rivularis-sublicia lineages, respectively. The greyish brown stipitate-capitate, relatively tall and folded apothecia are characteristic features of *H. japonica.* It contrasts *H. pezizoides* which has smaller and darker (blackish) apothecia and also differ micro anatomically by larger asci, (260–300 × 12–15 µm) and smaller, narrower ascospores, (14.5–15.3–16.5 × 8.5–9.0–9.6 µm). A vertical median section of a typical apothecium of *H. japonica* and other "hairy" *Helvella* spp., is shown in Fig. 6B (coll. O-F-253389). The description of *H. pezizoides ss*. Weber (1972) reminds of the present species.

Fallax – pezizoides lineage *sensu* Skrede *et al*. (2017):

Helvella bresadolae Skrede & T. Schumach., ***sp. nov.*** MycoBank MB 848115. Fig. 7A–C.

Etymology: Pertaining to the provisional name used by Rehm after having received the Austrian specimen from its collector Giacomo Bresadola.

Typus: **Norway**, Nordland, Saltdal, Junkerdalen, 10 Aug. 2016, *S. Bua Løken & T. Schumacher* (**holotype** TROM-F-610068)

Apothecia stipitate-capitate, saddle-shaped with recurved lobes when mature, hymenium dark brownish black, receptacle naked, pale to dark greyish black, cap 1–2.8 cm broad; stipe 1.5–3.5 cm tall, 0.25–0.40 cm wide, terete, solid, concolourous with receptacle or slightly paler towards base. *Medullary excipulum* of a dense *textura intricata*, hyphae 3–5 µm broad. *Outer excipulum* of *textura angularis*, cells intermixed (not in parallel rows), outermost cells club-shaped, individual cells to 20–30 µm long, by 10–15 µm broad. *Asci* subclavate to cylindrical, with a stout base, 200–240 × 14–17 µm, 8-spored. *Ascospores* ellipsoid, 16.8–17.5–18.5 × 10.8–11.3–12.2 µm, with one large internal oil drop and several small droplets towards poles, premature ascospores occasionally with external pustules. *Paraphyses* straight, 3–4.5 µm broad below, gradually enlarged to 6.5–8 µm at the clavate tips.

Specimens examined/sequenced: See Table 1.

Notes: A newly collected fresh specimen from Nordland, Norway, is selected as the holotype specimen (Fig. 7). This collection was made in a calcareous schistose rock area in Nordland County, Northern Norway. Two old and well-preserved specimens from the Austrian and French Alps ex herb. Rehm in the fungarium of Stockholm (S) have been molecularly linked to the newly collected material from Northern Norway (see Table 1). The small-sized asci and medium-sized ascospores discriminate *H. bresadolae* from morphologically lookalike species, *e.g. H. convexa, H. pezizoides*, *H. pulla* and *H. sublicia* (*cf.* Skrede *et al.* 2017, also providing a key to the three latter species). Judging from the original label of the Austrian specimen, Rehm seemingly acknowledged its status as a new species in a letter to the collector G. Bresadola, for which he provided the provisional name *H. bresadolae* (see collection label in Fig. 7C). Later he apparently changed his opinion and referred the specimen to *H. pezizoides* Afzelius (1783), a disposition later concurred by Dissing (1966) (*cf*. label in Fig. 7C).

DISCUSSION

Although easily distinguished from other macro-fungi by apothecial shapes, it is surprisingly difficult to morphologically distinguish species of *Helvella*. Large phenotypic plasticity as a response to ecological and biogeographic features in many species, and the lack of distinctive (species-specific) microscopic characters to discriminate among them are probably the reasons for these difficulties. This led previous mycologists to adopt a rather broad morphological species concept, which has turned out to be mostly incompatible with the present-day phylogenetic species concept that is to be preferred.

Early infrageneric subdivisions of *Helvella* based solely on gross morphology, hairiness of receptacular surface and stipe, and ascocarp ontogeny (Le Gal 1947, Dissing 1966, Weber 1972, Abbott & Currah 1997) have gained little support from recent studies that use genetic markers to infer monophyletic groups as basis for classification (Landeros *et al*. 2015, Skrede *et al*. 2017, 2020, Løken *et al*. 2020). This also accords to the three infrageneric lineages of *Helvella*, *i.e.* the / hypocrateriformis, the / fibrosa – macropus and the / fallax – pezizoides lineages under study (*cf.* Fig. 2).

In a first study by Skrede *et al*. (2017), species limits and naming of 55 European (phylogenetic) species were re-assessed and a number of morphospecies aggregates phylogenetically resolved, based on a sample of 432 specimens deposited in the fungaria of C and O. Five major clades (A–E) and 18 intrinsic evolutionary lineages were phylogenetically inferred from a *hsp* and *rpb2* and LSU dataset of 55 European and 27 extra-European species of *Helvella s.l*. In the present work, we add five new species that belong in the/ hypocrateriformis, / figrosa – macropus and / fallax - pezizoides lineages of *Helvella s.l.* (Fig. 2; *cf*. Skrede *et al*. 2017, Hansen *et al*. 2019).

Two species, *i.e. H. nordlandica* and *H. oroarctica,* are phylogenetically adhered to the / hypocrateriformis lineage (Skrede *et al.* 2017), which based on additions of one new species in Skrede *et al*. (2020), *i.e. H. platypodia*, and the two new species in the present work, now encompasses five species in Europe. Species of this lineage all have stipitate-cupulate apothecia.

The two new species added to the / fibrosa – macropus lineage, *i.e. H. convexa* and *H. japonica,* expand this lineage to include a wider spectrum of apothecial shapes, from regularly stipitate-cupulate to bi- to tri-lobed stipitate-capitate. Out of the five European species now adhered to this lineage, four species, *i.e. H. macropus*, *H. ephippioides*, *H. japonica* and *H. fibrosa*, also have a known distribution outside of Europe.

The stipitate-capitate *H. bresadolae* occupies a position as sister species to *H. pezizoides*, thus expanding the / fallax – pezizoides lineage to include *H. pulla*, *H. fallax*, *H. pezizoides* and *H. bresadolae.* Species of this lineage all have stipitate-capitate apothecia.

Fig. 7. *Helvella bresadolae*, coll. TROM-F-610068 – **holotype**; Norway, Nordland, Saltdal, Junkerdalen, 10 Aug. 2016, *leg. S. Bua Løken & T. Schumacher*. **A.** Dried specimens. **B.** Envelope, originally labelled *Helvella sp. nov*. **C.** Coll. S-F-126515 – Austria, Süd Tyrol, *leg. G. Bresadola* 1883, original envelope of collection labelled "*Helvella Bresadolae* Rehm *nov. spec. in lett. ad Bres*. 31/XII 83", stamped MUS. BOT. STOCKH. EX HERB. REHM, collection later annotated *Helvella pezizoides*.

Biodiversity

Skrede *et al*. (2017) reported on 55 European *Helvella* species, of which seven were new to science, based on materials from one or more of the Nordic countries. In the follow-up study focusing on evolution and generic limits in the family *Helvellaceae*, three *Helvella* species were transferred to a new genus *Dissingia*, one species (*i.e. H. silvicola*) to *Midotis*, one species (*i.e. H. terrestris)* re-installed in *Pindara*, and one species (*i.e. H. aestivalis*) accommodated in the formerly putatively pure underground genus *Balsamia* (Hansen *et al*. 2019). Thus, 49 species remained in the restricted circumscription of the genus (*i.e. Helvella s. str.*). Løken *et al*. (2020) published a taxonomic review of the *Helvella corium* species aggregate, including one newly described species, *i.e. H. pseudoalpina*, providing biogeographic and ecological notes on six species from the Nordic countries. A subsequent study of Skrede *et al*. (2020) recorded on 30 spp. of *Helvella* from Southern Europe (Spain), adding seven new species to the list of European *Helvella* spp.

With the addition of five new species of *Helvella* from the present work, the list of European *Helvella* spp. now amounts to 62 species, of which altogether 54 occur in the Nordic countries (Table 2). In addition, three species of *Dissingia*, one species of *Pindara* and one of *Balsamia,* formerly placed in *Helvella s.l.*, are parts of the diversity of *Helvellaceae* in the Nordic region (*cf*. Table 2).

Biogeography and ecology

Through this expanded survey of old and newly collected fresh specimens of *Helvella* from the Nordic countries, we have gained a much better understanding of the occurrence and biogeographic patterns of some species and subgroups of *Helvella* within the Nordic region. However, it should be noted that we have mainly collected in Norway and investigated the *Helvella* collections in the fungaria C, S, UPS, TRH, TROM and O.

Some *Helvella* species have a restricted distribution in the Nordic region. *Helvella semiobruta* has a single record from Gotland, Sweden, a distribution assumed to be governed by

local climatic and ecological features on this island of the Baltic Sea. This species, which is common in the Mediterranean region (Filippa *et al*. 2013, Skrede *et al*. 2020), finds similar climatic and ecological conditions in the Nordic region only in the hemiboreal islands of Gotland and Öland. Three species are known from Denmark only, probably due to preference for a temperate European climate, not much abundant in the rest of the Nordic region. This applies to *H. phlebophoroides*, *H. platypodia* and *H. queletiana.* Four species, in addition to *H. semiobruta,* are known from Sweden only, *viz. H. hypocrateriformis, H. ephippioides, H. japonica* and *H. retinervis*. *Helvella hypocrateriformis*, commonly recorded under its synonymous name *H. cupuliformis*, is a relatively short-stipitate, cupulate species that has been poorly understood in the past. Judging from published descriptions and illustrations of this apparently uncommon species in Europe, most records in the literature are suggested to represent the more common look-alike species *H. scyphoides* and *H. rivularis* (Dissing & Sivertsen 1980, Peric 2011, Van Vooren 2014). Eleven species are exclusively found in the arctic-alpine biome of Norway and Sweden, and partially in Greenland, Iceland and Svalbard, *i.e.*, *H. alpestris, H. alpina, H. arctoalpina, H. bresadolae, H. capucina, H. dryadophila*, *H. macrosperma, H. nordlandica, H. oroarctica*, *H. philonotis, H. pseudoalpina*. Further, three species are so far known only from Northern (arctic) Norway, *i.e.*, *H. bresadolae, H. nordlandica* and *H. oroarctica*.

The knowledge of distribution of a single species is dependent on sufficient collections and correct species delimitation. As we observed for the *Helvella corium* species aggregate, where we have done detailed morphological and molecular examinations of all material in the larger extant Nordic fungaria supplemented with additional field collection efforts from unexplored areas (Skrede *et al*. 2017, Løken *et al*. 2020), the discerned species have highly variable distribution patterns. A distribution map based on *H. corium s.l*. would have indicated one widespread species that occur in all habitats. Cryptic species with highly divergent distribution patterns and habitat choices have been documented for a number of fungal morphospecies in other genera as well; *e.g.*, in *Serpula himantioides* (Carlsen *et al*. 2011), *Amanita muscaria* (Geml 2006), *Skeletocutis nivea* (Korhonen *et al*. 2018), *Heterobasidion annosum s.l*. (Garbelotto *et al*. 1998, Dalman *et al*. 2010) and the lichen forming *Parmelia mayi* (Molina *et al*. 2011).

The distribution map presented here may indicate some climatic demands of the species in question. However, the ecological roles of the species in the local ecosystems are largely unknown and needs further investigation. In the study by Løken *et al*. (2020), where molecular sequences of old, preserved and newly collected specimens were used to define species limits in the *H. corium* aggregate, one of the new species, *H. alpestris*, produced an ITS sequence that was identical to a sequence obtained earlier in a root tip of *Salix reticulata* taken on the same spot (Weidemann 1998). With the data available at that time, Weidemann (1998) could not match the sequence from the root tip to the sequence she had obtained from an apothecium of *H. corium* collected at another locality. Thus, she suggested that it had to be a close relative of *H. corium* that formed the observed ectomycorrhizal root tip of *S. reticulata*. With the current data available we can conclude that *H. alpestris* is an ectomycorrhizal associate with *S. reticulata*, and represents the unknown *Helvella* species in the work of Weidemann (1998). Whether the other species of the *H. corium* complex also associates with plant roots, is highly suggestive as they often co-occur with specific plant species as well. However, whether they are ectomycorrhizal or exhibit other biotrophic relationships with their "hosts" needs to be investigated.

Many *Helvella* species have been suggested to have an ECM lifestyle (*e.g* see Tedersoo *et al*. 2006, Nguyen *et al*. 2013, Hwang *et al*. 2015). Both Hwang *et al*. (2015) and Tedersoo *et al*. (2006) found *Helvella* ITS sequences in plant root tips, similarly as we have done when comparing to Weidemanns (1998) study. Nevertheless, Hwang *et al*. (2015) also found clades with no evidence of ECM associations, *e.g.* the elastica group [clade VI in Hwang *et al*. (2015), clade E in Skrede *et al*. (2017)]. Thus, it appears that the ecology is highly variable within the genus *Helvella*. Further studies of the ecology of *Helvella* species are urgently needed as these species may have important ecosystem functions in a number of natural habitats.

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Conflict of interest: The authors declare that there is no conflict of interest.

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