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The genera *Helvella* and *Dissingia* (*Ascomycota*: *Pezizomycetes*) in Europe – Notes on species from Spain

I. Skrede[1*], L. Ballester Gonzalvo[2], C. Mathiesen[1], T. Schumacher[1]

[1]Department of Biosciences, University of Oslo, P.O. Box 1066, 0316 Oslo Norway
[2]Calle Octavio de Toledo 25, 50007, Zaragoza, Spain

*Corresponding author: inger.skrede@ibv.uio.no

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Abstract: Phylogenetic analyses of 115 newly collected *Helvella* specimens from Spain using three genetic markers [heat shock protein 90 (*hsp*), RNA polymerase II second largest subunit (*rpb2*) and the nuclear large subunit ribosomal DNA (LSU)] confirm the assignment of the Spanish collections to one *Dissingia* and 30 *Helvella* species. The analyses were supplemented with an additional sample of 65 Spanish and extralimital *Helvella* specimens from the fungaria of Oslo (O), Trondheim (TRH), Copenhagen (C), Uppsala (UPS), Stockholm (S) and Venice (MCVE). Nine species are described as new, *i.e. Helvella fuscolacunosa, H. hispanica, H. iberica, H. inexpectata, H. neopallescens, H. phlebophoroides, H. poculiformis*, *H. retinervis*, and *H. terricola*. We present photographs of a selection of fresh specimens and provide descriptions of all species of this diverse South European Mediterranean element of the genera in Europe.

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INTRODUCTION

Helvella is a species-rich genus of apothecial ascomycetous fungi (*Pezizomycetes: Pezizales: Helvellaceae*) of terrestrial biomes of the northern and southern hemispheres. Many authors have contributed to the species-level taxonomy of the genus, the more comprehensive are those of Boudier (1905–1910), Nannfeldt (1932, 1937), Dissing (1966a, b, Dissing & Nannfeldt 1966), Weber (1972, 1975), Harmaja (1977b, 1979), Häffner (1987), Abbott & Currah (1997), Vooren (2010, 2014), Landeros *et al.* (2012, 2015), and Skrede *et al*. (2017). In Dissing's monograph of "The genus *Helvella* in Europe" (Dissing 1966a), he recognised 26 species in Europe, a list that was later expanded to 28 (Dissing 1972) and to 38 in a survey 30 yr later, but then confined to species of the Nordic countries only (Dissing 2000). Meanwhile, Häffner (1987) accepted 41 species of *Helvella* from Germany and the European continent.

In a preceding study by Skrede *et al*. (2017), we used a multilocus genealogical approach to re-assess species limits, phylogeny and species-level taxonomy within the genus. Based on a selection of fungarium collections and newly collected specimens from North and Central Europe, Skrede *et al*. (2017) assigned molecular specifics and morphological characteristics to altogether 55 phylogenetic species of *Helvella* in Europe. In that work, however, specimens from Southern Europe were seriously under-represented. This paved the way for a review of *Helvella* specimens from Southern Europe using sequence data. The present work adds nine species to the checklist of *Helvella*-species from the European continent.

In a recent account on the generic limits and phylogeny of the family *Helvellaceae,* Hansen *et al*. (2019) erected the segregate genus *Dissingia* to encompass the morphological and molecular distinct members, previously recognised as the /leucomelaena lineage of *Helvella sensu lato* (Landeros *et al.* 2015, Skrede *et al.* 2017). This genus has been included in this revisionary study.

Calonge & Arroyo (1990) published an annotated species list of the genus *Helvella* in Spain, following the species concepts in Dissing (1966b). Their material, deposited at the fungarium of the Botanic Garden of Madrid, comprised 22 species and one variety assumed to include all species that occurred in the country. For a survey of early studies on Spanish *Helvella* species, the reader is referred to the introductory notes and bibliography presented in the work by Calonge & Arroyo (1990).

MATERIALS AND METHODS

Table 1 summarises Spanish and extralimital samples of *Helvella* specimens included in this study that are deposited in the fungaria of Copenhagen (C), Oslo (O), Sociedad de Ciencias Aranzadi (ARAN), Stockholm (S), Trondheim (TRH), Uppsala (UPS), and Venice (MCVE). In addition, *Dissingia leucomelaena* specimens from Spain were included as a suitable outgroup in the phylogenetic analyses. A selection of *in situ* photographs of typical specimens of all species of the Spanish specimens is given.

The morphological analyses follow the outline in Skrede *et al.* (2017). For the ascospore measurements, 10 ejected mature

Table 1. Locality, identification, and type information for *Helvella* and *Dissingia* specimens included in the study. The ID column contains type information and sequencing fungarium identification numbers. The columns LSU, *hsp* and *rpb2* contain GenBank accession numbers. Accession numbers in italics are new accessions from this study, accession numbers in bold are included in maximum likelihood analyses resulting in Fig. 1.

Species	ID	LSU	*hsp*	*rpb2*	Locality	Coll. date	Collector – Collector ID
D. leucomelaena	H1930 (O-F-256543)	–	***MN598130***	***MN626787***	Spain, Navarra, Viana	12.03.2016	A. Ezquerro – AEA0010
	H1931 (O-F-256544)	–	***MN598131***	***MN626788***	Spain, Rioja, Logrono	11.03.2017	A. Ezquerro, L. Ballester – LB17031101
	H2892 (TRH-12603)	–	*MN598182*	–	Spain, Balearic Islands, Mallorca, Galilea	04.02.1989	S. Sivertsen
	H2893 (TRH-12606)	–	*MN598183*	–	Spain, Balearic Islands, Mallorca, Galilea	29.12.1997	S. Sivertsen
	H2894 (TRH-12615)	–	*MN598184*	–	Spain, Balearic Islands, Mallorca, Galilea	29.12.1987	S. Sivertsen
	H2895 (TRH-12616)	–	*MN598185*	–	Spain, Balearic Islands, Mallorca, Formentor	07.04.1982	L. Sivertsen
	H2896 (TRH-12619)	–	*MN598186*	–	Spain, Balearic Islands, Mallorca, Lluch	08.04.1982	S. Sivertsen
	H2898 (TRH-12628)	–	*MN598187*	–	Spain, Balearic Islands, Mallorca, Son Torrella	28.01.1979	S. Sivertsen
	H2899 (TRH-12629)	–	*MN598188*	–	Spain, Balearic Islands, Mallorca, Son Torrella	28.01.1979	S. Sivertsen
	H2900 (TRH-12630)	–	*MN598189*	–	Spain, Balearic Islands, Mallorca, Massanella	30.01.1979	S. Sivertsen
H. acetabulum	H1927 (O-F-256511)	–	***MN598127***	***MN626784***	Spain, Cadiz, Castellar de la Fontera	05.03.2017	M. Plaza – AH0170305
	H1934 (O-F-256512)	–	*MN598134*	–	Spain, Zaragoza, Paniza	30.04.2006	L. Ballester – LB06043001
	H1935 (O-F-256513)	–	*MN598135*	–	Spain, Rioja, Banos de Rio Tobia	02.04.2016	A. Ezquerro – AEA0026
	H1936 (O-F-256514)	–	*MN598136*	–	Spain, Girona, S. Marti d'Empuries	12.03.2017	M. Perez de Gregorio – PG120317
	H1940 (O-F-256515)	–	*MN598140*	–	Spain, Rioja, Sorzano	24.06.2013	R. Martinez, L. Ballester – LB13062401
	H1942 (O-F-256516)	–	*MN598141*	–	Spain, Rioja, Ventas Blancas	29.04.2012	G. Munoz – GM2507
	H1943 (O-F-256517)	–	*MN598142*	–	Spain, Rioja, Almarza de Cameros	28.04.2016	G. Munoz – GM2920
	H2876 (TRH-12717)	–	*MN598166*	–	Spain, Balearic Islands, Mallorca, Lluch	08.04.1982	L. Sivertsen

Table 1. (Continued).

Species	ID	LSU	*hsp*	*rpb2*	Locality	Coll. date	Collector – Collector ID
	H2877 (TRH-12620)	–	*MN598167*	–	Spain, Balearic Islands, Mallorca, Coma Freda	08.04.1982	E. Dahl
	H2878 (TRH-12622)	–	*MN598168*	–	Spain, Balearic Islands, Mallorca, Coma Freda	08.04.1982	G. Gulden
	H2879 (TRH-12626)	–	*MN598169*	–	Spain, Balearic Islands, Mallorca, Coma Freda	26.04.1984	L., S. Sivertsen
	Epitype, H410 (C-F- Fungi. Exs. Suec. 1354)	**KY773154**	**KY784506**	**KY772752**	Sweden, Östergötland	14.09.1945	J. A. Nannfeldt
H. atra	H1019 (O-F-256518)	***MN644503***	–	***MN626770***	Spain, Bizkaia, Gorliz-Berreaga	17.11.2012	A. Melendez, A. Ayala PIPE0966
	H233 (O-253245)	**KY773063**	**KY784351**	**KY772600**	Georgia, Caucasus	13.07.1988	E. Johannesen
	Epitype, H406 (C-F- Fungi. Exs. Suec. 2066)	–	**KY784502**	**KY772748**	Sweden, Uppland	13.07.1938	S. Lundell
H. calycina	Epitype, H022 (O-253255)	**KY772915**	**KY784198**	**KY772442**	Norway, Oppland, Dovre	07.08.2009	T. Carlsen, T. Schumacher, I. Skrede
	H382 (C-F-21122)	**KY773143**	**KY784480**	**KY772727**	Denmark, Klim Bjerg	18.10.1993	Jytte, Lässøe
	H384 (C-F-41038)	**KY773144**	**KY784482**	**KY772729**	Denmark, Klim Bjerg	16.07.1999	L. Hansen, J. Vesterholt
	H845 (O-F-256519)	–	*MN598102*	–	Spain, Rioja, Autol	08.05.2009	G. Munoz – GM1504
	H846 (O-F-256520)	–	*MN598103*	–	Spain, Palencia, Duenas	30.04.2016	A. Calzada – ACD1844
	H847 (O-F-256521)	–	*MN598104*	–	Spain, Rioja, Sorzano	24.06.2013	R. Martinez, L. Ballester – LB13062404
	H848 (O-F-256522)	–	*MN598105*	–	Spain, Rioja, Ventas Blancas	29.04.2015	R. Martinez, L. Ballester – RM2338
	H849 (O-F-256523)	–	*MN598106*	–	Spain, Valladolid, Aldeamayor de San Martin	14.05.2016	F. Bellido – FB160514
H. costifera	H131 (O-68514)	**KY772982**	**KY784264**	**KY772514**	Norway, Akershus	27.07.2007	P.A. Bergersen
	H247 (O-253283)	**KY773074**	**KY784365**	**KY772613**	Norway, Oppland. Vågå	29.08.1998	S. Kjølner
H. crispa	H135 (O-18774)	**KY772986**	**KY784268**	**KY772518**	Norway, Akershus	15.10.2004	P. Marstad
	H2624 (O-F-256524)	–	***MN598151***	***MN626795***	Spain, Balearic Islands, Menorca, Binimoti, Ferreries	08.12.2007	J. L. Melis – GM071208-6
	H2626 (O-F-256525)	–	*MN598153*	*MN626754*	Spain, Huesca, Villanúa	12.10.2007	L. Ballester – LB07101201
	H2634 (O-F-256526)	–	***MN598161***	–	Spain, Huesca, Bergua	03.11.2017	J. Garcia, A. Hereza – LB17110301
	H2880 (TRH-12605)	–	*MN598170*	–	Spain, Balearic Islands, Mallorca, Galilea	29.12.1997	S. Sivertsen

Table 1. (Continued).

Species	ID	LSU	*hsp*	*rpb2*	Locality	Coll. date	Collector – Collector ID
	H2881 (TRH-12612)	–	*MN598171*	–	Spain, Balearic Islands, Mallorca, Formentor	01.01.1988	S. Sivertsen
	H2882 (TRH-12625)	–	*MN598172*	–	Spain, Balearic Islands, Mallorca, Reg. Escorca	24.10.1984	T. Schumacher
	Epitype, H408 (C-F- Fungi. Exs. Suec. 2062)	–	**KY784504**	**KY772750**	Sweden, Blekinge	5-14.10. 1946	S. Lundell, S. Wickland
H. dalgeri	H1924 (O-F-256527)	–	***MN598125***	***MN626782***	Spain, Girona, Serinya	04.02.2001	M. Perez de Gregorio – PG250217
	H2984 (O-F-256528)	–	***MN598202***	***MN626814***	Spain, Albacete, Masegoso	02.05.2009	A. Rodriguez – AR090502
H. danica	H058 (O-253288)	**KY772942**	**KY784222**	**KY772469**	Norway, Akershus	16.09.2009	T. Schumacher, I. Skrede
	Holotype, H263 (O-253288)	**KY773083**	**KY784378**	**KY772627**	Denmark, Jutland	18.09.2008	J. Heilmann-Clausen
H. elastica	H066 (O-253311)	**KY772950**	**KY784230**	**KY772476**	Sweden, Hallan	16.09.2009	G. Holden
	H329 (C-F-51672)	–	**KY784433**	**KY772684**	Russia, Sakha	21.08.1999	H. Knudsen
	H443 (O-253310)	**KY773167**	**KY784531**	**KY772775**	Norway, Akershus	00.00.2009	Ø. Stensrud
H. fibrosa	H343 (C-F-92103)	–	**KY784446**	**KY772697**	Iceland, Merkurhraun	26.08.1984	S. Elborne
	H357 (C-F-53774)	**KY773125**	**KY784458**	**KY772708**	Norway, Nordland	11.09.1975	H. Dissing
H. fusca	H2632 (O-F-256529)	–	***MN598159***	***MN626800***	Spain, Rioja, Ventas Blancas	09.04.2016	L. Ballester – LB16040903
	H304 (C-F-89381)	–	**KY784414**	**KY772663**	Netherlands, Zuid-Holland	14.05.1983	C. Bas
	H305 (C-F-92122)	**KY773101**	**KY784414**	**KY772663**	Hungary, Kiskunsag National Park	11.05.1978	M. Babos, A. Friesz
	Epitype, H817 (S-F-124424)	**JX993065**	***MN598098***	***MN626765***	Italy, Ex Herb. Rehm In Trento	05.1888	G. Bresadola
	H835 (S-F-023173)	–	*MN598099*	*MN626753*	Spain, Valladolid, La Cisterniga, Fuentes de Duero	21.04.1991	J. C. Santos
H. fuscolacunosa	H1020 (O-F-256530)	***MN644493***	–	–	Spain, Huesca, Banastas	08.12.2012	J. Garcia, L. Ballester – LB12120804
	H1024 (O-F-256531)	***MN644494***	***MN598086***	***MN626772***	Spain, Rioja, Villarroya	15.05.2016	G. Munoz – GM2930
	Holotype, H2883 (TRH-12618)	***MN644495***	***MN598173***	–	Spain, Balearic Islands, Mallorca, Formentor	07.04.1982	L. Sivertsen
	H2889 (TRH-12623)	***MN644496***	***MN598179***	–	Spain, Balearic Islands, Mallorca, Lluch	24.10.1984	T. Schumacher
H. griseoalba	H306 (C-F-92112)	–	**KY784416**	**KY772665**	USA, Michigan	09.06.1973	C. Nimke
H. helvellula	H1928 (O-F-256532)	–	***MN598128***	***MN626785***	Spain, Badajoz, Campillo de Llerena	11.03.2017	M. Plaza – AH0170311-1
	H278 (C-F-45506)	**KY773090**	**KY784393**	**KY772641**	France	20.04.1977	R. Schumacher

Table 1. (Continued).

Species	ID	LSU	*hsp*	*rpb2*	Locality	Coll. date	Collector – Collector ID
	Epitype, H308 (C-F-92128)	–	**KY784418**	**KY772667**	Spain, Canary Islands, Hierro, toward Taibique	07.01.1977	R. Korf, Fogel, Hennebert, L. Kohn
	H309 (C-F-45469)	**KY773103**	**KY773103**	–	France, Region des Landes	01.03.1981	F. Candoussau
	H521 (O-F-256533)	–	*MN598090*	–	Spain, Rioja, Villarroya	02.05.2010	G. Munoz – GM1832
	H523 (O-F-256534)	–	***MN598085***	***MN626760***	Spain, Rioja, Avellaneda	14.04.2007	R. Martinez – RM321
	H525 (O-F-256535)	–	*MN598093*	–	Spain, Rioja, Entrena	21.02.2015	R. Martinez, L. Ballester – LB15022101
	H836 (S-F-023260)	–	***MN598100***	***MN626766***	Spain, Valladolid, La Parrilla, Monte Bayón	28.03.1991	J. C. Santos
H. hispanica	H1023 (O-F-256536)	***MN644504***	***MN598112***	***MN626771***	Spain, Rioja, Santa Lucia	06.04.2015	A. Melendez – PIPE0833
	Holotype, H1929 (O-F-256537)	–	***MN598129***	***MN626786***	Spain, Rioja, Ventosa	11.03.2017	L. Ballester – LB17031103
H. hypocrateriformis	H275 (C-F-57126)	–	**KY784390**	**KY772638**	Switzerland, Graubünden	07.09.1982	H. Dissing
	Epitype, H301 (C-F-85205)	–	**KY784411**	**KY772660**	Sweden, Uppland	21.07.1948	R. Molander
H. iberica	H1016 (O-F-256538)	***MN644597***	***MN598108***	***MN626767***	Spain, Rioja, Tudelilla	03.04.2016	G. Munoz – GM2907
	Holotype, H1018 (O-F-256539)	***MN644498***	***MN598109***	***MN626769***	Spain, Rioja, El Rasillo	13.04.2013	R. Martinez – RM2373
H. inexpectata	H1017 (O-F-256540)	–	***MN598192***	***MN626768***	Spain, Rioja, Sojuela	05.01.2013	R. Martinez – RM1088
	Holotype, H2621 (O-F-256541)	–	***MN598148***	***MN626792***	Spain, Rioja, Sojuela	05.03.2016	A. Ezquerro – AE160305
H. juniperi	Holotype, H2973 (ex MCVE 20997 (no 501))	–	***MN598194***	***MN626807***	Italy, Lu, Viareggio	16.03.1996	G. Baiano, M. Filippa, D. Garofoli
	Isotype, H2974 (ex MCVE 20998 (no 501/a))	–	***MN598195***	***MN626808***	Italy, Lu, Viareggio	16.03.1996	G. Baiano, M. Filippa, D. Garofoli
	H415 (C-F-42193)	–	**KY784510**	**KY772754**	Portugal, Minho, S of S. Bartolomeu do Mar, N of Esposende	15.11.2000	P. Boisen Hansen
H. lactea	H262 (C-F Fungi. Exs. Suec. 1355)	–	**KY784377**	**KY772626**	Sweden, Uppland	25.07.1939	N. Hylander
	H374 (C-F-39379)	–	**KY784473**	**KY772722**	Denmark, Zealand	27.08.1961	H. Dissing
H. lacunosa	H153 (O-285214)	**KY773002**	**KY784285**	**KY772536**	Norway, Sør-Trøndelag	10.06.2007	R. Haugan – S07415
	Epitype, H407 (C-F Fungi Exs. Suec. 2065)	**KY773152**	**KY784503**	**KY772749**	Sweden, Femsjö. Skatåker	04.10.1948	S. Lundell, G. Haglund
H. leucophaea	H2628 (O-F-256545)	–	***MN598155***	***MN626797***	Spain, Huesca, Banastás	08.12.2012	J. Garcia, L. Ballester – LB12120805
H. macropus	H073 (O-253326)	**KY772954**	**KY784233**	**KY772480**	Norway, Oslo	03.09.2009	M. F. M. Bjorbaekmo

Table 1. (Continued).

Species	ID	LSU	*hsp*	*rpb2*	Locality	Coll. date	Collector – Collector ID
	H1933 (O-F-256546)	–	*MN598133*	–	Spain, Huesca, Cerler	12.09.2015	C. Rojo, L. Ballester – LB15091205
	H1948 (O-F-256547)	–	*MN598147*	–	Spain, Rioja, Lumberas	04.10.2008	G. Munoz – GM1324
	H257 (O-253325)	–	**KY784373**	**KY772622**	Norway, Oppland, Dovre	08.08.2009	T. Carlsen, T. Schumacher, I. Skrede – TS09-36
	H351 (C-F-56087)	–	**KY784452**	**KY772703**	USA, Alaska, Anchorage	14.08.1980	H. Dissing
H. maculata	H303 (C-F-45400)	–	**KY784413**	**KY772662**	USA, Alaska, Eklutna Lake	24.08.1973	V. L. Wells, P. E. Kempton
H. monachella	H2631 (O-F-256548)	–	***MN598158***	***MN626799***	Spain, Rioja, Ventas Blancas	29.04.2015	R. Martinez, L. Ballester – LB15042904
	Epitype, H268 (C-F-92121)	–	**KY784373**	**KY772622**	Hungary, Szelid	14.05.1979	M. Babos, L. Albert, J. Bukei, A. Friesz
	H269 (C-F-92120)	**KY773084**	**KY784384**	**KY772632**	Hungary, Szelid	24.05.1965	I. Ferencz, E. Toth, E. Vessey, S. Vasali
	H843 (S-F-022128)	–	*MN598101*	–	Spain, Valladolid, Tudela de Duero, Fuente del Rey	18.04.1990	J. C. Santos
H. neopallescens	H1021 (O-F-256549)	–	*MN598110*	–	Spain, Rioja, Ventosa	18.01.2014	L. Ballester – LB14011801
	Holotype, H1022 (O-F-256550)	***MN644500***	***MN598111***	–	Spain, Rioja, Logrono	07.02.2015	R. Martinez – RM2397
	H1025 (O-F-256551)	–	***MN598113***	***MN626773***	Spain, Bizkaia, Gorliz-Urezarantza	18.01.2014	A. Melendez – PIPE0753
	H1026 (O-F-256552)	–	*MN598114*	–	Spain, Rioja, Sorzano	28.03.2013	L. Ballester – LB13062402
	H1032 (O-F-256553)	–	*MN598117*	–	Spain, Rioja, Villarroya	27.04.2006	G. Munoz – GM495
	H2639 (O-F-256554)	–	***MN598165***	***MN626806***	Spain, Bizkaia, Derio	03.10.2017	A. Melendez – PIPE1063
	H2884 (TRH-12607)	***MN644501***	***MN598174***	–	Spain, Balearic Islands, Mallorca, Galilea	29.12.1997	S. Sivertsen
	H2885 (TRH-12609)	***MN644502***	***MN598175***	–	Spain, Balearic Islands, Mallorca, Formentor	01.01.1988	S. Sivertsen
	H2886 (TRH-12610)	–	*MN598176*	–	Spain, Balearic Islands, Mallorca, Lluch	28.12.1987	S. Sivertsen
	H2887 (TRH-12611)	–	*MN598177*	–	Spain, Balearic Islands, Mallorca, Puert de Canonge	29.12.1987	S. Sivertsen
	H2888 (TRH-12613)	–	*MN598178*	–	Spain, Balearic Islands, Mallorca, Puert de Canonge	29.12.1987	S. Sivertsen

Table 1. (Continued).

Species	ID	LSU	*hsp*	*rpb2*	Locality	Coll. date	Collector – Collector ID
	H2890 (TRH-12624)	–	*MN598180*	–	Spain, Balearic Islands, Mallorca, Lluch	24.10.1984	W. Holm
	H2891 (TRH-12627)	–	*MN598181*	–	Spain, Balearic Islands, Mallorca, Reg. Escorca	24.10.1984	T. Schumacher
	H2983 (O-F-256555)	–	***MN598201***	***MN626813***	Spain, Rioja, Clavijo	01.12.2018	R. Martinez – RM2482
	H401 (C-F-49767)	–	*MN598089*	–	France, Avignon	22.10.1974	H. Dissing
H. nigra	Epitype, H063 (O-253345)	**KY772947**	**KY772947**	**KY784227**	Sweden, Hallan, Halmstad	16.09.2009	G. Holden
	H1029 (O-F-256556)	***MN644491***	**KY784573**	**KY772815**	Spain, Rioja, Castroviejo	09.08.2014	A. Melendez, R. Martinez, C. Perez – PIPE0829
	H1030 (O-F-256557)	–	**KY784572**	**KY772816**	Spain, Bizkaia, Urkiola	19.10.2007	G. Munoz – GM1085
	H2622 (O-F-256558)	***MN644492***	***MN598149***	***MN626793***	Spain, Navarra, Suarbe	07.10.2017	C. Echavarri – CE17100701
H. pallescens	H136 (O-220306)	**KY772987**	**KY784269**	**KY772519**	Norway, Hordaland, Ulvik	28.08.2001	G. Flatabø
	Epitype, H138 (O-66205)	**KY772988**	**KY784271**	**KY772521**	Norway, Møre og Romsdal, Norddal	29.08.2003	D. Holtan
	H2630 (O-F-256559)	–	***MN598157***	***MN626798***	Spain, Rioja, Sojuela	24.06.2013	R. Martinez, L. Ballester – LB13062407
	H2633 (O-F-256560)	–	***MN598160***	***MN626801***	Spain, Zaragoza, Tarazona	01.11.2017	J. Genova, L. Ballester – LB17110103
	H2638 (O-F-256561)	–	***MN598164***	***MN626805***	Spain, Rioja, Montemediano de Cameros	23.06.2007	R. Martinez – RM378
H. palustris	H019 (O-253358)	**KY772914**	**KY784196**	**KY772440**	Norway, Oppland, Dovre	07.08.2009	T. Carlsen, T. Schumacher, I. Skrede
	H043 (O-253359)	**KY772933**	**KY784214**	**KY772458**	Norway, Oppland, Dovre	07.08.2009	T. Carlsen, T. Schumacher, I. Skrede
	H350 (C-F-55330)	**KY773123**	**KY784451**	**KY772702**	Finland, Kuusamo	15.08.1978	H. Dissing
H. panormitana	Epitype, H064 (0-253363)	**KY772948**	**KY784228**	**KY772474**	Sweden, Hallan, Laholm	16.09.2009	C. C. Mellberg
	H145 (O-203499)	**KY772994**	**KY784278**	**KY772528**	Norway, Møre og Romsdal, Stordal	18.09.2005	P. Larsen
	H2627 (O-F-256563)	–	***MN598154***	***MN626796***	Spain, Huesca, Villanúa	12.10.2007	L. Ballester – LB07101202
H. paraphysitorquata	Isotype, H271 (C-F-45305)	**KY773085**	**KY784386**	**KY772634**	Spain, Teruel	03.06.1988	Arroyo, Calon
H. pezizoides	Epitype, H061 (O-253366)	KY772945	***KY784225***	***KY772471***	Sweden, Hallan, Halmstad	16.09.2009	S. Lund
	H2636 (O-F-256564)	–	–	*MN626756*	Spain, Rioja, Castroviejo	09.08.2014	R. Martinez – RM2274
	H431 (C-F-52986)	**KY773161**	**KY784525**	**KY772768**	Denmark, N Jutland	06.10.1997	M. Christensen, K. Hansen

Table 1. (Continued).

Species	ID	LSU	*hsp*	*rpb2*	Locality	Coll. date	Collector – Collector ID
H. phlebophora	H273 (C-F-45405)	**KY773087**	**KY784388**	**KY772636**	Iceland, Austur Skaftafellsysla	20.08.1981	H. F. Gøtzsche – 84/31
H. phlebophoroides	Holotype, H1031 (O-F-256565)	***MN644506***	***MN598116***	***MN626775***	Spain, Rioja, Anguiano	02.07.2011	R. Martinez – RM2193
	H1709 (C-F-39531)	–	***MN598087***	***MN626777***	Denmark, Jutland, Hansed Skov N Horsens	22.08.1960	H. Dissing
	H1846 (C-F-17373)	***MN644507***	***MN598088***	***MN626779***	Denmark, NEZ, København	31.07.1985	J. Vesterholt
H. platypodia	H1792 (C-F-39481)	–	*MN598120*	–	Denmark, Zealand, Allindelille, N Ringsted	24.08.1961	B. & M. Lange, H. Dissing
	H1795 (C-F-39482)	–	*MN598121*	–	Denmark, Zealand, Lellinge, E Køge	30.08.1961	L. Hansen, M. Lange, H. Dissing
	H1796 (C-F-64490)	–	*MN598122*	–	Denmark, EJ, Tudsedamsmosen at Varna	13.10.1981	S. A. Elborne
	Epitype, H1939 (O-F-256566)	–	***MN598139***	***MN626790***	Spain, Rioja, Sorzano	11.06.2013	L. Ballester – LB13061103
H. poculiformis	Holotype, H1944 (O-F-256567)	–	***MN598143***	***MN626791***	Spain, Zaragoza	10.11.2009	G. Munoz – GM1702
H. pulla	Epitype, H149 (O-253370)	KY772623	KY784282	KY772532	Norway, Møre og Romsdal	26.09.2008	T. Læssøe
	H259 (O-253370)	**KY773080**	***KY784374***	***KY772623***	Norway, Østfold	18.09.2013	K. Varenius
	H2623 (O-F-256568)	–	***MN598150***	***MN626794***	Spain, Rioja, Montemediano de Cameros	21.06.2008	F. Martinez – FM574
	H2629 (O-F-256569)	–	*MN598156*	MN626758	Spain, Rioja, Sorzano	11.06.2013	L. Ballester – LB13061101
	H2635 (O-F-256570)	–	***MN598162***	***MN626803***	Spain, Rioja, Castroviejo	02.08.2014	R. Martinez – RM1161
	H2977 (O-F-256571)	–	*MN598196*	MN626757	Spain, Rioja, Hornos de Moncalvillo	19.12.2018	R. Martinez, L. Ballester – LB18121901
H. queletiana	H1716 (C-F-39372)	–	***MN598119***	***MN626778***	Denmark, Zealand, Gribskov	05.06.1973	P. M. Petersen, H. Dissing
	H2981 (O-F-256572)	–	***MN598200***	***MN626812***	Spain, Rioja, Canales de la Sierra	20.06.2009	R. Martinez – RM0749
	Neotype, H403 (C-F-45303)	**KY773151**	**KY784499**	**KY772746**	Denmark, Zealand, Boserup Skov	29.04.1995	B. T. Olsen
H. retinervis	H1000 (O-F-256573)	–	*MN598107*	–	Spain, Zamora, Villalazan	24.04.2016	H. Perez – 2404-16HP1
	Holotype, H1925 (ex ARAN3008363)	–	***MN598126***	***MN626783***	Spain, Gipuzkoa, San Sebastian	21.05.2009	J. M. Lekuona
	H1926 (ex ARAN5037657)	–	*MN598193*	MN626755	Spain, Navarra, Huitzi-Basakaitz	24.06.2009	J. M. Lekuona
	H778 (UPS-F-006175)	–	***MN598096***	***MN626763***	Sweden, Skåne, Ivö	09.08.1987	B. Hägg

Table 1. (Continued).

Species	ID	LSU	*hsp*	*rpb2*	Locality	Coll. date	Collector – Collector ID
	H779 (UPS-F-122183)	–	***MN598097***	***MN626764***	Sweden, Närke, Hallsberg	31.07.1981	S. Ryman
H. semiobruta	H1922 (O-F-256574)	–	***MN598123***	***MN626780***	Spain, Rioja, Logrono, Pinar del Gitano	11.03.2017	A. Ezquerro, L. Ballester – LB17031102
	Isotype, H277 (C-F-45507)	***MN644499***	KY784392	KY772640	France, Rhone, D'Aubagne	15.12.1972	J. C. Donadini
	H2901 (TRH-12614)	–	*MN598190*	–	Spain, Balearic Islands, Mallorca, Galilea	27.12.1987	S. Sivertsen
	H522 (O-F-256575)	–	***MN598091***	***MN626759***	Spain , Rioja, Ventosa	28.02.2015	R. Martinez, L. Ballester – RM2302
	H524 (O-F-256576)	–	*MN598092*	–	Spain, Rioja, Lardero	30.01.2016	R. Martinez – AC5335
	H526 (O-F-256577)	–	***MN598094***	***MN626761***	Spain, Rioja, Lardero	21.03.2015	R. Martinez, L. Ballester – LB15032101
	H529 (O-F-256578)	–	***MN598095***	***MN626762***	Spain, Alava, Laguardia	12.03.2016	A. Ezquerro – AE16031201
	H1366 (C-F-45419)	–	***MN598118***	***MN626776***	Sweden, Gotland, at Skansudd S of Fröjel	28.05.1968	P. M. Petersen
H. solitaria	H1923 (O-F-256579)	–	***MN598124***	***MN626781***	Spain, Huesca, Villanua	23.05.2016	J. Garcia, L. Ballester – LB16052302
	H1937 (O-F-256580)	–	*MN598137*	–	Spain, Rioja, Ventas Blancas	29.04.2015	R. Martinez, L. Ballester – LB15042901
	H1938 (O-F-256581)	–	*MN598138*	–	Spain, Rioja, Sorzano	11.06.2013	L. Ballester – LB13061102
	H1945 (O-F-256582)	–	*MN598144*	–	Spain, Rioja, Ventas Blancas	29.04.2007	G. Munoz – GM1011
	H1946 (O-F-256583)	–	*MN598145*	–	Spain, Rioja, Tudelilla	29.04.2012	G. Munoz – GM2506
	H2902 (TRH-12608)	–	*MN598191*	–	Spain, Balearic Islands, Mallorca, Escorca, Pollenza	02.04.1985	L & S. Sivertsen
	H370 (C-F-45467)	–	***KY784470***	***KY772720***	Spain, Valdepenas	06.07.1975	Lundell, Morand
H. sublicia	H1932 (O-F-256584)	–	***MN598132***	***MN626789***	Spain, Rioja, Castroviejo	09.07.2016	R. Martinez – RM2390
	H1947 (O-F-256585)	–	*MN598146*	–	Spain, Asturias, Covandonga	22.07.2011	G. Munoz – GM2192
	H2625 (O-F-256586)	–	*MN598152*	–	Spain, Huesca, Villanova	01.08.2006	R.Tena & L. Ballester – LB06080101
	H2637 (O-F-256587)	–	***MN598163***	***MN626804***	Spain, Rioja, Santa Coloma	18.09.2014	R. Martinez – RM2286
	Epitype, H417 (C-F-39823)	**KY773155**	***KY784512***	***KY772756***	Denmark, Zealand, Sorø	02.10.1993	K. Hansen
H. sulcata	H1027 (O-F-256588)	***MN644505***	***MN598115***	***MN626774***	Spain, Rioja, Clavijo	22.11.2013	R. Martinez – RM2238

Table 1. (Continued).

Species	ID	LSU	*hsp*	*rpb2*	Locality	Coll. date	Collector – Collector ID
	Epitype, H152 (O-69282)	**KY773001**	**KY784284**	**KY772535**	Norway, Oslo	13.10.2006	O. Smith, A.-S. Karlsson
	H2979 (O-F-256589)	–	***MN598198***	***MN626810***	Spain, Huesca, Barbaruens	28.09.2018	R. Martinez, L. Ballester – LB18092809
	H2980 (O-F-256590)	–	***MN598199***	***MN626811***	Spain, Huesca, Barbaruens	28.09.2018	F. Pancorbo, L. Ballester – LB18092802
H. terricola	Holotype, H2978 (O-F-256562)	–	***MN598197***	***MN626809***	Spain, Huesca, Cerler	28.09.2018	F. Cervera, L. Ballester – LB18092810

spores from one individual were measured and the minimum – mean – maximum values are reported.

DNA was extracted from all specimens 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 ExoSAP-IT (GEhealthcare, Waukesha, WI). For primer sequences, detailed PCR conditions, and sequencing techniques, see the procedure in Skrede *et al.* (2017). In addition to the sequences produced in the present study, a representative selection of sequences from *Helvella* species from other geographic regions were downloaded from GenBank and included for reference. Information on specimens studied and all new and retrieved sequences with accession numbers in GenBank is given in Table 1. The sequences were automatically aligned using the MUSCLE v. 3.8.425 (Edgar 2004) plugin in Geneious Prime 2019.0.4 (Biomatters, Auckland). 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. The best ML tree from the analysis of a concatenated, partitioned alignment of three genetic markers is presented in Fig. 1. In this concatenated dataset, we allowed for the inclusion of some missing data by permitting individuals with only LSU, *rpb2* and *hsp*, *hsp* and LSU or *rpb2* and LSU. Bootstrap analyses using 1 000 pseudoreplications were included in all ML analyses. The concatenated alignment is available in Dryad (http://datadryad.org).

The ML analyses were the basis for species delimitation. A simplified genealogical concordance phylogenetic species recognition (Avise & Ball 1990, Taylor *et al*. 2000, Dettman *et al*. 2003) was used, where terminal clades with bootstrap support > 70 % from two or more genetic markers were considered to be species. Some intraspecific variation was allowed.

RESULTS

Phylogeny

A total of 118 *hsp*, 69 *rpb2* and 17 LSU sequences were produced and submitted to GenBank. The final concatenated alignment was 1 163 bp (279, 346, 538 bp for *hsp*, *rpb2* and LSU, respectively). The ML phylogenetic tree has high support on most nodes toward the tips of the branches and is highly discriminating among species (Fig. 1). Although the basal nodes are mainly not supported, most of the main lineages and clades in Skrede *et al.* (2017) were retrieved.

The resulting ML analyses demonstrated the presence of 27 Spanish species. Spanish representatives of four additional species, *i.e. H. calycina*, *H. crispa, H. macropus* and *H. pezizoides* were not included in the concatenated dataset, since only *hsp* sequences were obtained (Table 1). Thus, 31 Spanish species are included in the present survey. The sequenced specimens from our samples are assigned to major lineages and clades across the genus *Helvella.* Nine independent lineages are defined as new species, *i.e. H. phlebophoroides*, *H. hispanica*, *H. neopallescens*, *H. terricola, H. fuscolacunosa*, *H. iberica*, *H. inexpectata*, *H. retinervis* and *H. poculiformis*, of which seven are nested in the /lacunosa clade (indicated as A in Fig. 1). The other two new species are found elsewhere in the phylogeny, one as a sister species to the /lacunosa clade (*i.e*. *H. retinervis*) and one as sister to *H. sublicia* (*i.e. H. poculiformis*).

Taxonomy

Dissingia leucomelaena (Pers.) K. Hansen & X.H. Wang, *Persoonia* **42**: 198. 2019. Fig. 2A.
Basionym: *Peziza leucomelas* Pers., *Mycol. Eur.* **1**: 219. 1822.
Synonym: *Helvella leucomelaena* (Pers.) Nannf., in Lundell & Nannfeldt, *Fungi exs. Suec. Fasc*. **19-20**: 21, no. 952. 1941.
See Skrede *et al*. (2017) for additional synonyms.

Illustration: Dissing (1966b: fig. 8, as *H. leucomelaena*).

Apothecium stipitate-cupulate, cup 2–8 cm broad, 1–5 cm deep, with crenate margin and expanded into irregular lobes, *hymenium* greyish brown to dark brownish black, often with a violaceus tinge, *receptacle* surface pubescent, upper part whitish to dark greyish brown, below gradually paler to yellowish white. *Stipe* short, 0.5–2 cm high, 0.6–1 cm broad, with blunt irregular ribs and grooves, with internal chambers. *Medullary excipulum* thick, of dense *textura intricata*, hyphae 3–5 µm broad. *Outer excipulum* of *textura angularis*, cells 10–24 µm, interspersed with some narrow hyphae of prismatic cells, outermost cells in rows turning out perpendicular to receptacle surface giving rise to tufts of fascicled hyphae consisting of club-shaped cells. *Asci* aporhynchous, 320–380 × 12–14 µm. *Ascospores* ellipsoid, 19.4–21.6–24.0 × 10.6–12.1–13.0 µm. *Paraphyses* brownish, 4 – 5 µm broad below, clavately enlarged to 7–11 µm at the tips.

Specimens examined/sequenced: See Table 1.

Notes: This short-stipitate deeply cupulate species was recently re-combined in the new segregate genus *Dissingia* (Hansen *et al*. 2019), a genus molecularly and morphologically segregated from *Helvella s. s.* based on phylogenetic evidence (paraphyly) and asci that arise from simple septa. The often semi-immersed growth habit, with the whitish stipe buried in the soil, characterises the species.

Helvella acetabulum (L.) Quel., Hymenomycetes, Fasc. Suppl. (Alençon): 102. 1874. Fig. 2B, C.
Basionym: *Peziza acetabulum* L., *Sp. Pl.* **2**: 1181. 1753; Fr., *Syst. Mycol.* **2**: 44. 1822
Synonyms: See Skrede *et al.* (2017).

Illustration: Harmaja (1977b: figs 1–2).

Apothecium stipitate-cupulate, 2.5–10 cm broad, by 3–8 cm high, *hymenium* pale brown to medium brown, drying dark brown, *receptacle* concolourous or pale yellowish brown, sub-pubscent. *Stipe* 1.5–7.5 cm high, 1.5–5 cm broad, broad above and narrowing towards the base, hollow inside, outside whitish to yellowish, with 5 to 7 prominent, mostly double-edged sharp ribs branching upwards to the attachment point about half way to the apothecial margin. *Medullary excipulum* of *textura intricata*, hyphae 4–8 µm broad, light brown-walled. *Outer excipulum* of *textura angularis* to *textura prismatica*, individual cells 10–25 µm diam, outermost cells prismatic, hyaline, 5–15 × 4–8 µm, arranged in rows that turn out perpendicular to receptacle surface. *Asci* pleurorhynchous, 310–380 × 13–16 µm. *Ascospores* ellipsoid, uniguttulate, 15.5–17.4–19.2 × 10.5–11.4–13.2 µm. *Paraphyses* 3–5 µm below, brownish along their whole length, slightly enlarged at the clavate tips.

Specimens examined/sequenced: See Table 1.

Note: The Spanish collections are morphologically and molecularly identical to specimens recorded from Northern and Central Europe (*cf.* Skrede *et al*. 2017).

Helvella atra König in Oeder, *Flora Danica* **3** (9): 7. 1770. - *nom. sanct.* Fig. 3C.
Synonym: *Leptopodia atra* (König in Oeder) Boud., Icon. Mycol., liste prélim.: 2. 1904.
See Skrede *et al.* (2017) for additional synonyms.
Misapplied name: *Helvella atra* Holmsk., *Beata ruris otia Fungis Danicis impens*a **2**: 47. 1799.

Illustrations: Oeder (1770: pl. 534, fig. 1), Boudier (1906: n°. 121, pl. 228, as *H. lacunosa*, Filippa & Baiano (2011: figs 9–11, as *H. lacunosa*).

Apothecium stipitate-capitate, saddle-shaped or irregularly lobed, 1–4 cm broad, 3–12 cm high, cap margin adnate and attached to stipe at 3 to 4 points, *hymenium* blackish with a dark violet brown tinge, even or wrinkled, *receptacle* surface greyish brown to black, smooth, with inconspicuous ribs on outer surface. *Stipe* 0.5–2.5 cm broad, naked, greyish brown to black, paler towards base, hollow and chambered inside, outside with 4 to 7 sharp and partly double-edged prominent ribs attached to the reflexed apothecial margin at 3 to 4 points, between ribs with deep grooves and lacunae ('holes'). *Medullary excipulum* of *textura intricata*, hyphae 3–5 mm broad. *Outer excipulum* of *textura angularis*, cells 8–15 µm in diam, hyaline, outermost cells club-shaped, 10–30 × 5–15 µm. *Asci* pleurorhynchous, 260–10 × 14–18 µm. *Ascospores* ellipsoid, 15.5–17.1–18.5 × 10–11.3–12.5 µm. *Paraphyses* subhyaline to light brown, 3–4 µm broad below, increasingly brown towards the 6–8 µm broad clavate tips.

Specimens examined/sequenced: See Table 1.

Notes: An account of the nomenclatural history of this medium-size greyish black species of the *H. lacunosa* morpho-species complex was given by Filippa & Baiano (2011) and Skrede *et al*. (2017). *Helvella atra* is apparently less common in Southern compared to Northern Europe.

Helvella calycina Skrede *et al*., *Persoonia* **39**: 221. 2017. Fig. 2D–F.
Basionym: *Boletus calyciformis* Battara, Fungorum Arimin.: 25. 1759; Fr., *Syst. Mycol.* **2**: 45. 1822.
Synonyms: See Skrede *et al.* (2017).

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

Apothecium short-stipitate, at first cupulate, then expanded and irregularly folded, 2–7.5 cm broad, 1.5–4.5 cm high; *hymenium* brownish, *receptacle* surface greyish brown, pubescent to furfuraceous; *stipe* with 5 to 8 prominent, blunt-edged, yellowish-white ribs dichotomously branched when extending onto receptacle surface, not reaching the margin in fully developed specimens, receptacle with concentric, parallel connections between ribs, making the surface somewhat wrinkled. *Medullary excipulum* of hyaline *textura intricata*, hyphae 3–5 µm broad. Outer excipulum of *textura prismatica* to *textura angularis*, outermost cells brown-walled. *Asci* pleurorhynchous, cylindrical, 240–280 × 11–14 µm. *Ascospores* ellipsoid, uniguttulate, 14.5–16.2–17.6 × 9.5–10.8–12.0 µm. *Paraphyses* 2.5–3.5 µm broad below, straight, septate, gradually enlarged to 4–6 µm at the tips.

Specimens examined/sequenced: See Table 1.

Notes: The species was re-named and re-described in Skrede *et al*. (2017), based on a taxon originally described from Italy as *Boletus calyciformis* by Battara (1759). *Helvella calycina* seems common throughout Europe, and was recently also reported from China (Wang *et al*. 2019). The North European and Spanish specimens are molecularly identical and diverge genetically from its sister species *H. costifera* in one consistent *hsp* and two *rpb2* SNPs.

Helvella crispa (Scop.) Fr., *Syst. Mycol.* **2:** 14. 1822. Fig. 4B.
Basionym: *Phallus crispus* Scop., *Fl. Carniol.*, ed. **2**, **2**: 475. 1772; Fr., *Syst. Mycol.* **2**: 14. 1822.
Synonym: *Helvella pallida* Schaeff., *Fung. Bavar. Palat. Nasc.* **4**: 112. 1774.
See Skrede *et al.* (2017) for additional synonyms.

Illustrations: Boudier (1909b: n°. 490, pl. 225), Dissing (1966b: fig. 21).

Apothecium stipitate-capitate, 2–7 cm broad, irregularly bi- to tri-lobate, saddle-shaped, with inrolled, free margin, *hymenium*

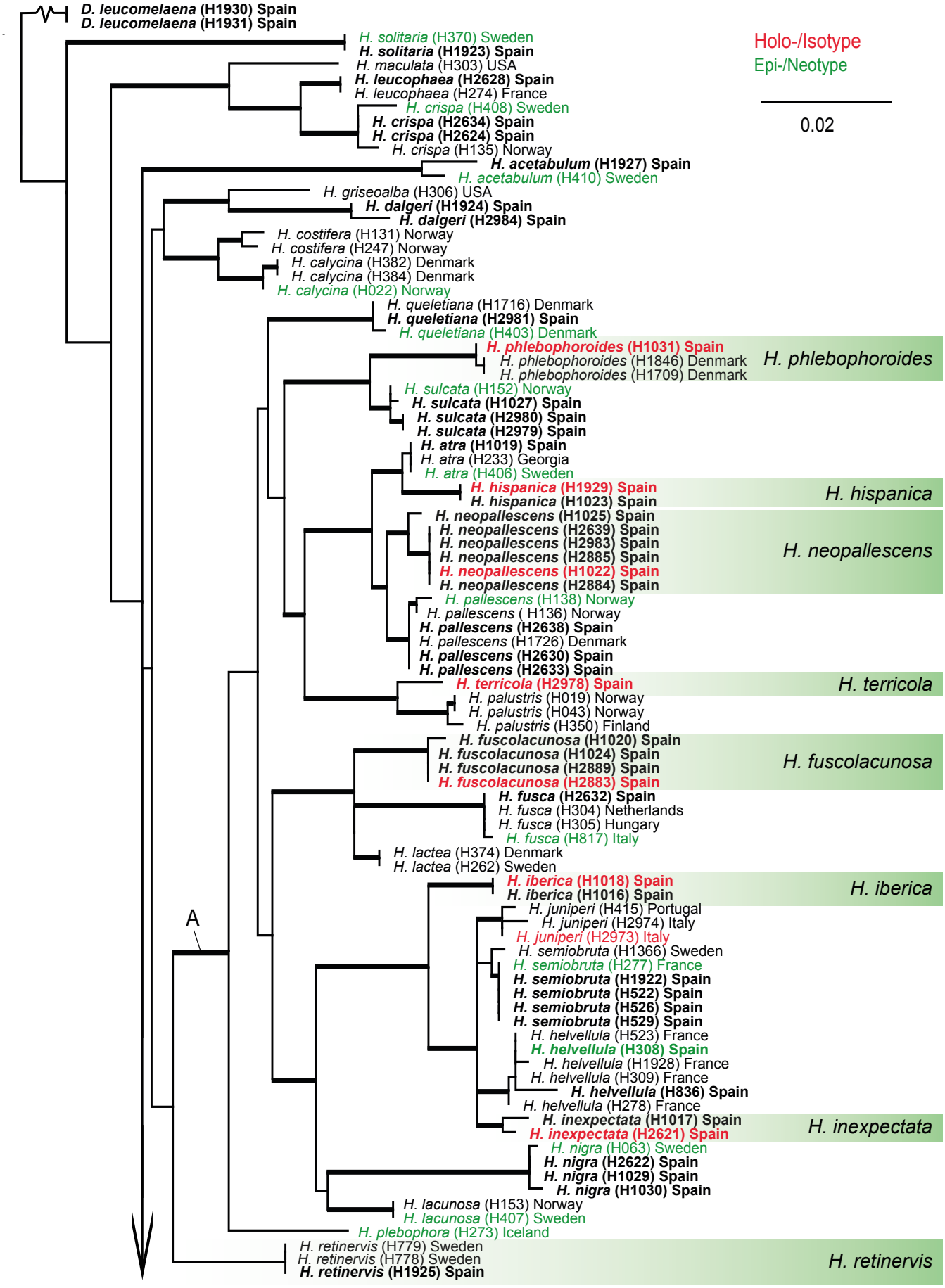

Fig. 1. Maximum likelihood tree of Spanish and other members of *Helvella* using parts of the RNA polymerase II second largest subunit (*rpb2*), heat shock protein 90 (*hsp*) and nuclear ribosomal large subunit DNA (LSU). Branches supported by ML bootstrap analyses (>70) are thickened. *Dissingia leucomelaena* is used as outgroup. Sequences from holo-/isotype (red) and epi-/neotype (green) are colour-coded. Green boxes indicate species described in the present study. Sequences from Spain are in bold.

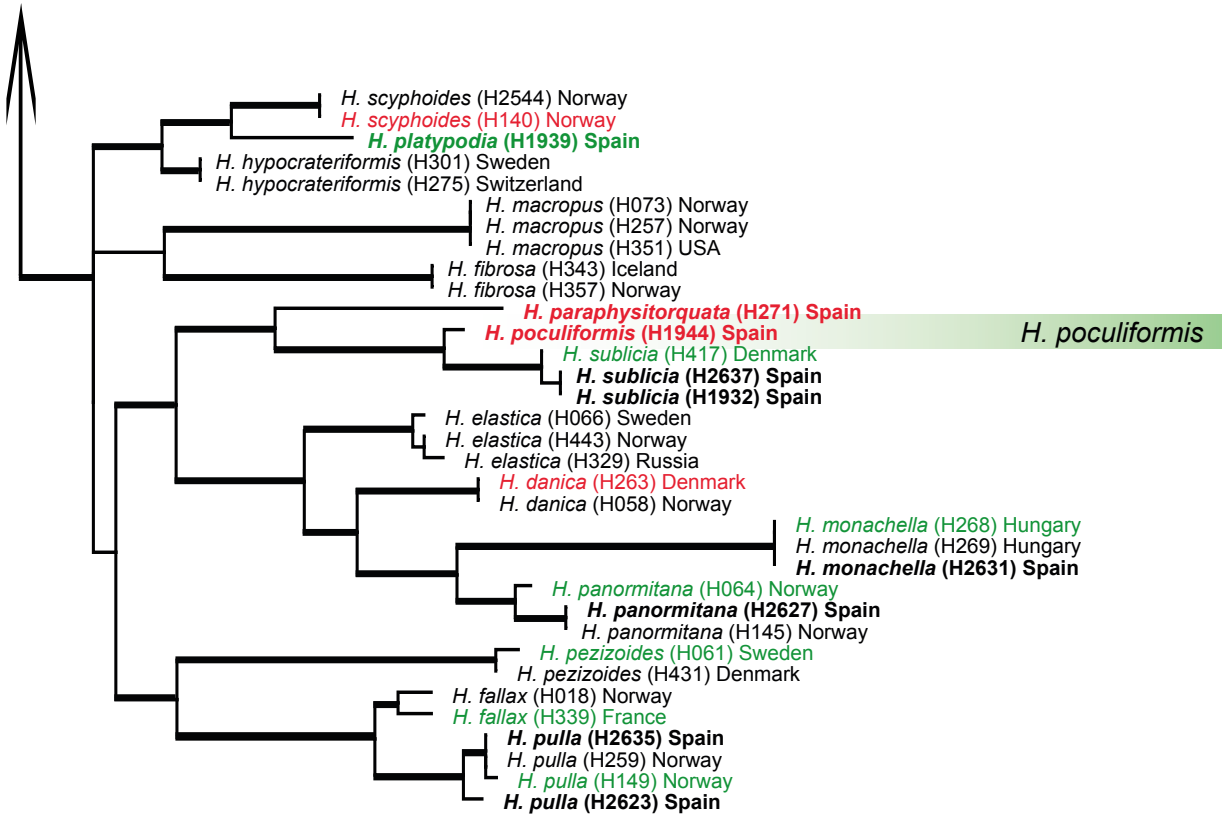

Fig. 1. (Continued).

white to light greyish white, drying yellowish to brownish, *receptacle* surface even, pubescent, pale to medium brown. *Stipe* prominent, 3–10 cm high, 1–3 cm broad, widest below, pure white when fresh, with densely set irregular longitudinal anastomosing ribs and dep grooves, hollow with longitudinal chambers inside. *Medullary excipulum* of *textura intricata*, hyphae 5–7 µm broad. *Outer excipulum* of *textura angularis*, cells irregular in shape and size, 12–25 × 5–25 µm, outermost cells prismatic to club-shaped, arranged in fascicled rows forming tufts of hyphae, walls pale brown. *Asci* pleurorhynchous, 260–310 × 12–16 µm. *Ascospores* ellipsoid, uniguttulate, 17.8–19.0–21.4 × 10.8–11.9–12.6 µm. *Paraphyses* 3–4 µm below, slightly enlarged to 6–9 µm at the clavate tips.

Specimens examined/sequenced: See Table 1.

Notes: European specimens of *H. crispa*, including the Spanish specimens, are morphologically uniform, but molecularly variable, however, still constituting a single distinct species in our phylogeny (*cf.* Fig. 1).

Helvella dalgeri Donadini, *Bull. Soc. linn. Provence* **35**: 136. 1985 [1984]. Fig. 2G, H.
Basionym: *Acetabula barlae* Boud., Hist. Class. Discom. Eur.: 40. 1907.
non Helvella barlae Boud. & Pat., J. Bot., Paris 2: 445. 1888.

Illustration: Boudier (1908b): n°. 349, pl. 245 (as *Acetabula barlae*).

Apothecium regularly short-stipitate cupulate, cup 3–5 cm broad, stipe 0.5–1.5 cm high, 0.7–1.5 cm broad, *hymenium* black, receptacle dark greyish black, with conspicuous, delicate white ribs extending from the stipe onto the receptacle; ribs on stipe and receptacle high and prominent, sharp-edged, branching, attachment points of ribs in periphery at the mid part of the receptacle surface. *Medullary excipulum* of compact *textura intricata*, hyphae multiseptate, 4–7 µm broad. *Outer excipulum* of *textura angularis*, cells 20–35 × 10–20 µm, outermost cells cylindrical to drum-shaped forming dense rows of cells turning out perpendicular to receptacle surface. *Asci* cylindrical, pleurorhynchous, 280–340 × 14–18 µm, with a long, flexuous, spore-free lower part. *Ascospores* ellipsoid, 18.2–19.2–20.5 × 9.4–10.1–11.4 µm, with one large internal guttule. *Paraphyses* 3–4 µm broad below, enlarged to a clavate apical cell segment 20–30 µm long, by 5–7 µm broad.

Specimens examined/sequenced: See Table 1.

Notes: This relatively large, greyish black, short-stipitate species was described as *Acetabula barlae* by Boudier (1908b). Since the earlier name *Helvella barlae* Boud. & Pat. (1888) exists, Donadini (1985) proposed the new name *H. dalgeri* for this South European species. The species was misinterpreted by Skrede *et al*. (2017) who, based on Boudier's plate and description (Boudier 1908b), placed *Acetabula barlae* in synonymy with *Helvella arctoalpina* Harmaja. The prominent white ribs on cup and stipe, which contrast with the dark-coloured receptacle surface, characterise the gross morphology of the species. In our phylogeny (Fig. 1) *Helvella dalgeri* is nested with *H. griseoalba* in a highly supported clade sister to the /costifera lineage in our phylogeny (*cf.* Fig. 1). A hypogeous *Helvella* specimen from Masegoso (Albacete) was shown molecularly identical to *H. dalgeri* (*cf.* Fig. 2G and Table 1).

Helvella fusca Gillet, *Champ. Fr., Discom*. **1**: 9. 1879. Fig. 5B.
Synonyms: See Skrede *et al.* (2017).

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

Apothecium stipitate-capitate, 1.8–3.5 cm broad, 0.7–4.5 cm high, irregularly bi- to tri- to tetralobate, saddle-shaped, with adnate, partly fused margin, *hymenium* light to medium to dark brown when fresh, drying brownish black, *receptacle* greyish white to pale brown, sub-pubescent, with low, anastomosing densely packed ribs on the receptacle surface. *Stipe* white to yellowish brown, 3–7 cm high, 1–2.5 cm broad, with longitudinal

Fig. 2. Photographs of apothecia in their natural habitat. **A.** *Dissingia leucomelaena* AEA0010 [H1930]. **B.** *Helvella acetabulum* LB13062401 [H1940]. **C.** *H. acetabulum* GM2507 [H1942]. **D.** *H. calycina* GM1504 [H848]. **E.** *H. calycina* RM2338 [H845]. **F.** *H. calycina* FB160514 [H849]. **G.** *H. dalgeri* AR090502 [H2984]. **H.** *H. dalgeri* PG250217 [H1924]. **I.** *H. retinervis* 2404-16HP1 [H1000]. **J.** *H. retinervis* ARAN3008363 [H1925]. Scale bars = 1 cm. All photographs taken by the collectors (confer Table 1).

anastomosing ribs and deep, partly lacunose furrows. *Medullary excipulum* of loosely interwoven *textura intricata*, hyphae 3–8 µm broad, hyaline. *Outer excipulum* of *textura angularis* to *textura prismatica*, brownish, outermost cells in rows perpendicular to receptacle surface, cells cylindrical to club-shaped, partly in few-celled fascicles (tufts). *Asci* pleurorhynchous, 260–320 × 14–16 µm. *Ascospores* uniguttulate, 17.4–18.7–20.8 × 11.0–12.1–13.2 µm. *Paraphyses* 3–4 µm broad below, with yellowish brown content, enlarged to 5–8 µm at the clavate tips.

Specimens examined/sequenced: See Table 1.

Fig. 3. Photographs of fresh apothecia and illustrations **A.** Authentic illustration of *Helvella sulcata* deposited in the fungarium of Uppsala (UPS), photograph taken by Åsa Kruys. **B.** *H. sulcata* RM2238 [H1027]. **C.** *H. atra* PIPE0966 [H1019]. **D.** *H. queletiana* RM0749 [H2981]. **E.** *H. phlebophoroides* RM2193 [H1031]. Scale bars = 1 cm. Photographs B, C, D and E are taken by the collectors (confer Table 1).

Fig. 4. Photographs of apothecia in their natural habitat. **A.** *Helvella leucophaea* LB121208 [H2628]. **B.** *H. crispa* LB07101201 [H2626]. **C.** *H. nigra* GM1085 [H1030]. **D.** *H. juniperi* MCVE 20997 [H2973]. Scale bars = 1 cm. All photographs taken by the collectors (confer Table 1).

Notes: *Helvella fusca* is a spring and early summer occurring species characterised by a stipitate saddle-shaped apothecium with brown hymenium and a white, lacunose stipe with delicate anastomosing ribs extending onto the receptacle surface. *Helvella fusca* occurs in association with *Populus* and is likely to form ectomycorrhiza with this host. See Notes of *H. fuscolacuonsa* for information on how to distinguish *H. fusca* from the morphologically similar species *H. fuscolacuosa*.

Helvella fuscolacunosa Skrede & T. Schumach. ***sp. nov.*** MycoBank MB834620. — Fig. 5A.

Etymology: Pertaining to the dark brown colour tinged with greyish and blackish (*adj*. fuscous) of the hymenium in combination with the ribbed, lacunose stipe.

Typus: **Spain**, Balearic Islands, Mallorca, Formentor, 7 Apr. 1982, *S. Sivertsen* (**holotype** TRH-12618).

Apothecium stipitate-capitate, 2.5–4.2 cm broad; irregularly saddle-shaped, trilobate, deflexed, that may mask its general shape; margin involute and wavy. *Hymenium* grey-brown to almost black, surface with ± bulges; receptacle pale grey, subpubescent, occasionally with inconspicuous veins. *Stipe* whitish, hollow, with internal chambers, up to 5 cm high and 2 cm broad, sub-pubescent, with 5 to 8 partly anastomosing, sharp ribs and deep grooves and a few lacunae between, ribs continuing onto the receptacle surface. *Medullary excipulum* of densely packed *textura intricata*, hyphae 3–7 µm broad, light brown-walled. *Outer excipulum* of *textura angularis* with some interwoven hyphae between, cells 7–30 × 5–20 µm, outermost cells cylindrical to club-shaped in rows terminating in a subcapitate up to 45 µm long end cell. *Asci* cylindrical, pleurorhynchous, 270–300 × 13–17 µm, ascospores often transversely arranged in young asci. *Ascospores* broadly ellipsoid, uniguttulate, 15.6–16.4–18.8 × 11.0–11.8–12.5 µm. *Paraphyses* 3–4 µm broad below, straight, enlarged to 6–8 µm at the clavate tips.

Specimens examined/sequenced: See Table 1.

Notes: *Helvella fuscolacunosa* shares stature and hymenium colour with *H. fusca* and *H. neopallescens*. However, while the stipe is interspersed with some lacunae (“holes”) in *H. fuscolacunosa* and *H. fusca*, these are lacking in *H. neopallescens*. Microanatomically, the ascospores in *H. fuscolacunosa* are smaller and broader than in *H. fusca* and *H. neopallescens*. Molecularly, *H. fuscolacunosa* deviates consistently in four *hsp*, three *rpb2* and 18 LSU substitutions from *H. fusca*, and in nine *hsp*, seven *rpb2* and 25 LSU substitutions from *H. neopallescens*.

Fig. 5. Photographs of apothecia in their natural habitat. **A.** *Helvella fuscolacunosa* LB12120804 [H1020]. **B.** *H. fusca* LB160409 [H2632]. Scale bars = 1 cm. Both photographs taken by the collectors (confer Table 1).

Helvella helvellula (Durieu) Dissing, *Rev. Mycol.* **31**: 204. 1966. Fig. 6E, F.
Basionym: *Peziza helvellula* Durieu, *Expl. Sci. Algerie* **1**: t. 27, f. 11. 1849.
Synonyms: See Skrede *et al*. (2017).

Illustrations: Durieu (1849): t. 27, f. 11, as *Peziza helvellula*, Boudier (1908a): nº. 346, pl. 247, as *Acetabula clypeata*), Caroti *et al*. (2007: pp. 33, 35, 41).

Apothecium subsessile to short-stipitate-cupulate, 1.2–2.5 cm broad; cupulate to irregular cupuliform to discoid, margin undulate and gently involute, *hymenium* black, receptacle surface furfuraceous, blackish, slightly sooty (fuliginous) towards the stipe. *Stipe* short, solid, cylindrical to flattened, 0.7–1.2 cm high, by 0.3–0.7 cm broad, somewhat thickened at the base, with 1 to 2 longitudinal grooves, at the top concolourous with the receptacle, paler towards the base which is almost always totally buried. *Medullary excipulum* of *textura intricata*, hyphae 3–5 µm broad. *Outer excipulum* of *textura angularis*, cells of uneven size, 10–25 µm broad, interspersed with some inflated, larger cells 20–45 × 10–15 µm. terminating into cylindrical to club-shaped cells towards the surface. *Asci* pleurorhynchous, 320–390 × 16–20 µm. *Ascospores* ellipsoid, obtuse, with one large and several small internal guttules, 21.8–24.0–27.3 × 12.8–13.8–15.4 µm. *Paraphyses* 3–4 µm broad below, slightly enlarged to 5–8 µm at the irregularly clavate tips.

Specimens examined/sequenced: See Table 1.

Notes: *Helvella helvellula* is a subsessile to short-stipitate black, cupulate species, described by Durieu (1849) based on a specimen in Herb. C Montagne (PC). Dissing (1966a) did not find any original specimen of this Mediterranean species in Montagne's Herbarium in Paris (PC). Caroti *et al.* (2007) later succeeded in finding an original specimen from Morocco collected by M. Roussel in 1836 and deposited in Montagne's herbarium in PC (see photograph on p. 41 in Caroti *et al*.). This specimen, which apparently is part of the original description of Durieu's species is probably too old to provide DNA for sequencing, thus the epitype selected by Skrede *et al.* (2017) from the Canary Islands is still in place to provide necessary information for a molecular identification of the species.

The Spanish collections are from acid soil, at altitudes from 500 to 1 100 m. a.s.l., always associated with *Cistus*, *i.e*. *Cistus albidus*, *C. salviifolius* and *C. laurifolius*. Short-stipitate specimens (see Fig. 6F) may be confused with *H. semiobruta,* which occurs in the same habitat, but, the apothecia in *H. semiobruta* are stipitate-capitate, with a bi- to trilobate convex cap and an elongate hollow stipe.

Helvella hispanica Skrede & T. Schumach. ***sp. nov.*** MycoBank MB834621. Fig. 7C, D.

Etymology: Referring to its place of origin (in Spanish language).

Typus: **Spain**, Ventosa, 11 Mar. 2017, *L. Ballester* LB17031103 (**holotype** O-F-256537).

Apothecium stipitate-capitate, cap 2.5–4.5 cm broad, irregular saddle-shaped, adnate, margin generally free but attached to the stipe at 2 to 4 points, *hymenium* dark greyish black to black, even or wrinkled folded, *receptacle* paler, greyish, smooth, with branching, blunt ribs. *Stipe* cylindrical, hollow, 2–7 cm high, 2–4.5 cm broad, whitish to grey, with 3 to 7 longitudinal, prominent, partly double-edged blunt ribs and deep grooves, occasional with some elongate lacunae. *Medullary excipulum* of dense *textura intricata*, hyphae 3–6 µm broad. *Outer excipulum* of *textura angularis* to *textura prismatica*, brownish, angular cells 10–20 µm interspersed with prismatic cells in rows, 8–14 µm broad, turning out perpendicular to receptacle surface, outermost cells club-shaped. *Asci* pleurorhynchous, 260–310 × 12–16 µm. *Ascospores* elongate-ellipsoid, 16.8–17.8–19.6 × 8.2–9.5–11.2 µm, with one large internal oil drop. *Paraphyses* straight, 3–5 µm below, indistinctly enlarged at the clavate tips.

Specimens examined/sequenced: See Table 1.

Notes: This new species is nested in the /atra-pallescens lineage, as delineated by Skrede *et al*. (2017). It resembles *H. lacunosa* in the ribbed, whitish stipe, the greyish-black to black hymenium, and the greyish-black outer cap surface. The apothecial margin

is generally free from the stipe. It genetically diverges from its sister species *H. atra* in two *hsp*, one *rpb2* and five LSU substitutions (*cf*. Fig. 1).

Helvella iberica Skrede & T. Schumach. ***sp. nov.*** MycoBank MB834622. Fig. 6A, B.

Etymology: Referring to its occurrence on the Iberian Peninsula.

Typus: **Spain**, El Rasillo, 13 Apr. 2013, *R. Martinez* RM2373 (**holotype** O-F-256539).

Apothecium stipitate-capitate, cap 1.5–3.5 cm broad, irregularly saddle-shaped with 2 to 4 lobes, adnate; margin free, *hymenium* dark greyish black to black, even or wrinkled folded, receptacle paler, light grey to greyish black, smooth, with branching blunt ribs continuing from stipe. *Stipe* cylindrical, 2–4 cm high, 0.7–1.5 cm broad, whitish to greyish, with deep, longitudinal, undulating furrows and blunt ribs, with some ± lacunae between. *Medullary excipulum* of loose *textura intricata*, hyphae 4–6 µm broad. *Outer excipulum* of *textura angularis*, individual cells 12–24 × 10–20 µm, light brown-walled, outermost cells club-shaped to sub-capitate. *Asci* pleurorhynchous, 260–310 × 15–21 µm. *Ascospores* elongate ellipsoid, 18.2–20.4–21.8 × 10.8–12.0–13.8 µm, with one large internal oil drop. *Paraphyses* straight, 4–6 µm below, slightly bent at tips, enlarged to 7–9 µm at the clavate tips.

Specimens examined/sequenced: See Table 1.

Notes: *Helvella iberica* is nested in the /helvellula lineage, as delineated by Skrede *et al*. (2017) (*cf*. Fig. 1). It resembles *H. juniperi* in colour and stature (Filippa & Baiano 1999). However, the free apothecial margin and five *hsp* and one *rpb2* substitutions separate it from the latter. See also Fig. 4D and 'Notes' under *H. inexpectata* and *H. semiobruta* below.

Helvella inexpectata Skrede & T. Schumach. ***sp. nov.*** MycoBank MB834623. Fig. 6G, H.

Etymology: Referring to the unexpected occurrence of yet another species of the /helvellula lineage on the Iberian Peninsula.

Typus: **Spain**, Sojuela (La Rioja), 5 Mar. 2016, *A. Ezquerro* AE160305 (**holotype** O-F-256541).

Apothecium stipitate-capitate, cap black to greyish black, 1.5–4 cm broad, in young specimens bi- to trilobate, later more irregular in shape, margin gently involute, deflexed and adhered to the stipe, *hymenium* greyish black to black, *receptacle* surface greyish, smooth to furfuraceous, covered by tiny veins. *Stipe* cylindrical, 1.2–4 cm high, by 0.5–4.5 cm broad, hollow with a few internal chambers, concolourous with receptacle or paler above, whitish below, with six to eight blunt, longitudinal ribs and deep grooves. *Medullary excipulum* of dense *textura intricata*, hyphae 2.8–5.5 µm broad, pale brown-walled. *Outer excipulum* of densely packed rows of angular to club-shaped cells, 10–30 × 7–15 µm, strongly constricted at septa, turning out perpendicular to receptacle surface. *Asci* pleurorhynchous, 280–320 × 14–18 µm. *Ascospores* oblong ellipsoidal, 18.4–19.6–21.4 × 10.6–11.7–12.8 µm, with one large and several small internal guttules. *Paraphyses* straight, 2.5–3.5 µm below, enlarged to 5–6.5 µm at the clavate tips.

Specimens examined/sequenced: See Table 1.

Notes: *Helvella inexpectata* has a convex cap and a short greyish white stipe with longitudinal blunt ribs and deep grooves between. It is nested with *H. helvellula, H. iberica, H. juniperi* and *H. semiobruta* in a highly divergent /helvellula lineage of the /lacunosa clade (Fig. 1, *cf*. also Skrede *et al*. 2017). The species resembles *H. juniperi* (Fig. 4D) and *H. iberica* (Fig. 6A, B) in shape and colour, but has smaller and more oblong, narrow ascospores than these 'look alike' species. The Spanish specimens of *H. iberica* and the Italian holo- and isotype specimens of *H. juniperi*, newly sequenced by us, differ in three and two *hsp*, and one and two *rpb2* substitutions, respectively.

Helvella leucophaea (Batt.) Pers., *Obs. mycol.* **2**: 19. 1799. Fig. 4A.
Basionym: *Boletus leucophaea* Battara, Fungorum Arimin.: 25. 1759.
Synonym: *Helvella pithyophila* Boud., *J. Bot.* **1**: 218. 1887.

Illustrations: Trattinia (1809: pl. 28, as *H. leucophaea* Pers.), Boudier (1887: pl. 3; 1904b: n°. 17, pl. 227, as *H. pithyophila*).

Apothecium stipitate-capitate, apothecia irregular saddle-shaped, 3–7 cm broad, *hymenium* pale olive brown, uneven bulged (wrinkled), margin crenate, reflexed, *receptacle* sub-pubescent, ochraceous brown, with low, branching, interconnected ribs. *Stipe* cylindrical, 6–10 cm high, by 1.5–3.5 cm broad, grey to dark greyish brown, sub-pubescent, with deep, longitudinal, irregular furrows and sharp-edged ribs, inside of stipe with uneven-sized longitudinal chambers. *Medullary excipulum* of interwoven septate, brown, branching hyphae, 3–5 µm broad. *Outer excipulum* of *textura angularis*, cells mostly 10–20 × 6–15 µm, outermost layer of cylindrical to club-shaped 3- to 5-celled protruding hyphae, 10–15 µm broad. *Asci* cylindrical, pleurorhynchous, 290–350 × 14–16 µm. *Ascospores* ellipsoid, with one large and numerous small internal oil drops, 16.2–18.8–20.4 × 10.2–10.8–12.0 µm. *Paraphyses* subhyaline, 3–4 µm broad below, enlarged to 6–10 µm at the irregular clavate tips, terminal cell thick-walled with incrusted, adhesive pigments.

Specimen examined/sequenced: See Table 1.

Notes: *Helvella leucophaea* resembles *H. crispa* in size and stature. However, the hymenium and stipe in fresh ascomata of the former are greyish to greyish brown, drying caramel brown. The two individuals from France and Spain are molecularly identical. Four consistent *rpb2* and two *hsp* substitutions separate *H. leucophaea* and its sister species *H. crispa* of the /crispa lineage (*cf.* Skrede *et al*. 2017).

Helvella macropus (Pers.) P. Karst., *Not. Sällsk. F. Fl. Fenn. Förh.* **11**: 224. 1870. Fig. 8F.
Basionym: *Peziza macropus* Pers., *Ann. Bot. (Usteri)* **15**: 26. 1795; Fr., *Syst. Mycol.* **2**: 57. 1822.
Synonyms: See Skrede *et al*. (2017).

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

Fig. 6. Photographs of apothecia in their natural habitat. **A.** *Helvella iberica* GM2907 [H1016]. **B.** *H. iberica* RM2373 [H1018]. **C.** *H. semiobruta* RM2302 [H522]. **D.** *H. semiobruta* AC5335 [H524]. **E.** *H. helvellula* RM321 [H523]. **F.** *H. helvellula* LB15002101 [H525]. **G.** *H. inexpectata* RM1088 [H1017]. **H.** *H. inexpectata* AE160305 [H2621]. Scale bars = 1 cm. All photographs taken by the collectors (confer Table 1).

Apothecium stipitate-cupulate, cup ± regular saucer-shaped, 1.5–3 cm broad, *hymenium* yellowish to greyish brown, receptacle concolourous, villose. Stipe terete, 2.5–12 cm high, 0.3–0.5 cm broad, pubescent. *Medullary excipulum* of loosely interwoven *textura intricata*, hyphae generally 4–6 µm broad, brownish, some hyphae with inflated cells 10–20 µm broad, constricted at septa. *Ectal excipulum* of *textura intricata*, innermost cells 10–30 µm broad, turning into fascicled rows of cylindrical cells 20–35 × 10–15 µm in outermost excipulum, some hyphae extending into 50–200 µm long fascicled hyphoid hairs. *Asci* pleurorhynchous, 240–300 × 13–16 µm. *Ascospores* ellipsoid-fusoid, with one large and two to three medium large internal guttules, 19.5–23.4–25.8 × 9–10.5–12.0 µm. *Paraphyses* 3–4 µm below, gradually enlarged to 5–9 µm at the clavate tips.

Specimens examined/sequenced: See Table 1.

Notes: Our molecular survey of *Helvella* species in Europe and the Nordic countries confirms the existence of five or six phylogenetic species in the *H. macropus* morphospecies complex (including *H. fibrosa*), of which *H. macropus* is the most common species in Europe.

Fig. 7. Photographs of apothecia in their natural habitat. **A.** *Helvella neopallescens* LB14011801 [H1021]. **B.** *H. neopallescens* LB13062402 [H1026]. **C.** *H. hispanica* LB16022002 [H528]. **D.** *H. hispanica* PIPE-0833 [H1023]. **E.** *H. terricola* LB18092810 [H2978]. **F.** *H. pallesens* RM378 [H2638]. Scale bars = 1 cm. All photographs taken by the collectors (confer Table 1).

Helvella monachella (Scop.) Fr., *Syst. Mycol.* **2**: 18. 1822. Fig. 8B.
Basionym: *Phallus monacella* Scop., *Fl. Carniol.*, ed. **2**, **2**: 478. 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.).
Synonyms: *Helvella albipes* Fuckel, *Jahrb. Nassau. Vereins Naturk*. **23–24**: 334. 1870.
Helvella leucopus Pers., *Mycol. Eur.* **1**: 213. 1822.

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

Apothecium stipitate-capitate, cap 1.5–4 cm broad, saddle-shaped or irregularly lobate, deflexed, margin occasionally reflexed, free, *hymenium* dark brown to brownish black, *receptacle* smooth, whitish to pale greyish. *Stipe* terete, hollow, whitish, 3–7 cm high, 1–2 cm broad, often with irregular groves. *Medullary excipulum* of *textura intricata*, hyphae 3–6 µm broad, some hyphae heavily pigmented, blackish. *Outer excipulum* of *textura angularis*, cells cylindrical to club-shaped, 15–40 × 6–20 µm, arranged in rows turning out perpendicular to receptacle surface. *Asci* pleurorhynchous, 260–310 × 15–18 µm. *Ascospores* ellipsoid, 20.6–22.0–23.8 × 12.7–14.1–15.2 µm, with one large internal oil drop. *Paraphyses* straight, 3–5 µm below, enlarged to 6–8 µm broad at the clavate tips.

Specimens examined/sequenced: See Table 1.

Note: The sequenced specimens from Spain have *hsp* and *rpb2* sequences identical to the rest of the sequenced specimens from Europe.

Helvella neopallescens Skrede & T. Schumach. ***sp. nov.*** MycoBank MB834625. Fig. 7A, B.

Etymology: Referring to it being genetically similar to *H. pallescens*.

Typus: **Spain**, Rioja, Logrono, La Grajera, 7 Feb. 2015, *R. Martinez* RM2397 (**holotype** O-F-256550).

Apothecium stipitate-capitate, cap 2.5–4.5 cm broad, irregularly saddle-shaped, margin reflexed but attached to stipe at 3 to 4 points, *hymenium* dark brownish to greyish black, even, *receptacle* paler, greyish, smooth, with ± anastomosing, delicate veins on the surface. *Stipe* whitish to greyish to dark grey, highly irregular in shape and length, ± cylindrical, 2–6 cm high, 0.8–2.5 cm broad, with 5–7 longitudinal blunt-edged ribs, hollow, with large chambers inside. *Medullary excipulu*m of densely interwoven *textura intricata*, hyphae 3–5 µm broad. *Outer excipulu*m of irregular *textura angularis*, cells relatively broad, 15–35 × 12–25 µm, outermost cells club-shaped, short-celled. *Asci* cylindrical, pleurorhynchous, 260–310 × 12.5–15 µm. *Ascospores* obtuse ellipsoidal, 16.1–16.8–18.2 × 9.2–9.6–11.4 µm, with one large internal oil drop. *Paraphyses* 3–5 µm below, enlarged to 7–8 µm broad at the clavate to spadiceiform tips.

Specimens examined/sequenced: See Table 1.

Notes: *Helvella neopallescens* is nested in the /atra-pallescens lineage, as delimited by Skrede *et al.* (2017). Morphologically, it resembles *H. hispanica, H. fuscolacunosa*, and *H. lacunosa* by the hollow, ribbed, and partly lacunose, whitish stipe and the contrasting brown to blackish cap, but is genetically distinct (*cf*. Fig. 1). It deviates from its morphologically dissimilar sister species *H. pallescens* in two *hsp*, one *rpb2* and four LSU substitutions.

Helvella nigra Berg., *Phytonom. univ.* **1**: t. 147. 1783. Fig. 4C.
non Helvella nigra Peck, *Bull. Torrey Bot. Club* **26**: 70. 1877, *nom. illeg.* (homonym).
See Skrede *et al*. (2017) for synonyms and typification.

Illustration: Bergeret (1783: pl. 147).

Apothecium stipitate-capitate, 2–6 cm across, cap saddle-shaped, bi- to trilobate, from 6 to 15 cm in height, apothecial margin adnate, firmly attached to the stipe at 4 to 6 points; *hymenium* wrinkled, dark grey to greyish black when fresh, drying darker, receptacle concolourous, smooth. *Stipe* concolourous or slightly paler, lacunose, *receptacle* surface concolourous or slightly paler, smooth, with distinct, branching ribs. *Stipe* 2.0–4.5 cm broad, naked, ribbed, ash grey to almost black, longitudinal ribs high and prominent, sharp, partly anastomosing and double-edged, with deep 'holes' (lacunae) between ribs, stipe hollow and 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 outgrowth of few cells colouring intensely in cotton blue. *Asci* pleurorhynchous, 290–330 × 14–16 µm. *Ascospores* ellipsoid, uniguttulate, 16.5–17.8–19.0 × 10.4–11.1–12 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: See Table 1.

Notes: *Helvella nigra* is characterised by greyish black ashen colours, a tall, slender stature, a ribbed, lacunose stipe, and a reflexed and lobed cap with prominent ribs on the receptacle surface. The apically bent paraphyses (like a "golf-club") are characteristic under the lens. Eight *hsp*, three *rpb2* and 25 LSU characters distinguish *H. nigra* and *H. lacunosa*.

Helvella pallescens Schaeff., *Fungi Bavar. Palat. Nasc.* **4**: 114. 1774 ('*Elvela*'). Fig. 7F.
Synonym: *Helvella sulcata* β (var.) *pallescens* (Schaeff.) Fr., *Syst. Mycol.* **2**: 16. 1822.

Illustration: Schaeffer (1774: pl. 322).

Apothecium 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 to 4 points, *hymenium* white to pale greyish drying brownish yellow; *receptacle* surface and stipe white to pale yellowish to brown, drying brown. *Stipe* long and slender, 0.5–1.5 cm broad, 4–6 cm high, hollow, with four to five longitudinal ribs and a few lacunae between. *Medullary excipulum* of an interwoven *textura intricata*, hyphae of variable thickness, 4–10 µm broad. *Outer excipulum* of *textura globulosa* to *textura angularis*, cells 20–40 µm diam, the outermost cells more elongated and prismatic

giving rise to a cover of densely packed club-shaped cells on receptacle surface. *Asci* pleurorhynchous, 280–310 × 14–15 µm, young asci with numerous cyanophilic ascospores with large pustules adhering to the spore wall. *Ascospores* broadly ellipsoid, 15.0–17.0–18.2 × 10.2–11.8–13.2 µm. *Paraphyses* hyaline, 2–3 µm broad, septate, gradually enlarged into irregular clavate tips, 6–10 µm broad.

Specimens examined/sequenced: See Table 1.

Notes: *Helvella pallescens* is a slender, whitish to greyish species that has been confused with *H. lactea*, with which it shares similar colours and microanatomy. Eight *rpb2* and nine *hsp* substitutions separate *H. pallescens* and *H. lactea.* The species is nested in the /lacunosa clade (Fig. 1).

Helvella panormitana Inzenga, *Funghi siciliani* **1**: 41. 1865. Fig. 8A.

Illustrations: Inzenga (1865: pl. 4. f.$1_{1–4}$).

Apothecium 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, receptacle smooth, white or pale yellow, concolourous with stipe, drying brownish orange. *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 hyphae, 3–4 µm broad, embedded in an amorphous gelatinous matrix. *Outer excipulum* a mixture of *textura intricata* and *textura angularis*, hyphae up to 8 µm broad, angular cells generally 25–40 µm in 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, 19–22.2–24 × 11.5–12.7–13.5 µm. *Paraphyses ca*. 3 µm broad below, septate, light brown, gradually enlarged to 6–8 µm at the clavate tips.

Specimens examined/sequenced: See Table 1.

Notes: *Helvella panormitana* was originally described from Sicily, Italy (Inzenga 1865). The species deviates from the morphologically similar *H. elastica* in 5 *hsp*, 11 *rpb2* and 10 LSU substitutions. The species is widely distributed in Europe (*cf*. Skrede *et al.* 2017).

Helvella pezizoides Afzel., *Kongl. Vetensk. Acad. Nya Handl.* **4**: 308. 1783. - *nom. sanct.* Fig. 9A, B, D, F.
Synonym: *Leptopodia pezizoides* (Afzel.) Boud., *Icon. Mycol., liste prelim*.: 2. 1904.

Illustrations: Afzelius (1783: pl. 10, f. 2), Dissing (1966b: 117).

Apothecium involute, stipitate, 0.5–1.5 cm broad, with edge permanently deflexed, *hymenium* black, *receptacle* surface pubescent, ash grey. *Stipe* brownish black, terete, pubescent, 1–2 cm high, 0.4–0.7 cm broad. *Medullary excipulum* of loose *textura intricata*, hyphae hyaline, 4–7 µm broad, interspersed with some distinct brownish black hyphae. *Outer excipulum* of *textura angularis*, cells thick-walled, brownish, turning out in dense rows perpendicular to receptacle surface, outermost cells irregularly club-shaped, constricted at septa, forming two-three-celled brownish dense individual hyphae to 50 µm long by 15 µm broad. *Asci* pleurorhynchous, 260–300 × 12–15 µm. *Ascospores* ellipsoid, 14.5–15.3–16.5 × 8.5–9.0–9.6 µm, with one large guttule in rehydrated material. *Paraphyses* straight, 3.5–4.5 µm broad below, gradually enlarged to 5.5–7 µm at the clavate tips.

Specimens examined/sequenced: See Table 1.

Notes: Morphologically, *H. pezizoides* resembles *H. fallax* and *H. pulla* in colour, but the pubescent receptacle and stipe separate it from the two latter species. In an ongoing study of *Helvella* in the Nordic countries, we discovered an authentic collection of *H. pezizoides* in the fungarium of Stockholm (S), and a colour plate of *H. pezizoides* in the fungarium of Uppsala (UPS) both examined and prepared by Adam Afzelius himself. The original specimen in S is three apothecia of Afzelius' original material mounted and glued to a sheet and filed under the name of *Peziza* (*stipitata*), a name which was also referred to by Afzelius in his original description of *H. pezizoides* (*cf.* Afzelius 1783, p. 308). The colour plate in UPS is a drawing of this fungarium sheet (now in S), which was also reproduced in an inverted version as a figure in the original work by Afzelius (1783, tab X, fig. 2). This figure was selected as a lectotype (iconotype) of *H. pezizoides* by Dissing (1966b). The original collection of Afzelius was tentatively referred to *H. villosa* [= *H. fibrosa* (Wallr.) Korf] by Dissing (1966b: 69).

Helvella phlebophoroides Skrede & T. Schumach. ***sp. nov.*** MycoBank MB834601. Fig. 3E.

Etymology: Pertaining to the prominent ribbed (*phlebus* = veined) outer surface of the receptacle similar to that observed in *H. phlebophora*.

Typus: **Spain**, Rioja, Anguiano, 2 Jul. 2011, *R. Martinez* RM2193 (**holotype** O-F-256565).

Apothecium stipitate-capitate, saddle-shaped to plane, cap 1.5–3.5 cm broad, attached to stipe at two to three points, when fully developed with a deflexed and free margin, *hymenium* greyish black, surface even or wrinkled, *receptacle* smooth, pale grey to whitish. *Stipe* grey to greyish white, 3–6 cm high, 1–1.5 cm broad, with 4 to 7 partly double-edged, blunt longitudinal ribs and deep furrows with a few lacunae between, ribs extending onto the receptacle forming delicate, radial ribs and veins (*cf.* Fig. 3E). *Medullary excipulum* of dense *textura intricata*, hyphae 4–6.5 µm broad. *Outer excipulum* of a mixture of *textura angularis*/*intricata*, the outermost cells bound in loosely interconnected rows of cells, brown-walled, 10–20 × 5–12 µm, turning out perpendicular to receptacle surface, outermost cell club-shaped. *Asci* cylindrical with a lengthy narrow sterile portion below, pleurorhynchous, 280–320 × 12–15 µm. *Ascospores* ellipsoid, with one large oil drop when fully mature, 15.2–16.6–17.8 × 9.0–9.6–10.4 µm. *Paraphyses* straight, 4–5 µm broad, enlarged to 6–8 µm at the tips.

Specimens examined/sequenced: See Table 1.

Notes: *Helvella phlebophoroides* is sister species to *H. sulcata* in our phylogeny (*cf*. Fig. 1). Four *hsp* and three *rpb2* characters

separate the two species. The species occurs in Denmark as well (Table 1). *Helvella phlebophoroides* may be confused with *H. phlebophora* and *H. queletiana*, due to the prominent radiating ribs of the outer receptacle surface. However, *H.*

Fig. 8. Photographs of apothecia in their natural habitat. **A.** *Helvella panormitana* LB07101202 [H2627]. **B.** *H. monachella* LB150429 [H2631]. **C.** *H. poculiformis* GM1702 [H1944]. **D.** *H. sublicia* RM22 [H2637]. **E.** *H. sublicia* RM2286 [H1932]. **F.** *H. macropus* LB15091205 [H1933]. **G.** *H. platypodia* LB13061103 [H1939]. **H.** *H. solitaria* GM1011 [H1945]. **I.** *H. solitaria* GM2506 [H1946]. Scale bars = 1 cm. All photographs taken by the collectors (confer Table 1).

phlebophoroides, like *H. queletiana* has fewer and more distantly set, irregularly radiating ribs on the receptacle surface compared to *H. phlebophora*. These three species all form distinct phylogenetic groups. *Helvella phlebophoroides* and *H. queletiana* is separated by nine *hsp*, 10 *rpb2* and 19 LSU substitutions, and *H. phlebophoroides* and *H. phlebophora* by 10 *hsp*, 14 *rpb2* and 20 LSU substitutions.

Helvella platypodia (Boud.) Donadini, *Bull. Soc. linn. Provence* **35**: 136. 1985. [1984]. Fig. 8G.
Basionym: *Cyathipodia platypodia* Boud., *Hist. Class. Discom. Eur.*: 39. 1907.

Typus: **Lectotype** designated here (MycoBank MBT390951): Boudier, Icones Mycol. Livr. 22: nº. 467, pl. 241, as *C. platypodia* 1909a. **Epitype** designated here (MycoBank MBT390950): **Spain**, Rioja, Sorzano, under *Corylus avellana*, 11 Jun. 2013, *L. Ballester* LB13061103 (**epitype** O-F-256566).

Illustration: Boudier (1909a: nº. 467, pl. 241, as *C. platypodia*).

Apothecium cupulate-stipitate, small to medium-sized, 1.5–3.5 cm broad, by 1–2.5 cm high, regular cupulate to saucer-shaped and recurved when fully mature, *hymenium* and *receptacle* greyish to olive grey, concolourous, *receptacle* and *stipe* pubescent, drying rusty brown, *hymenium* drying dark brown. *Stipe* whitish to yellowish, compressed (flattened - 'platypodia'), solid, to 3.5 cm high, 0.5–1.5 cm broad, with 2 to 3 longitudinal grooves. *Medullary excipulum* of *textura intricata*, hyphae 3–6 µm broad, septate. *Outer excipulum* of *textura angularis*, cells elongate club-shaped in rows, 20–30 × 10–15 µm, cells in periphery constricted at septa, outermost cells protruding into scattered loose tufts of fascicled, multiseptate hyphae (hyphoid hairs), 40–150 µm long, by 10–25 µm broad. *Asci* pleurorhynchous, 270–310 × 13–15 µm. *Ascospores* ellipsoid, 16.5–18.1–19.0 × 11.0–11.9–12.5 µm, with one large internal oil drop and some smaller guttules at the poles. *Paraphyses* 2–3.5 µm broad, not much enlarged to 5–6 µm at the tips.

*Specimens examined/sequence*d: See Table 1.

Notes: We have resurrected the name *H. platypodia* for this species, lectotypified by Boudier's plate (iconotype), and supported with an epitype from Spain, which contributes partial *hsp* and *rpb2* sequences to the species. *Helvella platypodia* belongs in the /hypocrateriformis lineage, as delineated by Skrede *et al*. (2017).

Helvella platypodia is a small to medium-sized grey to olive grey species with a contrasting white, compressed, furrowed stipe. The ascoma turn rusty brown when dried, matching the colours and description (in dry condition) in Boudier (1909a), and then resembling miniature ascomata of *Helvella solitaria* (see this species below). The Spanish collection is on acid soil in association with *Corylus avellana* and *Populus nigra*. The species occurs in Denmark as well (*cf*. Table 1). Based on gross morphology in dried condition, *H. platypodia* has been intermixed with the genetically unrelated *H. solitaria* (= *H. queletii*) of the /acetabulum - solitaria lineage with less greyish but more brown-coloured hymenium and more elongate, larger ascospores.

Helvella poculiformis Skrede & T. Schumach. ***sp. nov.*** MycoBank MB834627. Fig. 8C.

Etymology: Pertaining to the cup-shaped apothecia in this species.

Typus: **Spain**, Zaragoza, 10 Nov. 2009, *G. Munoz* GM1702 (**holotype** O-F-256567).

Apothecium stipitate-cupulate, 1–2.5 cm broad, by 1.5–3.5 cm high, regular cupulate to saucer-shaped, *hymenium* and *receptacle* dark grey to greyish, concolourous, *receptacle* drying rusty brown, hymenium dark brown. *Stipe* terete, cylindrical, whitish to greyish white, 0.3–0.5 cm broad. *Medullary excipulum* of *textura intricata*, hyphae brownish, 3–4 µm broad. *Outer excipulum* of *textura angularis*, cells elongate club-shaped of even size, 15–20 × 8–15 µm, outermost cells extending into scattered multi-celled hyphae (hyphoid hairs), 30–80 µm long, 7–15 µm broad. *Asci* pleurorhynchous, 240–280 × 11.5–15 µm, ascospores ± obliquely arranged in asci. *Ascospores* ellipsoid, slightly narrowing towards the poles, 18.5–19.2–20.5 × 9.2–10.0–11.0 µm, with one large and several minor internal guttules at the poles. *Paraphyses* 2.5–3.5 µm broad, enlarged to 6–9 µm at the slightly spadiceiform, clavate tips.

Specimen examined/sequenced: See Table 1.

Notes: *Helvella poculiformis* resembles *H. sublicia* in shape and colour and is nested in the /rivularis – sublicia lineage of Skrede *et al.* (2017). The ascoma is regularly cupulate to saucer-shaped, with a dark greyish black cup and a contrasting whitish to greyish, terete stipe. *Helvella poculiformis* differs from *H. sublicia* in three *hsp* and four *rpb2* substitutions.

Helvella pulla Holmsk., *Beata ruris otia Fung. Dan.* **2**: 49. 1799. - *nom. sanct.* Fig. 9C, E.
Synonym: *Helvella fuliginosa* Schaeff., *Fung. Bavar. Palat. Nasc.* **4**: 113. 1774.

Illustrations: Holmskjold (1799: pl. 26), Schaeffer (1774: pl. 320, as *Helvella fuliginosa*).

Apothecium 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, *receptacle* concolourous, subpubescent. *Stipe* grey, terete or slightly compressed, sub-pubescent, 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 *ca*. 2.5–4.5 µm broad, subhyaline, intermixed with some broader, brown-walled hyphae. *Outer excipulum* of *textura prismatica*, hyphae light brown-walled, 5–15 µm broad, arranged in rows turning out perpendicular to receptacle surface, outermost cells club-shaped, 15–30 × 10–20 µm. *Asci* pleurorhynchous, 275–310 × 13–15 µm. *Ascospores* ellipsoid, 17.6–18.3–19.0 × 10.6–11.4–12.0 µm. *Paraphyses* subhyaline, 3–4 µm broad below, gradually enlarged to 8–12 µm at the tips.

*Specimens examined/sequence*d: See Table 1.

Notes: This grey to blackish species of the /fallax - pezizoides lineage may resemble *H. poculiformis* and *H. sublicia* (of the

/ rivularis - sublicia lineage) in colour, however, both ascoma ontogeny (permanently saddle shaped and bilobate in *H. pulla* versus cupulate to applanate to compressed in *H. poculiformis* and *H. sublicia*) and microanatomy (ascospore mean values 18.3 × 11.4 µm in *H. pulla* versus 19.2 × 10.0 µm in *H. poculiformis* and 20.1 × 12.5 µm in *H. sublicia*) as well as molecular data easily discriminate among the three.

Fig. 9. Photographs of apothecia, an illustration and a fungarium specimen. **A**. *Helvella pezizoides* RM2274 [H2636]. **B**. Authentic plate of *H. pezizoides* deposited in the fungarium of Uppsala (UPS). **C**. *H. pulla* LB13061101 [H2629]. **D**. Original specimen of *H. pezizoides*, glued to cardboard in the fungarium of Stockholm (S). **E**. *H. pulla* RM1161 [H2635]. **F**. The envelope of the original material of *H. pezizoides*, annotated *Peziza stipitata*. Scale bars = 1 cm. Photographs A, C and E are taken by the collectors (confer Table 1) and photographs B, D and F by Åsa Kruys.

Helvella queletiana Sacc. & Trav., in Sacc., *Syll. Fung.* **19**: 850. 1910. Fig. 3D.
Synonyms: See Skrede *et al*. (2017).

Illustration: ? Weber (1972: fig. 34, as *H. phlebophora*?).

Apothecium stipitate-capitate, cap hemispheric, convex to flattened, 2–3.5 cm broad, 0.5–1.5 cm high, margin free to deflexed toward stipe, *hymenium* grey to light brownish grey, *receptacle* light grey to cream, drying darker, subtomentose, with conspicuous, branched, blunt ribs. *Stipe* 2.5–5 cm long, 0.8–1.5 cm broad, pubescent, paler or concolourous with receptacle, inside chambered, outside with 3 to 5 double-edged, sharp ribs continuing onto the receptacle surface. *Medullary excipulum* of *textura intricata*, hyphae septate, branching, hyaline, 4–10 µm broad. *Outer excipulum* of angular to club-shaped cells arranged in a palisade towards the surface, individual cells 15–35 × 5–20 µm, hyaline to brown-walled, outermost cells in rows forming hyaline hyphoid short-celled hairs. *Asci* pleurorhynchous, 270–320 × 12–17 µm. *Ascospores* ellipsoid, 17.0–17.8–19.2 × 11.2–12.3–13.5 µm. *Paraphyses* 3–4 µm broad below, subhyaline to pale brown-walled, at tips enlarged to 5–7 µm broad.

Specimens examined/sequenced: See Table 1.

Notes: *Helvella queletiana* is nested in an unsupported single-species lineage of the /lacunosa clade (clade B), as delineated by Skrede *et al.* (2017), a position retained in the present phylogeny (*cf.* Fig. 1). The photograph and description of *Helvella phlebophora* in Weber (1972, fig. 34) is suggestive of *H. queletiana.*

Helvella retinervis Skrede & T. Schumach. ***sp. nov.*** MycoBank MB834628. Fig. 2I, J.

Etymology: Referring to the veined (nerved) receptacle surface forming an incomplete network (reticulum).

Typus: **Spain**, Gipuzkoa, San Sebastian, 21 May 2009, *J.M. Lekuona* (**holotype** ARAN3008363).

Apothecium shortly stipitate-cupulate, cup 1.5–3.2 cm broad, *hymenium* greyish brown, smooth, often wrinkled, *receptacle* subpubescent, paler, greyish to whitish, with prominent branching ribs and interconnected veins forming a ± reticulate pattern, ribs reaching the margin or not, arising from a short stipe. *Stipe* indistinct, ribbed, 0.4–1 cm high. *Medullary excipulum* of tightly interwoven *textura intricata*, hyphae 3–6 µm broad. *Outer excipulum* of angular to prismatic cells, 10–20 × 5–20 µm broad, protruding in a loosely interwoven fasciculate, 3- to 6-celled tufts. *Asci* cylindrical, pleurorhynchous, 240–280 × 12–16 µm. *Ascospores* broadly ellipsoid to oval, uniguttulate, 14.0–14.6–15.8 × 11.3–12.0–13.3 µm, with one large internal oil drop. *Paraphyses* straight, 2.5–3.5 µm broad below, enlarged to 5–7.5 µm at the clavate to subcapitate tips.

Specimens examined/sequenced: See Table 1.

Notes: The species belongs in the *H. costifera* morphospecies complex, but constitutes a lineage of its own in our phylogeny (*cf.* Fig. 1). *Helvella retinervis* is distinguished from *H. costifera* and *H. calycina*, by two *hsp* and 12 *rpb2*, and four *hsp* and 12 *rpb2* substitutions, respectively. *Helvella retinervis* has also turned up among recently sequenced specimens of the *H. costifera* morpho-species complex from the fungarium in Stockholm (S), Sweden (see Table 1).

Helvella semiobruta Donadini & Berthet, *Bull. Soc. mycol. Fr.* **91**: 555. 1976. (1975). Fig. 6C, D.

Illustration: Donadini & Berthet (1975: figs 1–8).

Apothecium stipitate-capitate, cap convex, 1.5–3 cm broad, in young specimens folded and convex, later bilobate or trilobate and irregular in shape, margin undulate, gently involute or straight, in mature specimens deflexed and welded to the attachment points of the stipe, *hymenium* smooth, even or gibbose, folded, black, *receptacle* surface smooth to furfuraceous, at first greyish white, then greyish black in old specimens, covered by branched ribs and veins. *Stipe* 1.2–4 cm high, 0.5–2 cm broad, hollow, with 1 to 3 internal chambers, outside with three to five blunt and broad ribs and grooves, concolourous with receptacle or paler above, whitish below, in premature specimens stipe compressed with less protruding ribs. *Medullary excipulum* of dense *textura intricata*, hyphae 2.8–6.6 µm broad, with pale brown walls. *Outer excipulum* of brownish rows of angular to prismatic cells, 10–30 × 7–15 µm turning out perpendicular to receptacle surface. *Asci* pleurorhynchous, 300–370 × 14–18 µm. *Ascospores* oblong ellipsoidal, 19.8–22.1–24.5 × 12.2–13.8–14.8 µm, with one large and several small internal guttules. *Paraphyses* straight, 3–4 µm below, enlarged to 6–9 µm at the clavate tips.

Specimens examined/sequenced: See Table 1.

Notes: This Mediterranean species has a convex cap and a short greyish white stipe with a few longitudinal, blunt ridges and grooves. It is nested with *H. helvellula, H. iberica, H. inexpectata* and *H. juniperi* in a highly divergent lineage of the /lacunosa clade (Fig. 1, see also Skrede *et al.* 2017). A specimen from Gotland, Sweden, has been identified among specimens of the *H. lacunosa* morphospecies complex deposited in the fungarium of Stockholm (S). Filippa *et al.* (2013) gave an account of the morphology and ecology of the species in the Mediterranean region.

The Spanish specimens of *H. semiobruta* are all associated with *Cistus albidus* and collected from January to March between 500 to 700 m a.s.l. *Helvella semiobruta* may be confused with *H. juniperi*, with which it shares habitat and period of ascoma formation. In *H. juniperi* the stipitate-capitate ascoma is more irregularly saddle-shaped and has more numerous, prominent, longitudinal ribs and deep furrows on a cavernous, hollow stipe. Genetically, three *hsp* and three *rpb2* substitutions separate *H. semiobruta* and *H. juniperi. Helvella semiobruta* also shares habitat and fruiting time with *H. helvellula*, which is cupulate and never capitate as in *H. semiobruta.*

Helvella solitaria P. Karst., *Bidr. Känn. Finl. Nat. Folk* **19**: 37. 1871. Fig. 8H, I.
Synonyms: *Helvella queletii* Bres., *Rev. Mycol.* **4**: 211. 1882.
Helvella ulvinenii Harmaja, *Karstenia* **19**: 42. 1979.
See Skrede *et al.* (2017) for additional synonyms.

Illustrations: Dissing (1964: fig. 9; 1966b: fig. 18, as *H. queletii*), Dissing & Nannfeldt (1966: pl. 2: 2, as *H. queletii*), Weber (1972:

figs 27–28, as *H. queletii*), Harmaja (1977a: fig. 1, 1979: fig. 8, as *H. ulvinenii*), Schumacher & Mohn Jenssen (1992: 21, as *H. queletii*).

Apothecium stipitate-cupulate, cup to saucer-shaped, laterally compressed, 2.5–5 cm broad, *hymenium* dark greyish brown to brownish black, even, *receptacle* concolourous or paler, delicately pubescent. *Stipe* 1.5–6 cm high, by 0.8–2 cm broad, whitish or pale greyish, with 3 to 6 blunt ribs and grooves continuing onto the base of the cup. *Medullary excipulum* of densely interwoven *textura intricata*, hyphae 3–7 µm broad. *Outer excipulum* of *textura angularis*, cells slightly elongate, 25–50 × 20–40 µm, outermost cells giving rise to 3 to 6-celled hyphae in fascicled tufts, outermost cells cylindrical to club-shaped, 10–26 × 8–14 µm. *Asci* pleurorhynchous, 270–330 × 13–15 µm. *Ascospores* ellipsoid, uniguttulate, 18.2–20.1–21.8 × 11.4–12.5–13.2 µm. *Paraphyses* 3–4 µm broad below, brown-walled, with brownish granular content, enlarged to 5–8 µm at the clavate tips.

Specimens examined/sequenced: See Table 1.

Notes: The specimens from Spain show no intraspecific *hsp* and *rpb2* variation, as also observed among the Scandinavian populations (Skrede *et al.* 2017).

Helvella sublicia Holmsk., *Beata ruris otia Fung. Dan.* **2**: 51. 1799. Fig. 8D, E.
Synonym: *Helvella ephippium* Lev*., Ann. Sci. Nat. Bot., sér. 2,* **16**: 240. 1841.
See Skrede *et al.* (2017) for additional synonyms.

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

Apothecium stipitate-cupulate, at first cupulate and laterally compressed with inrolled margin, then expanding to saddle-shaped, adnate or reflexed, occasionally applanate, 0.5–2 cm broad, *hymenium* greyish to dark grey, occasionally whitish, even, *receptacle* sub-pubescent to villose, concolourous with hymenium. *Stipe* solid, terete, or compressed with one or two inconspicuous grooves below, concolourous with cap or paler to whitish. *Medullary excipulum* of *textura intricata*, hyphae 3–5 µm broad, walls brownish, intermixed with some blackish hyphae. *Outer excipulum* of *textura angularis*, cells 20–44 × 8–25 µm, outermost cells cylindrical to club-shaped in rows perpendicular to receptacle surface, 20–40 × 10–15 µm, outermost cells protruding to tufts of fascicled hyphae forming the villi of receptacle. *Asci* cylindrical, pleurorhynchous, 260–300 × 14–17 µm. *Ascospores* ellipsoid, uniguttulate, 18.8–20.2–21.5 × 10.7–11.6–12.4 µm. *Paraphyses* 2–3 µm below, slightly enlarged to 4–7 µm at the clavate tips.

Specimens examined/sequenced: See Table 1.

Notes: *Helvella sublicia* differs from other saddle-shaped *Helvella* species in its greyish colours and pubescent receptacle surface. The *hsp* and *rpb2* sequences of the Spanish and Nordic specimens are identical.

Helvella sulcata Afzel., *K. svenska Vetensk.-Acad. Handl.* **4**: 305. 1783. - *nom. sanct*. Fig. 3A, B.

Synonyms: See Skrede *et al*. (2017) for additional synonyms.

Illustration: Afzelius (1783: tab. 1, fig. 1), Schaeffer (1763: pl. 162, as '*Elvela decima qvarta*').

Apothecium stipitate-capitate, cap 1–4 cm broad, 3–6 cm high, saddle-shaped, bi- to trilobate, adnate, margin attached to stipe at 3 to 4 points, *hymenium* black, even or slightly wrinkled, *receptacle* surface greyish brown, 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) between, 4–6 along the circumference, almost no stipe flesh. *Medullary excipulum* of loose *textura intricata*, hyphae *ca*. 4–5 µm broad. *Outer excipulum* of angular to prismatic cells arranged in rows turning out perpendicular to receptacle surface, individual cells 8 – 15 µm, outermost cells more loosely arranged, club-shaped, 10–30 × 5–15 µm. *Asci* cylindrical, pleurorhynchous, 290–320 × 13–16 µm. *Ascospores* broadly ellipsoid, 14.8–16.2–16.8 × 10.5–12.1–13.2 µm. *Paraphyses* 3–4 µm broad, light brown below, medium brown above, enlarged to 5–6.5 µm at the clavate tips.

Specimens examined/sequenced: See Table 1.

Notes: Five *hsp*, nine *rpb2*, and 15 LSU substitutions distinguish *H. sulcata* and *H. lacunosa*.

Skrede *et al*. (2017) lectotypified *H. sulcata* with an authentic figure (iconotype) from the original work by Afzelius (1783, tab 1, fig. 1). A depiction of an authentic colour plate of *H. sulcata* prepared by Adam Afzelius himself, located in the fungarium of Uppsala (UPS), is shown in Fig. 3A. This colour plate constitutes the prototype for the figure of *H. sulcata* in Afzelius' work (Afzelius 1783, plate X, fig. 1).

Helvella terricola Skrede & T. Schumach. ***sp. nov.*** MycoBank MB834629. Fig. 7E.

Etymology: "dwelling on soil" as opposed to its "look-alike" sister species *H. palustris*.

Typus: **Spain**, Huesca, Cerler, 28 Sep. 2018, *F. Cervera & L. Ballester* LB18092810 (**holotype** O-F-256562).

Apothecium stipitate-capitate, cap 1.5–4 cm broad, 1–2 cm high, saddle-shaped, bi- to trilobate, deflexed but margin not attached to the stipe, *hymenium* greyish black, surface rugose with age, *receptacle* concolourous with hymenium or paler, glabrous or subtomentose, with ribs radiating from stipe apex. *Stipe* light grey to dark grey 3–7.5 cm long, 0.5–1.5 cm thick, slightly tapering above, solid, with 5 to 8 single- or double-edged longitudinal ribs. *Medullary excipulum* of *textura intricata*, hyphae hyaline, 4–8 µm broad. *Outer excipulum* of *textura globulosa-angularis*, cells 20–40 µm diam., hyaline or light brown-walled, the outermost cells more elongated and prismatic giving rise to a palisade of densely packed club-shaped cells turning out perpendicular to receptacle surface. *Asci* pleurorhynchous, 260 – 320 x 12 – 15 µm. *Ascospores* ellipsoid, 15.0–17.8–19.5 × 10.8–11.5–12.6 µm. *Paraphyses* light brown-walled, 2–3 µm broad, septate, gradually enlarged into an irregular clavate tip, 5–10 µm broad.

Specimen examined/sequenced: See Table 1.

Notes: *Helvella terricola* resembles *H. palustris* in shape and colour, but differs genetically in three *hsp* and three *rpb2* substitutions. The two species differ substantially in ecology; *H. palustris* grows in minerotrophic fens and marshes while *H. terricola* grows on naked, moist soil.

DISCUSSION

This follow-up study of *Dissingia* and *Helvella* of species from Spain focuses on Mediterranean South European species and adds to the current knowledge of the species composition and diversity of *Helvella* in Europe. This study complements the previous synopsis by Skrede *et al.* (2017) which was primarily focused on North European species. The Spanish samples amount to 31 species of *Dissingia* (1) and *Helvella* (30) and in total we add 11 species to the list of European helvellas, of which nine are described as new. Altogether, 67 species are now re-evaluated and molecularly characterized from Europe (Skrede *et al.* 2017, Løken *et al*. 2019). Two of the newly described species are also found in other European countries, *i.e. H. retinervis* in Sweden and *H. phlebophoroides* in Denmark (*cf.* Table 1). It is worth mentioning that *H. semiobruta*, with a mainly South European distribution, has been detected from the island of Gotland, Sweden, which has a geology and climate comparable to that of the Mediterranean countries (*cf*. Table 1). The diversity illustrated in our survey is astonishing based on the limited number of collections (115) available. This underlines the extent of the unexplored diversity of *Helvella* and is highly suggestive that many more species of *Helvella* await discovery and description, in particular in regions where few collections have been made and are available in fungaria.

The Spanish samples also highlight the extensive radiation and diversification of *e.g*. the /helvellula lineage. This highly divergent lineage of the /lacunosa clade detected by Skrede *et al*. (2017), included three species, *i.e. H. helvellula*, *H. semiobruta* and *H. juniperi*. In the present outline, after incorporation of two additional species, *i.e*. *H. iberica* and *H. inexpectata*, this lineage comprises five species (*cf*. Fig. 1). It is noteworthy that *H. juniperi*, which is known with certainty from Italy and Portugal (*cf.* Table 1), did not turn up among the Spanish samples. Instead, the two new species *H. iberica* and *H. inexpectata* were detected, apparently sharing the same type of habitat as *H. juniperi*. It is expected that *H. juniperi* is also present in Spain. Moreover, the morphological diversification of species of this lineage is remarkable, considering the common ancestry of the group. Both stipitate and sessile, as well as cupulate and capitate species characterised have derived among these genetically very closely related species.

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