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Four new species of *Hydnellum* (*Thelephorales*, *Basidiomycota*) with a note on *Sarcodon illudens*

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Abstract: Four new *Hydnellum* species are described. *Hydnellum roseoviolaceum sp. nov*. grows in dry pine heaths on acidic, sandy soil. It is close to *H. fuligineoviolaceum*, another pine-associated species, but differs by smaller spores, an initially rose-coloured instead of violet flesh in fresh basidiomata and a mild taste. *Hydnellum scabrosellum sp. nov*. grows in coniferous forests on calcareous soil. It shares a general morphology with *H. scabrosum*, which also is its closest relative. It differs by having smaller and slenderer basidiomata and by the yellowish ochraceous colour of flesh and spines in dried specimens compared to the whitish or reddish brown colour seen in *H. scabrosum*. *Hydnellum fagiscabrosum sp. nov*. is another species with morphological and phylogenetic affinities to *H. scabrosum*. However, it is associated with trees from *Fagales* whereas *H. scabrosum* is associated with *Pinaceae*. *Hydnellum nemorosum sp. nov*. is yet another species that associates with broadleaved trees. It seems to be a rare species, morphologically reminiscent of *H. fuligineoviolaceum*, *H. ioeides* and *H. scabrosum,* but it is phylogenetically close to *H. fennicum*. Sequences from the type specimens of *H. glaucopus*, *H. lepidum*, *H. scabrosum*, *Sarcodon illudens* and *S. regalis* are included in the analyses. Specimens given the provisional name "*Sarcodon pseudoglaucopus*" in Sweden are now shown to be referable to *S. illudens*. The analyses further showed that *S. illudens* is close to *H. lepidum*. The new combination *Hydnellum illudens* is proposed. *Sarcodon regalis* and *H. lepidum* are shown to be conspecific and, although their basionyms were simultaneously published, the name *S. regalis* was only validated in a later publication. *Hydnellum lepidum* therefore takes priority and *S. regalis* becomes a synonym.

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INTRODUCTION

The stipitate hydnoid fungi within *Thelephorales* have attracted a lot of interest from environmental and conservation authorities since they are rarely recorded and have shown strong population declines across continental Europe due to atmospheric pollution and unsuitable forestry practices (Hrouda 1999, Nitare 2006, Arnolds 2010, Ozinga *et al*. 2013, Holec & Kučera 2018, Nitare 2019). Global conservation assessments have been published for seven species, of which five are currently regarded as Vulnerable (IUCN 2020). Effective conservation measures require a precise knowledge about species diversity and species limits (Runnel *et al*. 2014). Fungi are often notoriously difficult to identify and morphological differences are often small and based on ambiguous or overlapping character states. The potential presence of cryptic species adds another layer of uncertainty to the evaluation of species ecology, occurrences, geographical distribution, and population trends. Stipitate hydnoid fungi are not exempt from these challenges (Ainsworth *et al*. 2010, Baird *et al*. 2013, Loizides *et al*. 2016).

The genera of the stipitate hydnoid *Thelephorales* have traditionally been distinguished using two characters, *viz*. basidiomatal texture and spore colour: dry corky basidiomata in *Hydnellum* and *Phellodon* and fleshy basidiomata in *Bankera* and *Sarcodon*; brownish spores in *Hydnellum* and *Sarcodon* and hyaline spores in *Bankera* and *Phellodon*. Information from DNA sequences has shown that this simple and practical classification cannot be maintained. A new classification instead relegates *Bankera* to the synonymy of *Phellodon* (Baird *et al*. 2013), while *Sarcodon* is much reduced and most of its species have been moved to *Hydnellum* (Larsson *et al*. 2019).

Maas Geesteranus successively introduced a subgeneric classification for *Sarcodon* with six sections (summarised in Maas Geesteranus 1975a). In this classification, most of the

species treated herein would belong either to section *Scabrosi* or to section *Violacei*. Both sections received moderate support, within the genus *Hydnellum*, in the phylogenetic analyses performed in Larsson *et al*. (2019).

Typifying section *Scabrosi*, *Hydnellum scabrosum* is based on *Hydnum scabrosum*, a species originally described by Fries from pine forests in Femsjö, SW Sweden (Fries 1836) and later neotypified with a collection from the same area (Maas Geesteranus & Nannfeldt 1969). Although this species continued to be regarded as a species of coniferous or, occasionally, mixed woodlands in North America (Harrison 1961, Harrison & Grund 1987), this was not the case in Europe. Maas Geesteranus (1956, 1975a) treated the species in a wider sense and accepted specimens from both broadleaved and conifer forests, a taxonomic view which has prevailed in Europe ever since (*e.g.* Phillips 1981, Breitenbach & Kränzlin 1986, Gulden & Hanssen 1992, Stalpers 1993, Pegler *et al*. 1997, Hrouda 1999, Arnolds 2003, 2010). However, preliminary analysis of the available molecular data suggested that specimens from broadleaved (*e.g.* in Brock *et al*. 2009) and coniferous (*e.g*. in Nitare & Högberg 2012) woodlands are genetically different. The British population of the former group was provisionally recognized as "*Sarcodon* sp. 1 (with *Fagaceae*)" and unofficially assessed as nationally Endangered (Smith *et al*. 2016). Intense collecting in Sweden and the UK and subsequent sequencing of material from both forest types was therefore carried out to investigate whether the formal recognition of two distinct species was warranted. While specimens with a *Hydnellum scabrosum* aspect collected in European broadleaved forests have been interpreted as the true *H. scabrosum*, specimens from coniferous forests have often been identified as other species within section *Scabrosi*, most commonly as *H. glaucopus* (Pegler *et al*. 1997, van der Linde *et al*. 2008).

In Sweden, the need for conservation measures for *Sarcodon* species was evaluated and an action plan developed (Nitare 2006). A rare species associated with *Pinus* was in that report erroneously identified as *S. glaucopus*. Intensified sampling due to the increased interest that followed from the publication of the report yielded many new collections, some of which could not be included in current species concepts. A provisional description of three potentially new *Sarcodon* species was published in Nitare & Högberg (2012), supported by a preliminary analysis of ITS1 sequences. The specimens previously misidentified as *S. glaucopus* were there reclassified as an undescribed species under the provisional name "*S. pseudoglaucopus*".

Here we formally describe three new species with a place in section *Scabrosi*, and one new species belonging to section *Violacei*. Our phylogenetic analyses further include sequences from the holo-, iso- or neotypes of *Hydnellum glaucopus, H. lepidum, H. scabrosum, Sarcodon illudens*, and *S. regalis*. Our aim is to provide an improved taxonomic framework for this group of stipitate hydnoids which will, in turn, lead to the generation of more accurate and reliable distribution and ecological data.

MATERIALS AND METHODS

Sampling

The specimens studied were collected in Denmark, Italy, the Netherlands, Norway, Spain, Sweden and the UK over the last two decades, either by ourselves or by colleagues sending material to us. Interesting specimens were also found in the fungaria in Göteborg (GB), Kew (K), Oslo (O), Stockholm (S) and Uppsala (UPS). Studied specimens are listed for each of the species described in the taxonomy section. DNA from a selection of specimens was extracted and sequenced. Our phylogenetic analyses also incorporated sequences downloaded from GenBank and UNITE (Nilsson *et al*. 2018). Specimens sequenced for this study and their GenBank accession numbers are listed in Table 1.

Microscopy

Specimens were mounted in 2 % KOH, Melzer's reagent or cotton blue in lactic acid and studied with a Zeiss Axioskop or an Olympus BH2 light microscope using bright field or phase contrast optics. Spore measurements were made without ornamentation and ornament height was recorded separately. Spore measurements are given as a range covering 90 % of measured spores with 5 % extreme values given within parentheses. The number of collections used (x) and spores measured (y) is provided in the form n = x/y. Spores were photographed in a Zeiss Axioskop microscope equipped with a ×100 DIC objective lens, a Zeiss MRc camera, and Zen Blue software. Photographed tissue was mounted in Melzer´s reagent.

Molecular methods

Sequences for the complete ITS region and about 1 200 base pairs (bp) of the 5´ end of the LSU (28S) of the nuclear ribosomal DNA were generated using the primers ITS1F (Gardes & Bruns 1993) and LR21, LR0R, and LR7 (Hopple & Vilgalys 1999). Genomic DNA was extracted from the specimens using the DNeasy Plant Mini Kit (Qiagen, Hilden) and PCR reactions were performed with illustra PuReTaq Ready-To-Go PCR beads (Cytiva, Marlborough) using 0.5 µM of each primer and 1–3 µL of the DNA extracts. PCR clean-up was carried out using the QIAquick PCR purification kit (Qiagen, Hilden). Sequences were generated by Macrogen Europe (Amsterdam, the Netherlands) using primers ITS1, ITS4 (White *et al*. 1990), Ctb6 (https://nature.berkeley.edu/brunslab/) and LR5 and LR3R (Hopple & Vilgalys 1999). Genomic DNA was extracted from old type specimens using a modified CTAB method (Larsson & Jacobsson 2004) and the ITS1 and ITS2 regions were amplified separately using primers ITS1F-ITS2 and ITS3-ITS4B respectively (White *et al*. 1990, Gardes & Bruns 1993). PCR reactions and clean up followed the methods described above. Primers used for sequencing were ITS1, ITS2, ITS3 and ITS4 (White *et al*. 1990).

Selected specimens preserved in K (vouchers prefixed K(M) in Table 1) were either processed according to the methods outlined in Parfitt *et al.* (2007) or using the following protocols. Genomic DNA was extracted using an enzymatic digestion and glass-fibre filtration method and the full ITS region amplified with ITS1F and ITS4 primers following Dentinger *et al*. (2010). DNA from the ectomycorrhizal root tip ALM363 was extracted using Extract-N-Amp (Sigma-Aldrich) and the full ITS region amplified using ITS1F and ITS4 following Suz *et al*. (2014). PCR products were purified with Exo-SAP-IT (USB) and sequenced bidirectionally using BigDye Terminator v. 3.1 Cycle Sequencing reagents in an ABI 3730 DNA Analyzer (Applied Biosystems).

Table 1. Specimen data and GenBank numbers for sequences published in this study.

				GenBank number	
Species	**Collector**	**Voucher**	**Country**	**ITS**	**LSU**
Hydnellum amygdaliolens	E. Larsson 333/19	GB-0202072	FR	MW144290	MW144290
Hydnellum fagiscabrosum	R.A. Alder	K(M)162048	GB	MW187570	n/a
	R.A. Alder	K(M)171979	GB	MW187571	n/a
	M. Nesbitt	K(M)172590	GB	MW187572	n/a
	A. Crotty ARL 660	K(M)197476	GB	MW187573	n/a
	A.M. Ainsworth	K(M)197472	GB	MW187574	n/a
	A.M. Ainsworth	K(M)197477	GB	MW187575	n/a
	J. Pitt	K(M)197490	GB	MW187576	n/a
	A. Leonard	K(M)181351	GB	MW187577	n/a
	L. Goodwin	K(M)160940	GB	MW187578	n/a
	F. Boccardo	K(M)197487	IT	MW187579	n/a
	I.-L. Fonneland 2014-005	O-F-251442	NO	MW144291	n/a
	R.-G. Carlsson 11/082	GB-0195625	SE	MW144292	MW144292
	R.-G. Carlsson 11/088	GB-0195621	SE	MW144293	MW144293
	J. Nitare	GB-0195805	SE	MW144294	MW144294
	R.-G. Carlsson 11/082j	GB-0195623	SE	MW144295	MW144295
	J. Olsson	GB-0195622	SE	MW144296	MW144296
	E. Larsson 169/19	GB-0195727	SE	MW144297	n/a
Hydnellum fennicum	E. Bendiksen 142/07	O-F-76339	NO	MW144298	MW144298
	A. Molia *et al*. AM 64/2010	O-F-22400	NO	MW144299	n/a
	T. Jacobsen *et al*.	O-F-303852	NO	MW144300	n/a
	G. Bollingmo	O-F-301661	NO	MW144301	n/a
	M. Øverby HST15-617	O-F-260304	NO	MW144302	n/a
	S. Westerberg	GB-0195634	SE	MW144303	MW144303
	S. Westerberg	GB-0129370	SE	MW144304	MW144304
	S. Westerberg	GB-0195636	SE	MW144305	MW144305
	R.-G. Carlsson 11/077	GB-0195637	SE	MW144306	MW144306
	R.-G. Carlsson 13/047	GB-0195635	SE	MW144307	n/a
	R.-G. Carlsson 11/072	GB-0195632	SE	MW144308	MW144308
	S. Westerberg	GB-0129369	SE	MW144309	MW144309
	R.-G. Carlsson 11/077j	GB-0195633	SE	MW144310	MW144310
Hydnellum fuligineoviolaceum	T.E. Brandrud 468/16	O-F-256729	NO	MW144311	n/a
	G. Gaarder	O-F-242766	NO	MW144312	MW144312
	W.E. Johansen	GB-0195815	NO	MW144313	n/a
Hydnellum glaucopus	T.E. Brandrud 474/16	O-F-256726	NO	MW144314	n/a
	G. Bollingmo	O-F-260241	NO	MW144315	n/a
	A. Molia & A.K. Wollan	O-F-22418	NO	MW144316	n/a
	A. Molia *et al*. AM 70/2010	O-F-22412	NO	MW144317	n/a
	R.-G. Carlsson 05/059j	GB-0195645	SE	MW144318	MW144318
	R.-G. Carlsson 08/071j	GB-0195644	SE	MW144319	MW144319
	E. Jansson	GB-0195638	SE	MW144320	MW144320
	R.-G. Carlsson 00/87j	GB-0195659	SE	MW144321	MW144321
	J. Nitare *et al*.	GB-0195642	SE	MW144322	MW144322
	K. Gahne & Å. Edvinsson	GB-0195820	SE	MW144323	MW144323
	E. Larsson 157/19	GB-0195938	SE	MW144324	n/a
	E. Arnolds 07/69	GB-0195788	SE	MW144325	n/a

Table 1. (Continued).

Species	Collector	Voucher	Country	GenBank number	
				ITS	LSU
	E. Larsson 261/11	GB-0195722	SE	MW144326	MW144326
	R.-G. Carlsson 10/047	GB-0195646	SE	MW144327	MW144327
	R.-G. Carlsson 11/069j	GB-0195639	SE	MW144328	MW144328
	L. & S. Stridvall 11/015	GB-0195648	SE	MW144329	n/a
	R.-G. Carlsson 08/092j	GB-0195641	SE	MW605222	MW605222
	J. Eriksson	UPS-F-013955	SE	MW144330	n/a
Hydnellum illudens	U. Roffler & B. Senn-Irlet BSI 07/115	ZT-Myc-64129	CH	MW187580	n/a
	J. Boiffard	L.09111973	FR	MW144331	n/a
	E. Arnolds 07/23	GB-0195786	IT	MW144332	n/a
	C.A. Hobart	K(M)197492	IT	MW187581	n/a
	H. Holien 17/07	O-F-68659	NO	MW144333	MW144333
	K. & E. Bendiksen 187/10	O-F-76340	NO	MW144334	MW144334
	G. Gaarder 6393	O-F-242769	NO	MW144335	MW144335
	T.E. Brandrud 469/16	O-F-256727	NO	MW144336	n/a
	T.E. Brandrud 451b/16	O-F-256728	NO	MW144337	n/a
	S. Svantesson 890	GB-0195937	NO	MW144338	MW144338
	E. Larsson 91/10	GB-0195721	SE	MW144339	MW144339
	E. Larsson 332BA/18	GB-0195723	SE	MW144340	n/a
	J. Nitare	GB-0195819	SE	MW144341	MW144341
	L. Andersson & T. Fasth	GB-0195651	SE	MW144342	MW144342
	L. Andersson & T. Fasth	GB-0195808	SE	MW144343	MW144343
	E. Larsson 333/18	GB-0195724	SE	MW144344	n/a
	J. Nitare	GB-0195802	SE	MW144345	n/a
	E. Arnolds 07/60	GB-0195787	SE	MW144346	n/a
	L. Andersson & T. Fasth	GB-0195654	SE	MW144347	MW144347
	L. Andersson & T. Fasth	GB-0195653	SE	MW144348	MW144348
	L. Andersson & T. Fasth	GB-0195652	SE	MW144349	MW144349
	J. Nitare	GB-0195649	SE	MW144350	MW144350
	L. Andersson & T. Fasth	GB-0195655	SE	MW144351	MW144351
	G. Aronsson	GB-0195650	SE	MW144352	MW144352
Hydnellum ioeides	A.M. Ainsworth	K(M)196064	GB	MW191881	n/a
	A.M. Ainsworth	K(M)196065	GB	MW191882	n/a
	D. Mills	K(M)236333	GB	MW187582	n/a
	F. Boccardo	K(M)197486	IT	MW187583	n/a
	R. Kristiansen	O-F-295820	NO	MW144353	MW144353
	A. & B. Nilsson	GB-0129376	SE	MW144354	MW144354
	R.-G. Carlsson 11/059j	GB-0195657	SE	MW144355	MW144355
	F. Papmehl-Dufay 006	GB-0195656	SE	MW144356	MW144356
	B. & K. Hjortstam	GB-0195660	SE	MW144357	MW144357
	R.-G. Carlsson 11/090j	GB-0195658	SE	MW144358	MW144358
Hydnellum lepidum	T. Borgen DMS-680077	GB-0207597	DK	MW144359	n/a
	M. Strandberg DMS-9213941	GB-0207598	DK	MW144360	n/a
	M. Strandberg DMS-168848	GB-0207599	DK	MW144361	n/a
	D.A. Reid *et al.*	K(M)38542	GB	MW187584	n/a
	Anonymous	K(M)197482	IT	MW187585	n/a
	R. Fortey	K(M)197483	IT	MW187586	n/a

Table 1. (Continued).

Species	Collector	Voucher	Country	GenBank number	
				ITS	LSU
	S. Skeates	K(M)197484	IT	MW187587	n/a
	R. Chrispyn EA 00/117	GB-0195785	NL	MW144362	n/a
	A. van der Berg EA 00/119	GB-0195784	NL	MW144363	n/a
	G. & H. Piepenbroek	L.0053426	NL	MW144364	n/a
	P. Marstad & T.N. Kristiansen 207/13	O-F-302063	NO	MW144365	n/a
	E. Larsson 374/17	GB-0202073	SE	MW144366	n/a
	R.-G. Carlsson 07/120	GB-0195670	SE	MW144367	MW144367
	F. Papmehl-Dufay 1401	GB-0195669	SE	MW144368	MW144368
	E. Larsson 358/16	GB-0195739	SE	MW144369	n/a
	C. Albinsson	GB-0195804	SE	MW144370	MW144370
	A. Alvarez-Lafuente ALM363	root tip	ES	MW192748	n/a
Hydnellum nemorosum	T. Borgen DMS-9211777	GB-0195939	DK	MW144371	n/a
	A.M. Ainsworth	K(M)197478	GB	MW187588	n/a
	A.M. Ainsworth	K(M)197481	GB	MW187589	n/a
	I.-L. Fonneland 11/191	O-F-242352	NO	MW144372	MW144372
	D. Broström 00/114	GB-0195631	SE	MW144373	MW144373
Hydnellum roseoviolaceum	B. Petterson	GB-0195936	SE	MW144374	MW144374
	D. Broström 08/033	GB-0195687	SE	MW144375	MW144375
Hydnellum scabrosellum	E. Larsson 317/16	GB-0195736	SE	MW144376	n/a
	J. Nitare	GB-0195806	SE	MW144377	MW144377
	G. Aronsson 130920	GB-0195791	SE	MW144378	MW144378
	J. Nitare	GB-0195689	SE	MW144379	MW144379
	G. Aronsson 130913	GB-0195792	SE	MW144380	MW144380
	J. Nitare	GB-0195807	SE	MW144381	MW144381
Hydnellum scabrosum	B. Wasstorp	GB-0195702	FI	MW144382	MW144382
	E. Larsson 378/16	GB-0195729	SE	MW144383	n/a
	E. & G. Grundel	GB-0195695	SE	MW144384	MW144384
	R.-G. Carlsson 99/071j	GB-0195696	SE	MW144385	MW144385
	E. Larsson 220/11	GB-0195731	SE	MW144386	n/a
	J.-O. Tedebrand	GB-0195691	SE	MW144387	MW144387
	R.-G. Carlsson 13/068	GB-0195694	SE	MW144388	MW144388
	E. Larsson 332B/18	GB-0195726	SE	MW144389	n/a
	V. Fägersten	GB-0195692	SE	MW144390	MW144390
	A. Pallin	GB-0195794	SE	MW144391	n/a
	R.-G. Carlsson 08/145j	GB-0195699	SE	MW144392	MW144392
	R.-G. Carlsson 11/095j	GB-0195701	SE	MW144393	MW144393
	R.-G. Carlsson 10/046	GB-0195698	SE	MW144394	MW144394
	R.-G. Carlsson 11/095	GB-0195700	SE	MW144395	MW144395
	L. Ljungberg	GB-0195690	SE	MW144396	MW144396
	R.-G. Carlsson	GB-0195697	SE	MW144397	MW144397
	A. Stridvall *et al*.	GB-0195693	SE	MW144398	n/a
	E. Larsson 268/18	GB-0195730	SE	MW144399	n/a
	S. Lundell	UPS F-013954	SE	MW144400	n/a
	T.E. Brandrud 536/13	O-F-249353	NO	MW144401	MW144401
	J. Pitt	K(M)25139	GB	MW202245	n/a
Sarcodon cyrneus	F. Boccardo	K(M)197488	IT	MW202246	n/a

Phylogenetic analyses

Three datasets were compiled and manually aligned in AliView v. 1.26 (Larsson 2014). In the first dataset we used 5.8S and *ca*. 900 bp from the 5' end of 28S from the nuclear ribosomal repeat. We based this alignment on Larsson *et al*. (2019) but restricted the dataset to *Hydnellum* and added *Sarcodon leucopus* as outgroup. We further added sequences from the five species that are the focus of this study together with sequences of *H. fuscoindicum* that, in Larsson *et al*. (2019), was recovered as a sister taxon to *H. fuligineoviolaceum*. The second and third datasets consisted of ITS sequences for the species in section *Scabrosi* and section *Violacei*, respectively, following the analyses in Baird *et al*. (2013) and Larsson *et al*. (2019). *Hydnellum aurantiacum* was selected as the outgroup for the *Scabrosi* dataset and *H. peckii* was the corresponding selection made for the *Violacei* dataset. We augmented our ITS datasets for each of our focus species with available sequences downloaded from the GenBank and UNITE databases.

Maximum Likelihood (ML) analyses were conducted with IQ-TREE (Nguyen *et al*. 2015) using the online server at http://iqtree.cibiv.univie.ac.at/ (Trifinopoulos *et al*. 2016). ITS1, 5.8S, ITS2 and 28S were treated as separate partitions (Chernomor *et al*. 2016). The best-fitting substitution model was estimated using ModelFinder implemented on the IQ-TREE server (Kalyaanamoorthy *et al*. 2017). Branch support was estimated through the SH-aLRT test (Guindon *et al*. 2010) and through ultrafast bootstrap (Hoang *et al*. 2018), both of which are available on the IQ-TREE server.

Bayesian Inference (BI) was calculated using MrBayes v. 3.2 (Ronquist *et al*. 2012) implemented on the CIPRES Science Gateway server v. 3.3 (Miller *et al*. 2010) and utilizing the BEAGLE library (Ayres *et al*. 2012). The same partitions as in the ML analyses were used. Substitution models were selected with MrModeltest v. 2 (Nylander 2004). Analyses of the *Hydnellum* and the *Violacei* dataset were run for 5 M generations, sampling trees every 1 000th generation. The *Scabrosi* dataset was run for 8 M generations with the same sampling frequency. Other program settings were the default ones.

RESULTS

For the present study 136 *Hydnellum* specimens and one ectomycorrhizal root tip were sequenced. This resulted in 137 full or partial ITS sequences and 67 LSU sequences, all of which are deposited in GenBank (Table 1).

All BI analyses reached stationarity long before termination and chain-mixing was satisfactory. For the *Hydnellum* analysis, a burn-in of 25 % was used but for the other two analyses a 50 % burn-in was necessary to ensure that only trees with average standard deviation of split frequencies below 0.01 were included when computing the consensus trees.

The trees are labelled with support values and only strong branch support is shown. The first number represents the SH-aLRT test from the ML runs and values from 80 % are indicated. The second number is the outcome of the ultrafast bootstrap from ML analyses and values from 95 % are shown. The third figure is the posterior probability from the BI analyses and here values from 0.95 are shown.

After alignment the *Hydnellum* dataset included 1 553 positions. Nine of these positions could not be reliably aligned and were discarded prior to analyses. ML and BI analyses of the *Hydnellum* dataset showed largely similar topology and the ML tree is presented here (Fig. 1). Sections *Violacei* and *Scabrosi* are recovered as strongly supported. In addition, *H. aurantiacum* and *H. auratile* form a supported clade. The relationships among these three clades and the rest of the species are not resolved. Twenty-five terminal clades with strong support from at least two branch support tests represent an equal number of species. In addition, the single sequence of *H. amygdaliolens* is recovered on a separate branch. Of the terminal clades four could not be connected to existing species names and are here interpreted as the new species *Hydnellum fagiscabrosum, H. nemorosum, H. roseoviolaceum*, and *H. scabrosellum* (see Taxonomy section below). The taxon provisionally called "*Sarcodon pseudoglaucopus*" can now be identified as *S. illudens* (Maas Geesteranus 1976) following our phylogenetic analyses which included a sequence derived from the holotype of that species. The new combination *Hydnellum illudens* is proposed.

European specimens of each species generally showed no or little genetic variation within the ITS region. On the other hand, the genetic infraspecific variation was often considerable, which caused difficulties for the alignment. We still decided not to discard any ambiguous nucleotide positions since our aim with the ITS trees was not primarily to evaluate the phylogenetic relationships among species but to visualize the amount of genetic difference between species and the extent of morphological identifications within species.

After alignment the *Violacei* dataset included 673 nucleotide positions. ML and BI analyses of the *Violacei* dataset are identical and the ML tree is presented here (Fig. 2). All terminal clades are supported by at least two branch support tests. Seven terminal clades represent four known species, one new species described here as *Hydnellum roseoviolaceum*, and two unidentified North American taxa, one of them represented only by environmental DNA.

After alignment the *Scabrosi* dataset included 694 nucleotide positions. ML and BI analyses of section *Scabrosi* are not fully congruent with respect to the placement of *Hydnellum scabrosum*. In the ML analysis *H. scabrosum* occupies a separate branch while in the BI analysis *H. scabrosum* is paraphyletic in relation to *H. fennicus, H. amygdaliolens, H. nemorosum* and an unidentified species. The ML tree is shown in Fig. 3. Nine terminal clades are supported by at least two branch support tests while the clade formed by *H. scabrosum* sequences, including that derived from the neotype, is visible in the tree but not supported. Supported clades correspond to six known species and three new species, here described as *Hydnellum fagiscabrosum*, *H. nemorosum*, and *H. scabrosellum*.

Taxonomy

Hydnellum fagiscabrosum A.M. Ainsw. & Nitare, ***sp. nov.*** MycoBank MB 837984. Figs 4A, C–F, 9A.

Etymology: Epithet derived from *fagi-*, referring to the association with *Fagales* (*e.g. Castanea*, *Fagus* and *Quercus*) and *scabrosum*, referring to the morphological similarity to *Hydnum scabrosum* Fr.

Typus: **Sweden**, Blekinge, Ronneby, north-eastern shore of lake Listersjön, close to a picnic area, near *Fagus sylvatica*, 56.320946/15.350357, 3 Sep. 2014, *J. Nitare* (**holotypus** GB-0195805; **isotypi** K(M)264450, UPS); GenBank accession: MW144294.

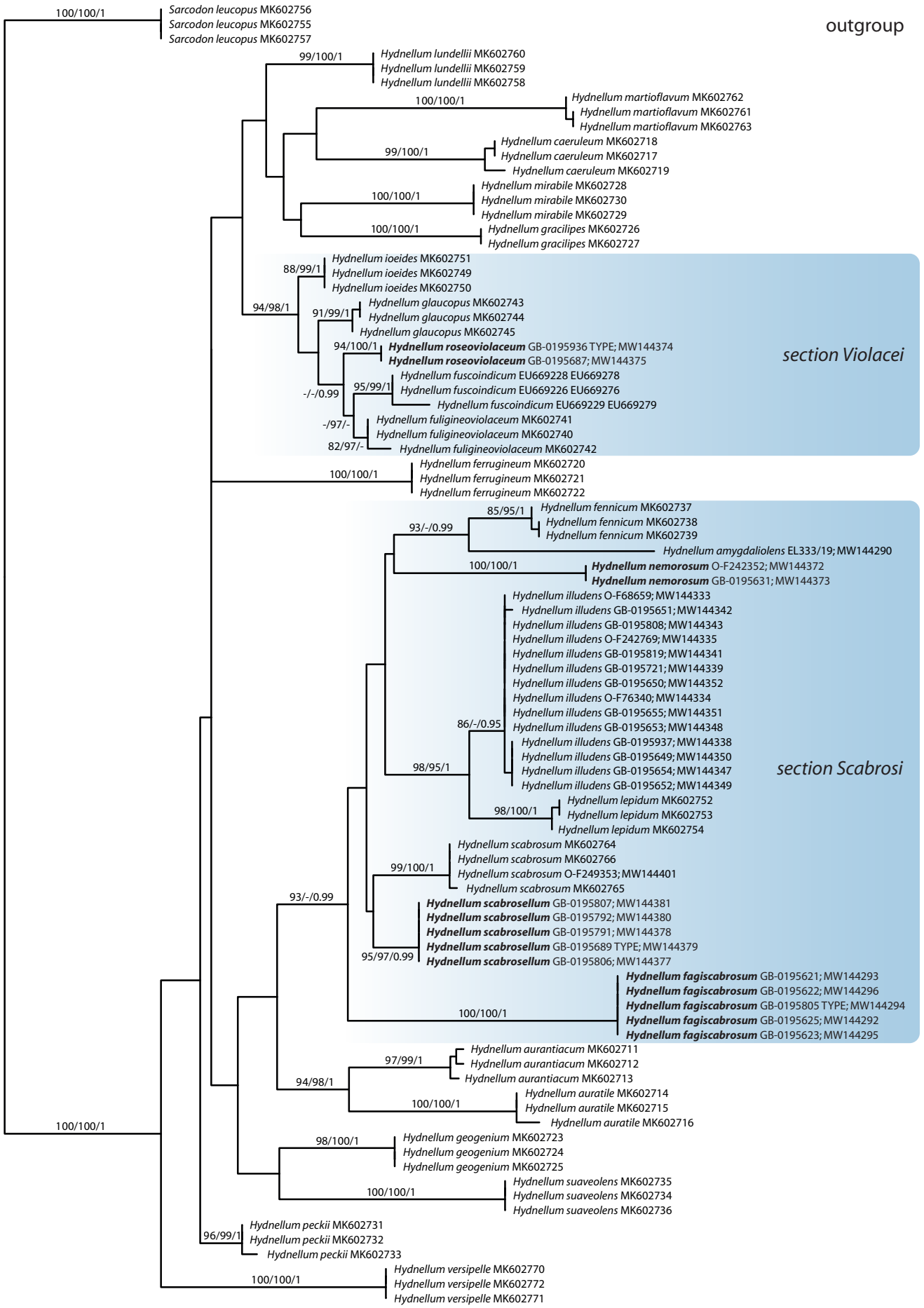

Fig. 1. Phylogram of *Hydnellum*. Maximum Likelihood tree based on nuclear ribosomal 5.8S and partial 28S sequences. Numbers on branches represent reliable support values from SH-aLRT test (≥ 80 %), ultrafast bootstrap (≥ 95 %), and Bayesian inference posterior probability values (≥ 0.95), respectively. Species described here are marked in bold face.

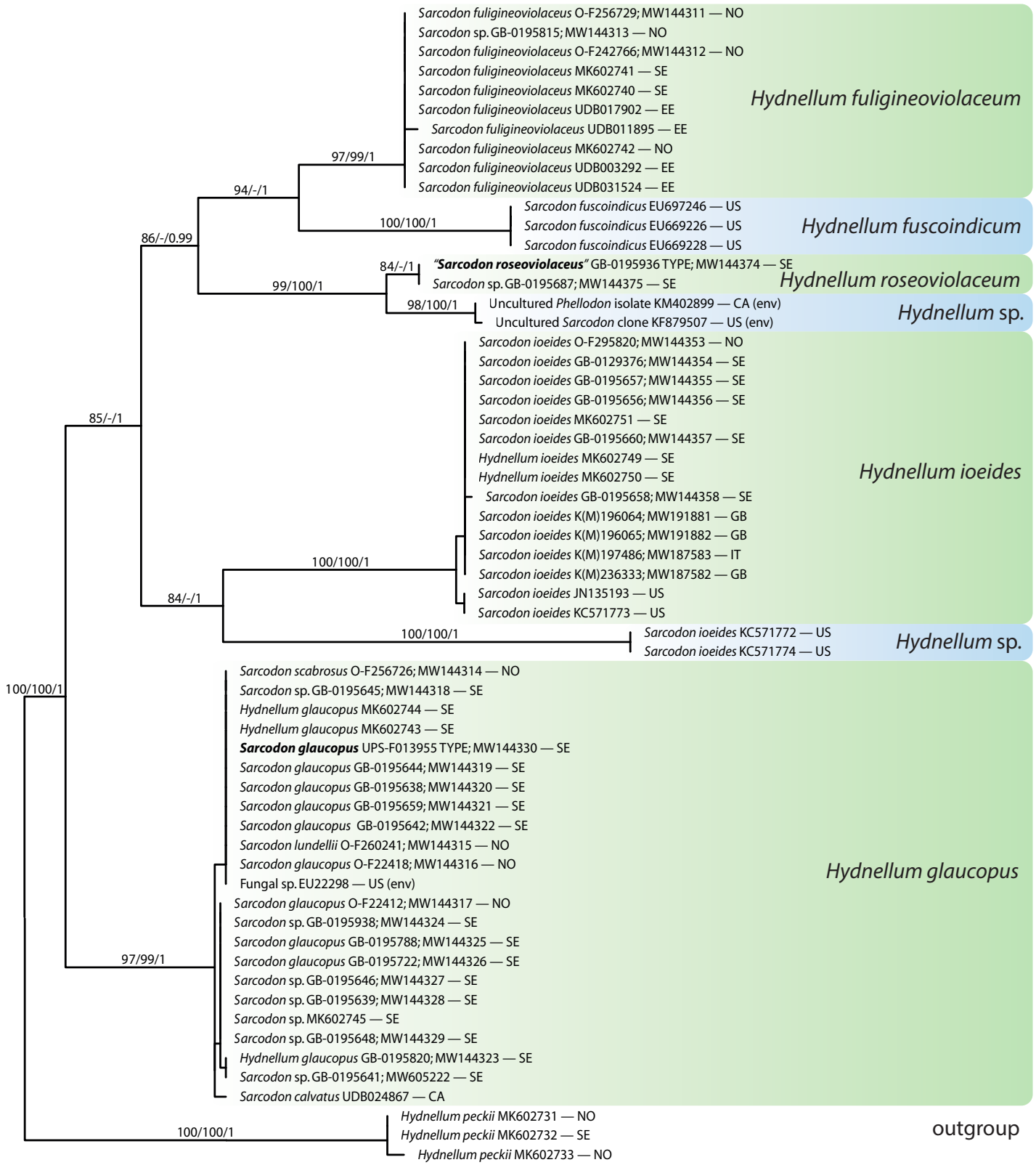

Fig. 2. Phylogram of *Hydnellum* section *Violacei.* Maximum Likelihood tree based on nuclear ribosomal ITS sequences. Numbers on branches represent reliable support values from SH-aLRT test (≥ 80 %), ultrafast bootstrap (≥ 95 %), and Bayesian inference posterior probability values (≥ 0.95), respectively. Terminal names are the original identification. Sequences from type specimens are marked in bold face. Sequences not generated from basidiomata are marked as env(ironmental).

Misapplication: *Sarcodon scabrosus* (at least in part) *sensu* European authors.

Selected illustrations (all labelled as *S. scabrosus*): Breitenbach & Kränzlin [1986: 235 (no. 279)], Maas Geesteranus (1975a: taf. 34 abb. a), Pegler *et al.* (1997: fig. 77 showing micromorphology of specimen K(M)30165 sequenced by Brock *et al.* 2009).

Description: *Basidiomata* terrestrial, stipitate, medium to rather large and fleshy, solitary or clustered, often in small groups.

Pileus 50–140 mm broad, irregularly rounded to lobate, initially convex, umbonate or plane, usually developing a depressed centre at maturity; margin thin, undulating and initially incurved; cuticle radially fibrillose, showing superficial tearing to produce marginal areolae and zones of concentric scales, sometimes terminating in an upturned pointed darker tip, and deeper tearing to produce radial fissures in the underlying paler context and a central zone of coarse block-like scales; initially pinkish red brown, sometimes showing lilac or pale violaceous tints, with whitish growing edge, becoming progressively darker towards the centre and entirely chestnut brown or black brown with age. *Stipe* 30–100 × 10–30 mm, cylindrical or basally tapered with smooth, scaly, longitudinally fibrillose texture or covered by rudimentary or entire spines; concolourous with the pileus at the apex and distinctly bluish-green to black at the base with whitish mycelium binding the soil. *Spines* not, slightly or strongly decurrent, up to 10 × 1 mm, light greyish brown with whitish tips at first, becoming progressively browner from the base. *Flesh* not zoned, whitish, with distinctive greyish- or bluish-green patch within the base of the stipe, smell farinaceous, taste farinaceous and bitter. *Chemical reaction*: when a drop of 3 % KOH is added to dry specimens, the pileipellis becomes darker brown and the flesh becomes pale brown. *Hyphal system* monomitic, all hyphae simple septate, tramal hyphae of spines up to 8 µm wide. *Basidia* clavate, with four sterigmata. *Basidiospores* brown, subglobose or short ellipsoid, irregularly tuberculate, with oblique apiculus, 4.5–6.3(–6.4) × (3.5–)3.8–5.3(–5.6) µm, av. = 5.4 × 4.7 µm, Q = 0.9–1.5 (n = 4/100, measurements from the lateral side without tubercles), tubercles numerous, up to 1.3 µm high, with rounded, flat-topped or exsculpate apices.

Ecology and distribution: We conclude that this species is ectomycorrhizal from the placement of GenBank sequence MF946050 which was obtained from an American ectomycorrhizal root tip of *Quercus* section *Lobatae* and identified as *S. scabrosus* in Rasmussen *et al*. (2018). From field observations we infer that *H. fagiscabrosum* is a mycorrhizal partner of *Fagus sylvatica*, *Quercus* spp. and *Castanea sativa*, including coppiced non-native *Castanea* in the UK. It is mostly found in the nemoral vegetation zone in sandy or gravelly soils, usually with other stipitate hydnoids, and often on mossy embankments, tracksides, ditchsides or in similarly nutrient poor microhabitats. The true extent of its European distribution is currently unknown due to its former inclusion within the circumscription of *S. scabrosus*, but we have produced molecular evidence for its presence in Norway, Sweden, UK and Italy and therefore suspect it is a very widespread, albeit relatively uncommon, member of the European *Fagaceae*-associated stipitate hydnoid community. Placement of GenBank sequences in Fig. 3 demonstrate that *H. fagiscabrosum* is also present in the southeastern USA in Florida, North Carolina and Tennessee where it has been assigned to *S. scabrosus* (Hughes *et al*. 2009, Baird *et al*. 2013, Rasmussen *et al*. 2018).

Additional specimens examined: **Italy**, Liguria, Savona, Sassello, Badami, on soil near *Castanea sativa*, 2 Sep. 2010, *F. Boccardo* K(M)197487 (as *S. regalis*). **Norway**, Agder, Tvedestrand, N of Øynesvann, trackside in *Quercus* forest, 23 Aug. 2014, *I.-L. Fonneland & D. Pettersen* O-F-251442. **Sweden**, Bohuslän, Lysekil par., Vägeröds dalar, on soil with *Quercus* sp. and *Tilia cordata*, *E. Larsson* GB-0195727; Sotenäs and Tossene par., Hogsäm, on soil under *Fagus sylvatica*, *R.-G. Carlsson* GB-0195621, GB-0195625; Tanum par., Lindö, on soil *with Quercus* sp*., Tilia cordata*, and *Corylus avellana*, *J. Olsson* GB-0195622; Västergötland, Sätila par., Ramhultafallet, on soil with *Quercus* sp. and *Corylus avellana*, *R.-G. Carlsson* GB-0195621. **UK**, Berkshire (VC22), Windsor Crown Estate, on soil near *Castanea sativa*, 28 Sep. 1979, *R. Phillips* K(M)119189 (as *S. scabrosus*); Windsor Crown Estate, Buttersteep area (dry ditch), (SU9065), on soil near *Castanea sativa*, 2 Sep. 2005, *A.M. Ainsworth* K(M)197477 (as *S. scabrosus*); Windsor Crown Estate, Buttersteep Hill, (SU9066), on soil near *Castanea sativa*, 29 Sep. 2008, *A.M. Ainsworth* K(M)197472 (as *Sarcodon* sp.); East Norfolk (VC27), St Faith's Common (TG181173), on soil near *Castanea sativa*, 22 Sep. 2011, *A. Crotty* K(M)197476 (as *S. scabrosus*); South Hampshire (VC11), New Forest, Brock Hill area (SU27020553), on soil near *Quercus* sp. and *Fagus sylvatica*, 9 Oct. 2011, *M. Nesbitt* K(M)172590 (as *S. scabrosus*); New Forest, Roydon Woods (SU313000), on soil, 11 Sep. 2002, *A. Leonard* K(M)181351 (as *S. scabrosus*); New Forest, Vinney Ridge (SU26290518), on soil near *Quercus* sp., 17 Sep. 2010, *A. Lucas* Hyd229 (as *S. scabrosus*); Surrey (VC17), Witley Common (SU92553982), on soil near *Quercus* sp. and *Castanea sativa*, 13 Sep. 2008, *L. Goodwin* K(M)160940 (as *S. scabrosus*); Woking (TQ018605), on soil near *Quercus* sp., *Castanea sativa* and *Pinus sylvestris*, 31 Jul. 2007, *R.A. Alder* K(M)162048 (as *S. scabrosus*); *ibid.*, 6 Sep. 2011, *R.A. Alder* K(M)171979 (as *S. scabrosus*); West Kent (VC16), Seal Chart (TQ567557), on soil near *Quercus petraea*, 11 Oct. 2010, *J. Pitt* K(M)197490; Tudeley Woods, on soil near *Castanea sativa*, 24 Sep. 1994, *N. Fletcher* K(M)30165, (as *S. scabrosus*); *ibid.*, 15 Oct. 1999, *J. Weightman* K(M)64653 (as *S. scabrosus*).

Notes: Historically, our species has been included in a broad concept of *Sarcodon scabrosus* which has an inferred association with both *Fagaceae* and *Pinaceae*, at least in Europe. However, based on its protologue, the discussion in Maas Geesteranus & Nannfeldt (1969) and the clustering of a sequence derived from its neotype with several sequences derived from conifer-associated basidiomata and mycorrhizal root samples (see Fig. 3), *Hydnellum scabrosum sensu stricto* was revealed to be an ectomycorrhizal partner of *Pinaceae* only. More specifically, it was detected in the roots of *Pinus sylvestris* in Estonia (UNITE UDB008050), of *Pinus densiflora* (GenBank AB251833) in Japan (Lian *et al*. 2006) and of *Pseudotsuga menziesii* (GenBank KM402896) in Canada (Kranabetter *et al*. 2015). Furthermore, European basidiomatal sequence and collection data indicate that it is usually found on poor sandy soils with *P. sylvestris* and never in pure stands of *Fagaceae*. It should also be noted in passing that the placement of GenBank sequence AF351870 in Fig. 3 indicates that, in Oregon at least, *H. scabrosum sensu stricto* can also form mycorrhizal associations with epiparasitic monotropoid plant roots (Bidartondo & Bruns 2001).

Hitherto, *H. fagiscabrosum* was recognized as "*Sarcodon* sp. 1 (with *Fagaceae*)" in the UK (Smith *et al*. 2016) and as "*H. fagiscabrosum nom. prov.*" in Sweden (Nitare 2019). We have not been able to find any usable existing name for this misinterpreted species, and old names such as *Hydnum amarescens* Quél., a fairly pale and minutely scaly species with a non-existent type *fide* Maas Geesteranus (1956), are all dubious and have been applied to other species (see *e.g.* discussion in Maas Geesteranus & Nannfeldt 1969). Therefore, we prefer to give this widely distributed species a new name.

The basidiomata of *H. fagiscabrosum*, *H. illudens* and *H. scabrosum* are similarly coarsely scaly when fully mature, but these species differ in their pileal pigmentation and ecological associations. In the field, *H. fagiscabrosum* can be distinguished from *H. scabrosum* by the relatively persistent, often broad and contrastingly whitish pileal margin of the former and its

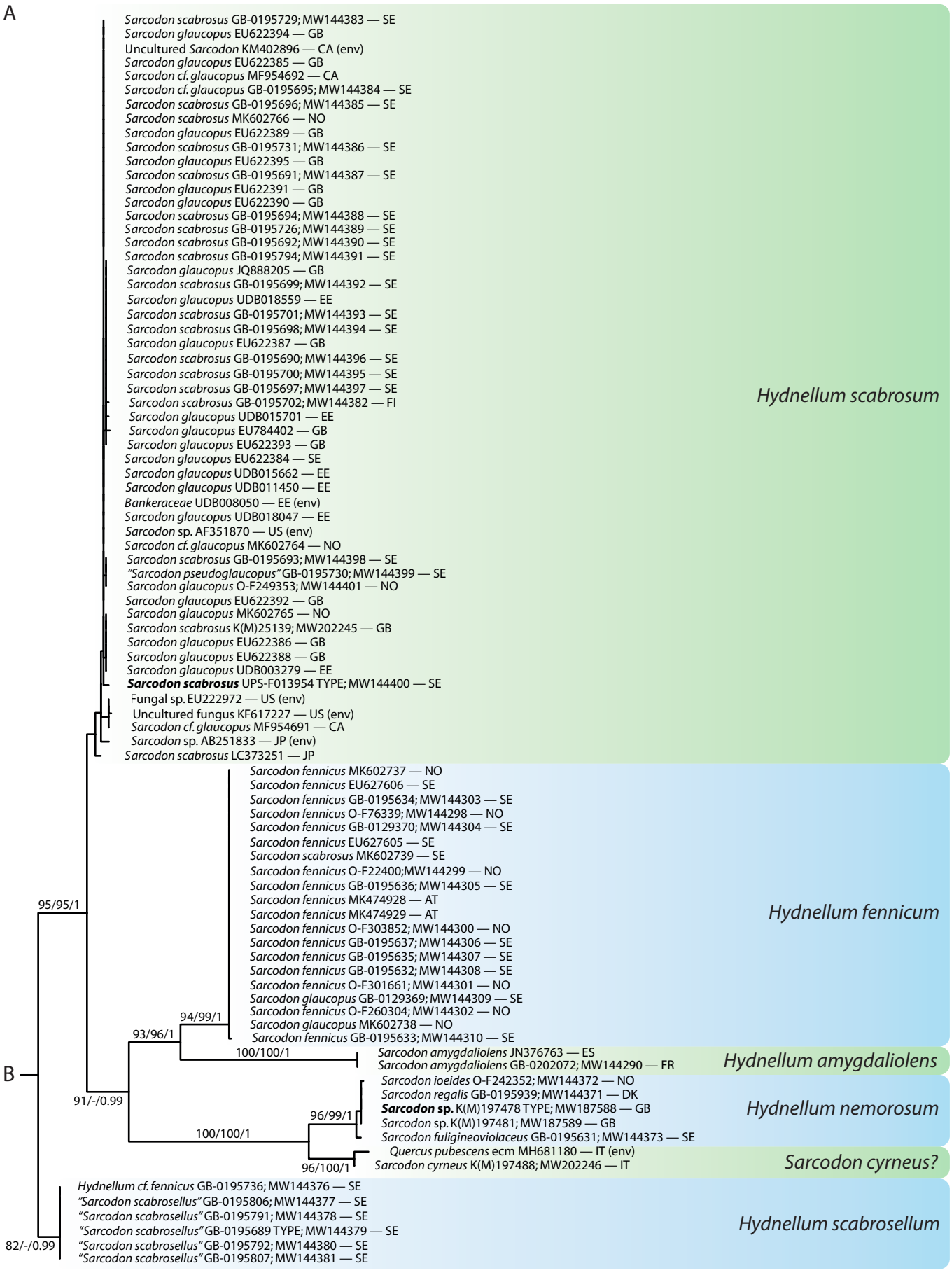

Fig. 3. Phylogram of *Hydnellum* section *Scabrosi.* Maximum Likelihood tree based on nuclear ribosomal ITS sequences. Numbers on branches represent reliable support values from SH-aLRT test (≥ 80 %), ultrafast bootstrap (≥ 95 %), and Bayesian inference posterior probability values (≥ 0.95), respectively. Terminal names are the original identification. Sequences from type specimens are marked in bold face. Sequences not generated from basidiomata are marked as env(ironmental).

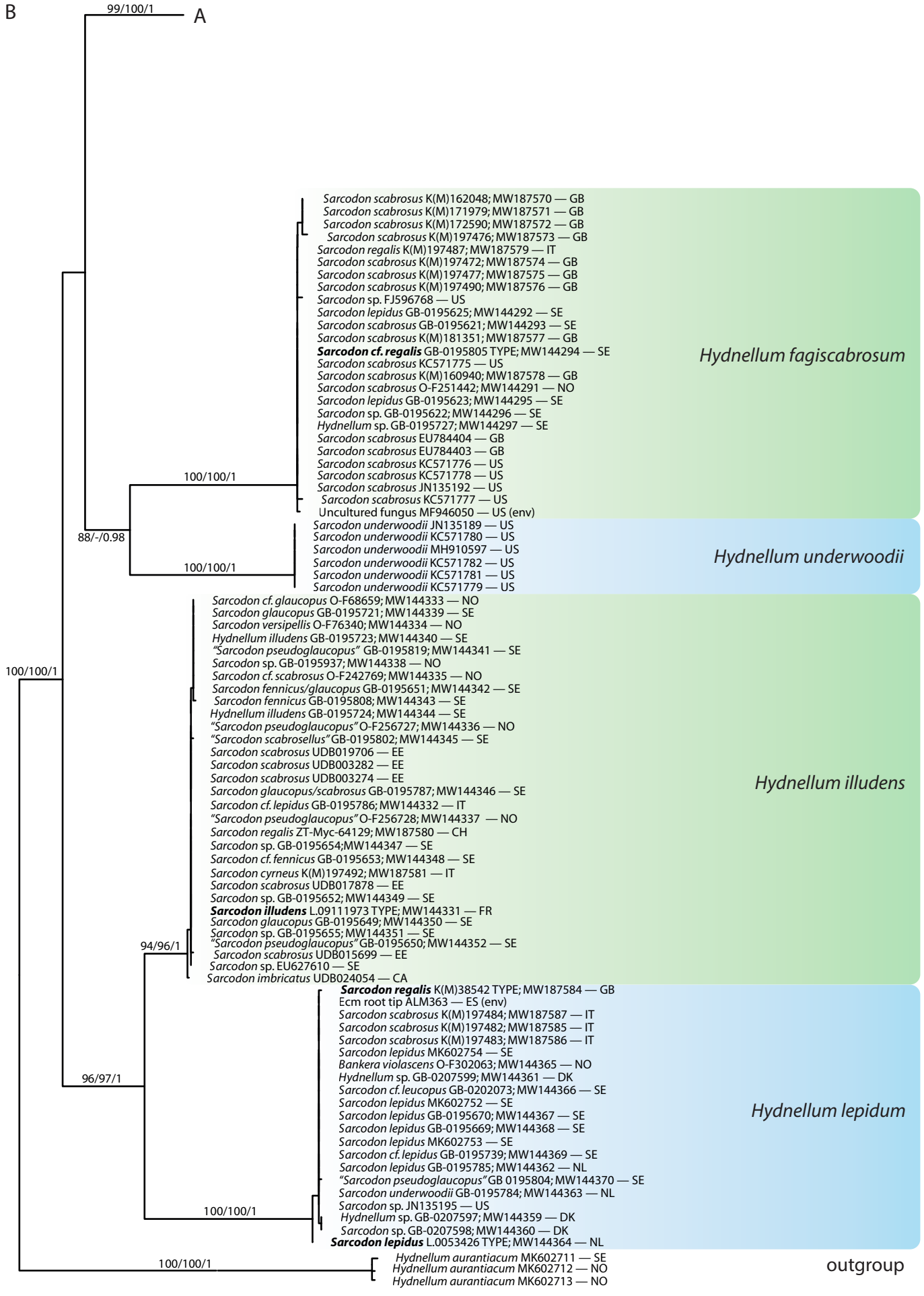

Fig. 3. (Continued).

Fig. 4. A. *Hydnellum fagiscabrosum* GB-0195727. **B.** Collecting site for GB-0195727. **C.** *H. fagiscabrosum* holotype, GB-0195805. **D.** *H. fagiscabrosum* O-F-251442, photo I.-L. Fonneland. **E.** *H. fagiscabrosum* Hyd229, photo A. Lucas **F.** *H. fagiscabrosum* GB-0195622, photo J. Olsson. **G.** *Hydnellum lepidum* DMS-680077, photo T. Borgen. **H.** *H. lepidum* GB-0202073.

association with *Fagaceae*. *Hydnellum scabrosum* has a more concolorous pileal margin and it associates with *Pinaceae*. Although *H. illudens* and *H. fagiscabrosum* might be found in similar habitats in southern Europe, they differ in basidiomatal colours. The pileal surface is yellowish brown in *H. illudens* and the dried flesh also assumes a yellowish colour, whereas the pileus is reddish brown in *H. fagiscabrosum* and the flesh remains greyish when dried. Furthermore, basidiomata of *H. illudens* have a strongly farinaceous taste, whereas those of *H. fagiscabrosum* are rather sour and acrid.

Hydnellum fagiscabrosum is distinguished from *H. nemorosum* and *H. lepidum*, both of which are associated with broadleaved trees, by its more coarsely scaly pileus. Of these species, *H. nemorosum* differs the most with its pinkish to vinaceous-brown pileus which is fissured but not really scaly, whereas in *H. lepidum* the scales are small and more or less adpressed all over the pileal surface.

Hydnellum illudens (Maas Geest.) Nitare, ***comb. nov.*** MycoBank MB 837988. Figs 5A–D, 9C.
Basionym: *Sarcodon illudens* Maas Geest., *Proc. K. Ned. Akad. Wet.,* Section C **79**(3): 285. 1976.
Synonym: "*Sarcodon pseudoglaucopus*", Nitare *nom. prov.* in Nitare & Högberg (2012).

Misapplication: *Sarcodon glaucopus sensu* Nitare, 2006, *non* Maas Geesteranus & Nannfeldt, 1969.

Selected illustrations (as "*Sarcodon pseudoglaucopus*" Nitare *nom. prov*.): Nitare & Högberg (2012: fig. 9A–F).

Typus: **France**, Vendée, Saint-Hilaire-de-Talmont, "Le Veillon", under an old *Quercus ilex*, 4 Nov. 1973, *J. Boiffard* L.09111973 (holotype).

Description: *Basidiomata* terrestrial, stipitate, fleshy and compact, single or concrescent. *Pileus* 70–120 mm, convex to plano-convex, centrally somewhat depressed, ochraceous to fulvous brown, sometimes darker in the middle. Cuticle initially slightly tomentose, dry, first loosely covered by a thin cottony tomentum-layer of ephemeral whitish to pale rose hyphae (mostly whitish, but sometimes with slightly pinkish tints, often seen only in the expanding margin), with age becoming smooth, more or less glabrescent, from the centre more or less cracked into areoles and small adnate scales. *Stipe* 40–60 × 15–30 mm, above concolourous with the pileus, tapering downwards with a short rooting point, at the base white-tomentose or greyish blue to olivaceous grey (usually only at the rooting point, but sometimes developing a blue-grey base of the stipe). *Spines* strongly decurrent, but rarely reaching the middle of the stipe, up to 5 mm long, crowded, at first pallid, then becoming yellowish brown, when dried yellowish to ochraceous. *Flesh* not zoned, when fresh pale greyish, when dry (exsiccates) yellowish to ochraceous. *Smell* subfarinaceous, taste at first strongly farinaceous, mild or slightly acid or bitterish, after a short while leaving a more intensely bitter taste with farinaceous components. *Chemical reaction*. When adding 3 % KOH on dry specimens, only the pileipellis (not the flesh) immediately changes colour to charcoal black. *Hyphal system* monomitic, all hyphae simple septate, spine trama hyphae up to 7 µm wide. *Basidia* clavate, with four sterigmata. *Basidiospores* pale brownish, globose or irregularly subglobose, tuberculate, with oblique apiculus, 4.7–5.7(–6.1) × 3.5–4.5 µm, $\bar{x}$ = 5.2 × 4.0 µm, Q = 1.2–1.5 (n = 3/90, measurements from the lateral side without tubercles), tubercles numerous, 0.4–0.9 µm high, with rounded, flat-topped or exsculpate apices.

Ecology and distribution: Associated with *Picea*, *Pinus* or *Quercus* on calcareous or somewhat base-rich soils, often in sandy and dry places. In addition to the type locality in France it is known from calcareous ground in several districts in Sweden within the hemiboreal, southern boreal and middle boreal vegetation zones. It is confirmed also from southern to central Norway, Estonia, Switzerland, and Italy. A sequence (UDB024054) deposited in the UNITE database under the name *Sarcodon imbricatus* proved to be this species. The sequence was generated from a basidioma collected in conifer forest in NW British Columbia, Canada, making it the first report of *Hydnellum illudens* from North America.

Additional specimens examined: **Italy**, Puglia, Bari, Casamasella 14 km E of Maglia, old forest of *Quercus ilex* on calcareous soil, 6 Jan. 2007, *E. Arnolds* GB-0195786; Sardinia, Baldo, near *Quercus suber, Cistus, Arbutus*, 12 Nov. 2006, *C.A. Hobart* K(M)197492 (as *S. cyrneus*). **Norway**, Nord-Trøndelag, Steinkjer, Kalvøya, on soil with *Pinus sylvestris*, *H. Holien*, O-F-68659; Hedmark, Hamar, Furuberget nat. res., *K. & E. Bendiksen* O-F-76340; Viken, Ringerike, SW of Ultvedt, on soil in conifer forest, *G. Gaarder* O-F-242769; Ultveitvatnet nat. res., on soil in conifer forest, 25 Sep. 2010, *S. Svantesson* GB-0195937; Ultvedtåsen, calcareous *Pinus* forest, 16 Sep. 2016, *T.E. Brandrud & B. Dima* O-F-256728; Nordbyåsen, calcareous *Pinus* forest with some *Picea*, 20 Sep. 2016, *T.E. Brandrud & B. Dima* O-F-256727. **Sweden**, Dalarna, Rättvik, Rättviksheden, "Gropen", sandy *Pinus* heath, 5 Sep. 2004, *J. Nitare* GB-0195825 (fig. 9E & F in Nitare & Högberg 2012; ITS1 JX999975); Kalkverket SO, lichen-rich *Pinus* forest, 21 Aug. 2010, *E. Larsson* GB-0195721; Enån nat. res., Kungshol, sandy *Pinus* heath, 7 Sep. 2018, *E. Larsson* GB-0195723, GB-0195724; Gotland, Gothem, Åminne, Tjälders, on soil in mixed conifer forest on limestone, 23 Aug. 2005, *J. Nitare* GB-0195803 (ITS: 1 JX999984); 26 Sep. 2011, *J. Nitare* GB-0195649; Gästrikland, Gävle, Limön, Oxharen, mixed conifer forest, 18 Aug. 2012, *L. Andersson & T. Fasth* GB-0195651; NE of the café, *Picea* forest with some *Pinus* on diabase, 18 Aug. 2012 *L. Andersson & T. Fasth* GB-0195808; Limön 18 Aug. 2012, *L. Andersson & T. Fasth* GB 0195652, GB-0195653, GB-0195654, GB-0195655; Uppland, Älvkarleby, Billudden, Brämsand, on soil in calcareous sandy *Pinus sylvestris* forest, 12 Sep. 2007, *J. Nitare* GB-0195818 (fig. 9A in Nitare & Högberg 2012; ITS: 1 JX999985); 10 Oct. 2010, *G. Aronsson* GB-0195650 10; 14 Sep. 2009, *J. Nitare* GB-0195819 (fig. 9B & 9C in Nitare & Högberg 2012); Västland, Östervret, calcareous *Picea* forest, 16 Sep. 2016, *J. Nitare* GB-0195802; Öland, Böda, Böda kronopark, *Pinus* forest on wind-blown coastal sand-dunes, 8 Oct. 2007, *E. Arnolds* GB-0195787.

Notes: This species differs macroscopically from *Hydnellum scabrosum*, *H. fagiscabrosum* and *H. glaucopus* by its ochraceous to fulvous brown cuticle (almond-brown or like café-au-lait) without copper-rufous (reddish) or violaceous colours and in dried exsiccates by its yellowish-ochraceous flesh and hymenium (spines). Both *H. illudens* and *H. scabrosum* can associate with *Pinus*, but *H. illudens* is found on base-rich soils whereas *H. scabrosum* is found mostly on acidic soils. *Hydnellum illudens* usually produces smaller and more compact and sturdier basidiomata compared to *H. scabrosum*. *Hydnellum glaucopus* can also be distinguished from the others by its smaller basidiospores which are 4–4.5 µm, evenly subglobose

Fig. 5. A. *Hydnellum illudens* TU106275 (UDB003274), photo V. Liiv. **B.** *H. illudens* GB-0195724. **C.** *H. illudens* TU106475 (UDB015699), photo V. Liiv. **D.** *H. illudens* GB-0195818. **E.** *Hydnellum scabrosum* TU106993 (UDB015662), photo V. Liiv. **F.** *H. scabrosum* TU106280 (UDB003279), photo V. Liiv.

and ornamented with rather slender evenly spread spines that are rarely twinned. By contrast, the larger basidiospores (up to 6.5 µm long) of *H. fagiscabrosum*, *H. illudens* and *H. fagiscabrosum* are slightly irregular and ornamented with rather coarse, frequently twinned (exsculpate) spines.

Maas Geesteranus (1976) regarded *H. lepidum* (as *Sarcodon*) as the most closely related species. This observation is confirmed by the molecular phylogeny where the two species cluster together with high support.

Since its description from a single specimen the species has been little reported and seemingly ignored or misunderstood by European mycologists. The specimens we have sequenced were either not fully identified or assigned to *Sarcodon cyrneus*, *S. fennicus, S. glaucopus, S. regalis, S. scabrosus, S. versipellis* or to the provisional name "*S. pseudoglaucopus*".

Two sequenced Italian specimens (GB-0195786, K(M)197492) were collected under *Quercus ilex* and *Q. suber*, respectively, which is also the normal habitat for *Sarcodon cyrneus*. The possibility that *H. illudens* can associate with *Quercus* trees implies that ecology alone may not suffice to separate *H. illudens* from *H. lepidum*. See also notes to *H. nemorosum* below.

Hydnellum nemorosum A.M. Ainsw. & E. Larss. ***sp. nov.*** MycoBank MB 837985. Figs 6A, C, D, 9E.

Fig. 6. A. *Hydnellum nemorosum* K(M)197481. **B.** *H. nemorosum* type locality. **C, D.** *H. nemorosum* holotype, K(M)197478.

Etymology: The epithet *nemorosum* refers to broadleaved trees which are thought to be the mycorrhizal partners of this species. *Typus*: **UK**, Berkshire (VC22), Windsor Great Park, Johnson's Pond (SU96676951), on a moss-covered (*Leucobryum*) sandy mound near *Castanea sativa,* with *Pinus sylvestris* and *Quercus robur* further away, 51.416389/-0.611111, 15 Sep. 2008, *A.M. Ainsworth* (**holotypus** K(M)197478; **isotypus** GB-0207601); GenBank accession: MW187588.

Description: *Basidiomata* terrestrial, stipitate, medium-sized and fleshy, solitary or clustered, often in small groups. *Pileus* 40–100 mm broad, irregularly rounded to lobate, initially convex or umbonate, becoming more plane with age and sometimes developing a depressed centre; margin thin, undulating and remaining long incurved; cuticle initially almost smooth, matt, becoming pellicular and sometimes shiny in places, occasionally showing superficial tearing to produce a few marginal areolae and zones of poorly-developed appressed scales, and more frequently becoming deeply lacerated to produce radial fissures in the underlying paler context and a central zone of coarse block-like scales; initially pinkish or vinaceous brown, with whitish growing edge, becoming progressively darker reddish or vinaceous brown towards the centre and blackening with age. *Stipe* 20–60 × 10–30 mm, cylindrical or basally tapered with a smooth or fibrillose texture and sometimes covered by rudimentary or entire spines; concolourous with the young pileus at the apex, darker below and distinctly bluish–green to black at the base with whitish mycelium binding the soil. *Spines* to some degree decurrent, up to 5 × 1 mm, pinkish brown with whitish tips at first, becoming progressively vinaceous and browner from the base. *Flesh* not zoned, whitish with pink tinges becoming more vinaceous when exposed to the air by tearing of pileal surface, with distinctive greyish- or bluish-green patch within the base of the stipe, smell farinaceous but with a penetrating fruity element, taste farinaceous and bitter. *Chemical reaction*: when a drop of 3 % KOH is added to dry specimens, the pileipellis becomes darker brown and the flesh becomes pale brown. *Hyphal system* monomitic, all hyphae simple septate, tramal hyphae of spines up to 6.5 µm wide. *Basidia* clavate, with four sterigmata. *Basidiospores* brown, subglobose or short ellipsoid, irregularly tuberculate, with oblique apiculus, (3.0–)3.4–5.1(–5.3) × (2.8–)3.0–3.8(–4.5) µm, av. = 4.1 × 3.4 µm, Q = 1.0–1.6 (n = 4/100, measurements from the lateral side without tubercles), tubercles numerous, 0.2–0.8 µm high, with rounded, flat-topped or exsculpate apices.

Ecology and distribution: We are of the opinion that this species is ectomycorrhizal, although we are currently unaware of any ectomycorrhizal root tip DNA evidence to confirm this. From field notes accompanying the specimens sequenced, we conclude that, although records are comparatively sparse, this species is found in mixed or broadleaved woodland and is therefore almost certainly a mycorrhizal partner of various broadleaved tree species. Hosts are likely to include *Castanea sativa*, *Fagus sylvatica* and *Quercus* spp. It should be noted, however, that there were no representatives of *Fagaceae* recorded near our species in the mixed woodland present at the sampled Swedish locality (see *Additional specimens examined*). Our choice of

epithet for this species therefore reflects our greater degree of uncertainty regarding the range of its mycorrhizal partners compared to our state of knowledge regarding *H. fagiscabrosum*. It has been found in sandy or gravelly soils, sometimes with other stipitate hydnoids, and seemingly with a preference for raised or sloping ground or similarly nutrient poor microhabitats. The true extent of its European distribution is currently unknown due to the current paucity of known collections. It may have been misdetermined as a range of *Sarcodon* species in the past, but there are so few records to date that it could well be a genuine rarity. Thus far, we have produced molecular evidence for its presence in northern and western Europe (Denmark, Norway, Sweden and the UK), although this is currently restricted to just a single site in each country.

Additional specimens examined: **Denmark**, Jylland, Silkeborg, Kobskov, on mineral soil on sloping ground near *Fagus sylvatica*, 15 Sep. 2017, *T. Borgen* DMS-9211777 (GB-0195939) (as *S. regalis*). **Norway**, Aust-Agder, Grimstad, Bakken Nord, on soil in steep southwest facing *Quercus*-dominated broadleaved woodland, 19 Sep. 2011, *I.-L. Fonneland* O-F-242352 (as *S. ioeides*). **Sweden**, Dalarna, Rättvik, Rättviksheden, on soil amongst mosses in mixed forest (but no *Fagus* or *Quercus* present), 8 Sep. 2000, *D. Broström* GB-0195631 (as *S. fuligineoviolaceus*). **UK**, same details as for holotype, 25 Sep. 2010, *A.M. Ainsworth* K(M)197481 (as *Sarcodon* sp.)

Notes: This species has been described and illustrated online under the name *Sarcodon regalis sensu* Strandberg & Borgen in Danmarks svampeatlas (Strandberg & Borgen 2020) wherein it was documented repeatedly at a single Danish location between 2002 and 2019. It has also been recognized as "*Sarcodon* sp. 2" in an unofficial species conservation assessment (Data Deficient) in the UK (Smith *et al*. 2016). Two other names (see above) have been misapplied to this species in Norway and Sweden and both are likely to have arisen due to the dominant dark purplish brown pigmentation of its mature basidiomata. We do not know if this species occurs in southern Europe but, if it is present in any historical collections, there is at least one further name that should be included in the search, namely *S. cyrneus*. This is another broadleaved tree associate which was described from two Corsican collections (Maas Geesteranus 1975a, b). Its protologue refers to its pinkish and purplish brown colours and poorly defined pileal scales, morphological characters which are reminiscent of *H. nemorosum*, but, critically, the two species differ in the pigmentation at the base of the stipe. Indeed, Maas Geesteranus (1975a) keys his species in section *Squamiceps* rather than section *Scabrosi* based on its lack of bluish or greenish colours in the stipe base. Furthermore, the illustration of the dried holotype in Maas Geesteranus (1975a) seems too pale to be *H. nemorosum* and there is also a difference in spore length. Bearing in mind that Maas Geesteranus' (1971) spore measurements of *Hydnellum* and *Sarcodon* always included the ornamentation, he stated that the length of "probably not mature" spores of *S. cyrneus* ranges from (5.8–)6.3–7.3 µm whereas the corresponding values obtained for our specimens of *H. nemorosum* (n = 100) are 4.5–5.8(–6.0) µm. It would have been very interesting to include authentic *S. cyrneus* in our analyses but, unfortunately, our attempts to generate a sequence from type material were unsuccessful (see Discussion for further remarks on *S. cyrneus*).

Hydnellum roseoviolaceum Nitare ***sp. nov.*** MycoBank MB 837986. Figs 7A–C, 9F.

Etymology: Epithet derived from *roseo* (L) = rose, referring to the rosy (rose-coloured) basidiomatal context, combined with *violaceum* (violet-coloured) referring to its tendency to change colour to violet-lilac.

Typus: **Sweden**, Härjedalen, Sveg, Fisktjärnområdet, Ytterberg, in dry, lichen-dominated, seminatural old pine heath forest on acidic sand together with *Cladonia* spp., 62.072398/14.541843, 19 Sep. 2009, *B. Petterson & S. Pratheepchuang* (**holotypus** GB-0195936; **isotypi** O, UPS); GenBank accession: MW144374.

Description. *Basidiomata* terrestrial, stipitate, fleshy and compact, simple, often rather small and slender. Pileus (30–)50–80 mm broad, convex to plano-convex, somewhat depressed in the centre, with undulating edge, ochraceous brown, tobacco/cigar-brown to reddish brown, with blackish spots in old or damaged parts. Pileus becoming more-or-less dirty black-spotted due to blackening of the hypodermis. Cuticle (pileipellis) dry, epidermis in young basidiomata forming a very thin brown tomentum, later becoming almost smooth, with no radially arranged fibrils, but with short and very small adnate hairy tufts from agglutination of tomentum hyphae (only seen under a lens), in patches sometimes cracked into small areoles. Dry specimens sometimes with small yellowish dots of excreted matter. *Stipe* 40–60 × (5–)10–15 mm, concolourous with the pileus, tapering downwards and with a short greyish-blue rooting point. *Spines* strongly decurrent, but rarely reaching the middle of the stipe, up to 5 mm long, crowded, with age dark brown, but for a long time pallid at the tip. *Flesh* not zoned, first pinkish to rosy, becoming violaceous to lilac in about 20 s, at least in the central parts of the basidioma, more-or-less blackening when drying. No particular smell, taste mild. *Chemical reaction*. When adding 3 % KOH to dry specimens, both the pileipellis and flesh (trama) immediately change colour to charcoal black. *Hyphal system* monomitic, all hyphae simple septate, tramal hyphae in spines up to 10 µm wide. *Basidia* clavate, clampless, with 4 sterigmata. *Basidiospores* pale brownish, globose or subglobose, tuberculate, with oblique apiculus, 4.3–5.1 × 3.2–4.2 µm, av. = 4.7 × 3.6 µm, Q = 1.1–1.5 (n = 2/48, measurements from the lateral side without tubercles), tubercles numerous, 0.5–0.8 µm high, with prominent rounded apices.

Ecology and distribution: Presumably ectomycorrhizal with *Pinus sylvestris.* Found in old, seminatural *Pinus* stands (pine heaths) on dry, acidic sandy soil with *Cladonia* lichens. Only known from three records (two localities) in eastern central Sweden, within the middle and northern boreal vegetation zones in areas with a rather continental climate.

Additional specimens examined: **Sweden**, Härjedalen, Sveg, Fisktjärnområdet, Ytterberg, 29 Aug. 2008, *P. Hedberg* (UPS) (= first record at the type locality); Dalarna, Vårmhus, Kumbelnäs, Bonäsheden, old pine heath on fossil eolian sand-dunes, 8 Sep. 2008, *D. Broström* GB-0195687.

Notes: Among the hydnoid fungi associated with *Pinus sylvestris*, *Hydnellum roseoviolaceum* seems to be very close to, and has been mistaken for, *H. fuligineoviolaceum* due to its tendency to assume a lilac flesh. It differs by smaller spores, colour changes in the flesh from rose to violet (not being violet from the beginning

Fig. 7. A–C. *Hydnellum roseoviolaceum*, holotype, GB-0195936, photos B. Pettersson. **D.** *H. roseoviolaceum* type locality, photo B. Pettersson. **E.** *H. fuligineoviolaceum* TU106391 (UDB011895), photo V. Liiv. **F.** *H. fuligineoviolaceum* GB-0195817.

as in *H. fuligineoviolaceum*) and its mild taste (*N.B.* some people cannot detect the very acrid taste of *H. fuligineoviolaceum*). It differs from *H. glaucopus e.g.* by its more intense rose-lilac flesh and by being associated with *Pinus* (not *Picea*) on acidic, non-calcareous sites. The pictures, and partly the description, of *S. fuligineoviolaceus*, by Maas Geesteranus (1975a, *e.g.* plate 38) seem very similar to those of this new species (collections from Greece not checked) and this may be due to a misapplication of the name.

To compare the newly described species with Kalchbrenner and Fries' original concept of *Hydnum fuligineo-violaceum*, the Carpathian collection from pinewoods at Olaszi (now Spišské Vlachy in Slovakia) made in Sept. 1870 and bearing Fries' handwriting (UPS, F-173546) was studied. The collection is selected as the type by Maas Geesteranus (1975a) but he refrained from a precise designation by writing "(Holo?)Typus". This is probably the original collection Fries refers to as *v. s.* (= *vidi siccam*; I have seen it dry) (Fries 1874). The material consists of

Fig. 8. A. *Hydnellum scabrosellum*, young basidiomata from the type locality, GB-0195806. **B.** *H. scabrosellum* holotype, mature basidiomata, GB-0195689. **C.** *H. scabrosellum* GB-0195791, photo G. Aronsson. **D.** *H. scabrosellum*, collecting site for GB-0195791, photo G. Aronsson.

one small basidioma divided in three slices. The flesh is typically bluish-violet-grey (also in the spines) and the spores are 5.1–6.2 × 3.4–4.4 µm, av. = 5.6 × 3.7 µm (n = 32, measurements from the lateral side without tubercles), tubercles 0.6–0.8 µm high. Kalchbrenner's collection therefore represents, without doubt, the present concept of *Hydnellum fuligineoviolaceum*.

An ITS BLAST search in GenBank brings up two western North American sequences as the closest matches at 95–96 %. These sequences are both generated from ectomycorrhizal root-tips, one from a *Pinus muricata* stand in northern California (Moeller *et al*. 2014), the other from *Pseudotsuga menziesii* in British Columbia (Kranabetter *et al*. 2015). The sequence difference to *H. roseoviolaceum* consists of 15 indels and 14 gaps. We currently cannot suggest any name for this American sister taxon, if any exists. If the basidiomatal colours are like those of *H. roseoviolaceum*, it is likely to become misidentified as *H. fuscoindicum.*

Hydnellum scabrosellum Nitare ***sp. nov.*** MycoBank MB 837987. Figs 8A–C, 9G.

Etymology: Epithet derived from *scabros*[*um*] and *-ellum* (L. dim.) referring to "the small *scabrosum*" (= *Hydnum scabrosum* Fr.).

Typus: **Sweden**, Uppland, Börstil parish, Tvärnö, Tuskö, Tuskösundet nat. res. ("Återvändan"), in herb-rich conifer forest dominated by *Picea abies* with some scattered old *Pinus sylvestris*, on strongly calcareous moraine on the edge of an old abandoned mine-shaft, 60.22267/18.49009, 13 Sep. 2012, *J. Nitare* (**holotypus** GB-0195689; **isotypi** O, UPS); GenBank accession: MW144379.

Description: *Basidiomata* terrestrial, stipitate, thin and slender, single or concrescent. Pileus 30–60(–100) mm broad, plano-convex to depressed, with undulating thin margin. Cuticle fibrillose and scaly, cracking up from the centre, at first rosy to pinkish, with whitish growing edge, with age becoming coppery or vinaceous reddish-brown to purplish-brown, with darkening blackish-brown scales in the centre. *Stipe* 30–60 × 5–10 mm, above ochraceous pinkish-brown or concolourous with the pileus, tapering downwards, at the base bluish-grey or blackish-green under a white mycelial cover. *Spines* strongly decurrent, often reaching the middle of the stipe, up to 5 mm long, crowded, at first pallid and whitish, by age becoming yellowish brown, when dry yellowish to ochraceous. *Flesh* not zoned, fresh pale, when dry (exsiccates) yellowish-ochraceous brown. *Smell* subfarinaceous, taste bitterish. *Chemical reaction.* When adding 3 % KOH to dry specimens, only the pileipellis (not the flesh) immediately changes colour to charcoal black. *Hyphal system* monomitic, all hyphae simple septate, generative hyphae up to 10 µm wide. *Basidia* clavate, with four sterigmata. *Basidiospores* pale brownish, globose or irregularly subglobose, tuberculate,

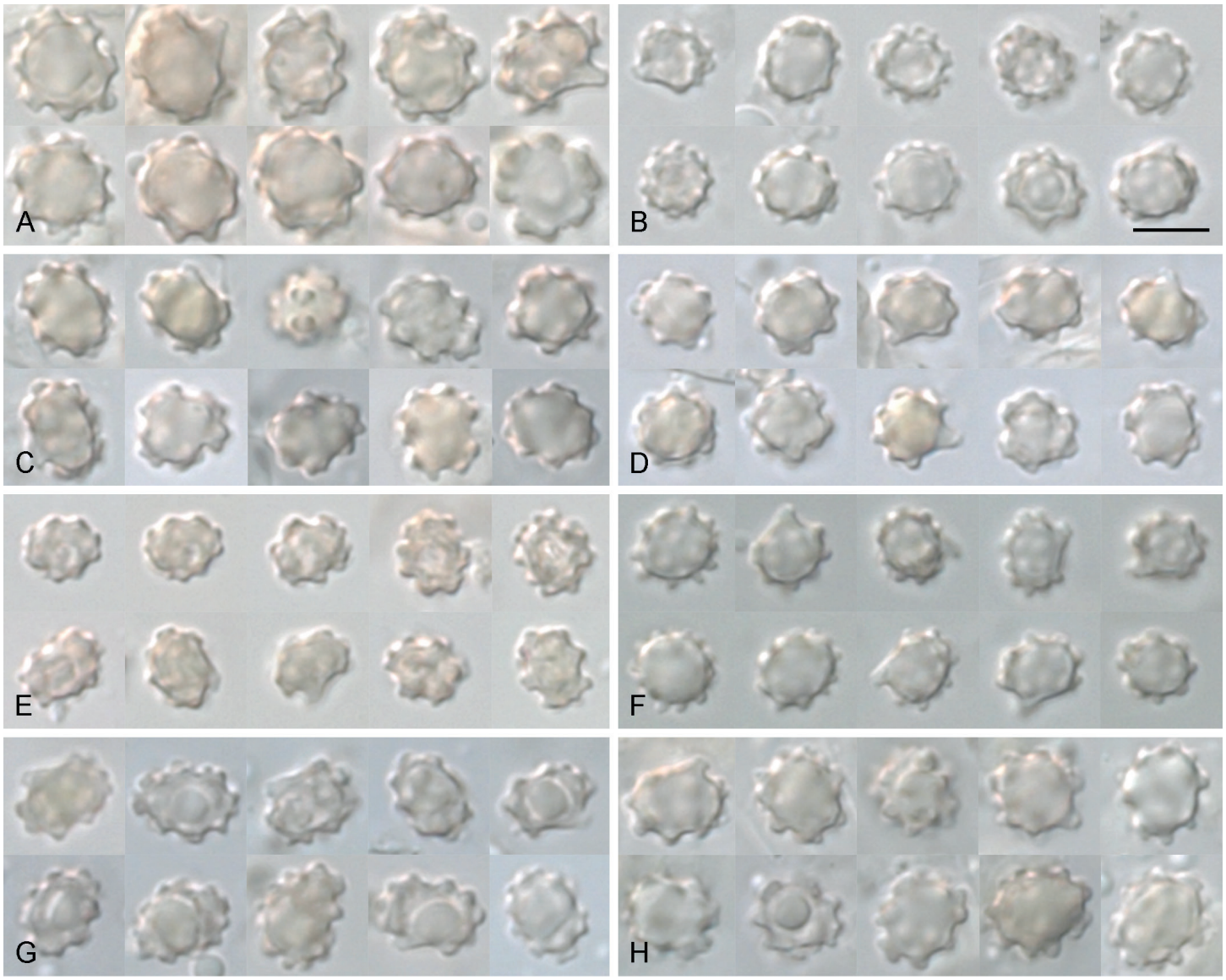

Fig. 9. *Hydnellum* basidiospores. **A.** *H. fagiscabrosum* (holotype, GB-0195805). **B.** *H. glaucopus* (GB-0195722). **C.** *H. illudens* (GB-0195937). **D.** *H. lepidum* (GB-129373). **E.** *H. nemorosum* (O-F-242352). **F.** *H. roseoviolaceum* (holotype. GB-0195936). **G.** *H. scabrosellum* (holotype, GB-0195689). **H.** *H. scabrosum* (GB-0195731). Scale bar = 5 µm.

with oblique apiculus, 5.1–6.6 × 3.4–4.7 µm, av. = 5.8 × 4.0 µm, Q = 1.2–1.7 (n = 3/90, measurements from the lateral side without tubercles), tubercles numerous, 0.6–0.9 µm high, with prominent, rounded, flattened, flat-topped to exsculpate apices.

Ecology and distribution: Presumably ectomycorrhizal with conifers (mixed forest with *Pinus* and *Picea*, associated tree-species not exactly known but probably *Pinus sylvestris*), strongly calciphilous. Mostly known from coniferous forests situated close to the coast (Gulf of Bothnia) in the province of Gästrikland and northern Uppland, east-central Sweden (at the northern limits of the hemiboreal vegetation zone). This so far Swedish species can be expected to occur in pine forests on calcareous ground around the Baltic Sea.

Additional specimens examined: **Sweden**, Gästrikland, Hamrånge, Bergby, Näset nat. res., calcareous conifer forest, 15 Sep. 2011, *J. Nitare* GB-0195807; Uppland, Börstil, Tvärnö, Tuskö, Tuskösundet, 5 Sep. 2008, *J. Nitare* GB-0195806 (from the same spot as the holotype, fig. 12A in Nitare & Högberg 2012); Älvkarleby, Lanforsen, Tippön, calcareous *Pinus sylvestris* forest (with scattered *Picea abies),* 20 Sep. 2013, *G. Aronsson* GB-0195791; Askön, calcareous *Pinus sylvestris* forest (with scattered *Picea abies*), 13 Sep. 2013, *G. Aronsson* GB-0195792; Östergötland, Västra Tollstad, Omberg, Ombergsliden nat. res., on soil in calcareous *Picea abies* forest with *Pinus sylvestris* and *Betula* sp., 13 Sep. 2016, *E. Larsson* GB-0195736.

Notes: Among the hydnoid fungi associated with conifers, *Hydnellum scabrosellum* is most similar to *H. scabrosum* but has smaller and slenderer basidiomata and looks like a dwarf form of the latter species. The size difference is particularly obvious when considering the stipe diameter which rarely exceeds 1 cm in *H. scabrosellum* but is usually 2–5 cm in mature specimens of *H. scabrosum*. The yellowish-ochraceous hymenium and flesh (when dry) and the occurrence on base-rich soil, also differs from the non-calciphilous *H. scabrosum*. The coastal region in Gästrikland, where most collections were made, is characterized by its extremely calcareous-rich soils (moraine), depending on the geological features and recent land uplift during the postglacial period.

DISCUSSION

Species in *Hydnellum* seem to be sensitive to nitrogen deposition and to modern forestry practices (Nitare 2019) and are of conservation concern across Europe. Fewer than 350 fungi are currently included in the IUCN's Red List of threatened species but, already, four European *Hydnellum* species (*H. compactum*, *H. gracilipes*, *H. ioeides* and *H. mirabile*) have been assessed as globally Vulnerable (IUCN 2020). In many European countries several species are evaluated as threatened and included on national Red Lists. Furthermore, rich assemblages of *Hydnellum* and other stipitate hydnoids are increasingly being used in the selection of sites for legal protection and/or habitat-specific conservation management, *e.g*. in the Netherlands (Ozinga *et al*. 2013), Sweden (Nitare 2019) and the UK (Bosanquet *et al*. 2018).

However, conservation assessments and measures require that species definitions are unambiguous and that habitat preferences are reasonably documented. Through the present study and similar earlier studies supported by molecular data, it has become clear that the morphological species concepts used for *Hydnellum* species in Europe are, in many cases, problematic. Names may cover several species and concepts may also differ between countries, leading to misidentifications. Furthermore, for all the species discussed here it is important to note that basidiomatal morphology and pigments change during development and are also influenced by growth patterns and weather conditions (compare for example the two specimens of *H. lepidum*, Fig. 4G, H). For a safer identification both young and fully developed basidiomata ought to be examined. It is also clear that not enough attention has been paid to host associations. *Hydnellum* species probably all form ectomycorrhizal partnerships and their host ranges may be more limited than suggested by maps and descriptions found in the literature. Indeed, we recommend that the identification process should always start with careful observation of the habitat and potential ectomycorrhizal partners. If the habitat is a conifer forest, *H. glaucopus*, *H. illudens* and *H. scabrosum* may be present. *Hydnellum glaucopus* will be found in mesic to moist *Picea* forest on somewhat base-rich soil while *H. scabrosum* grows in dry pine forest on base-poor, often sandy soil. *H. illudens* probably has a broader habitat choice and seems able to associate with both *Picea* and *Pinus*, albeit always on base-rich soil. If, on the other hand, the habitat is a hardwood forest then *H. fagiscabrosum, H. illudens, H. nemorosum* and *H. lepidum* must be considered during identification. If the habitat is a mixed forest, a morphology-based identification alone may not produce reliable results and DNA sequencing should be considered.

Maas Geesteranus (1971, 1975a) introduced section *Scabrosi* (under *Sarcodon*) and included *S. scabrosus* (section type), *S. fennicus*, *S. glaucopus*, *S. lepidus* and *S. regalis*. Commenting on a key to the section, Maas Geesteranus (1975a) wrote "Die Unterscheidung bereitet öfters Schwierigkeiten!". *Sarcodon illudens* was a later addition (Maas Geesteranus 1976) and in the present paper three new species, *H. fagiscabrosum*, *H. nemorosum*, and *H. scabrosellum*, add further complexity to the section. Furthermore, sequences from specimens identified as *S. cyrneus* and *H. underwoodii* were also recovered within section *Scabrosi*. If these sequences are correctly named, the placement is at odds with that of Maas Geesteranus (1971, 1975a) who referred both species to his section *Squamiceps*.

Section *Squamiceps* was distinguished from section *Scabrosi* by its lack of a blue-green stipe base and context (Maas Geesteranus 1975a). Our sequences of two Italian collections initially identified as *S. cyrneus* were either left as named (K(M)197488) in the absence of an appropriate reference sequence, or redetermined as *H. illudens* (K(M)197492). However, our molecular evidence indicates that both collections belong in section *Scabrosi*. They would therefore be expected to have the characteristic blue-green stipe pigmentation, which is contrary to the original description of *S. cyrneus*. Indeed, in Sardinia at least, some morphological interpretations of *S. cyrneus* can include specimens with blue flesh at the base of the stipe (Brotzu 1998). We cannot be sure whether the terminal cluster comprising K(M)197488 and the GenBank sequence (MH681180) derived from an Italian ectomycorrhizal root tip of *Quercus pubescens* (Fig. 3) represents *S. cyrneus sensu typi* or yet another undescribed species. Further study of collections morphologically identified as *S. cyrneus* is urgently needed.

With the exception of *Hydnellum glaucopus*, phylogenetic analyses support the validity of section *Scabrosi sensu* Maas Geesteranus. *Hydnellum glaucopus* is here recovered as a member of section *Violacei*. *Hydnellum glaucopus* and *H. scabrosum*, the type of section *Scabrosi*, are often confounded. Maas Geesteranus (1975a: 65) was aware of the problem and, commenting on the description of *H. glaucopus*, he concluded "Es gehört Erfahrung dazu, um vorliegende Art von dem vielgestaltigen *S. scabrosus* zu unterschieden". The confusion partly stems from the failure to recognize *scabrosum*-like specimens growing with *Fagaceae* as a separate species. Such specimens have mostly been considered to be the true *H. scabrosum* while similar-looking specimens collected in conifer forests have, to some extent, been named *H. glaucopus*. The latter species is, however, morphologically distinguishable since it has a subtomentose to somewhat glossy pileal surface that is smooth or with age rupturing in the centre to expose the paler flesh. The pileal colour is greyish brown with rosy or violet tints and it darkens where touched or damaged to dark chocolate brown.

In our phylogenetic ITS analyses of section *Violacei* (Fig. 2), a sequence identified as *Sarcodon calvatus* (UNITE UDB024867) and generated from a basidioma from British Columbia, Canada, showed 99.2 % similarity to European *Hydnellum glaucopus*. If it can be shown that this specimen is identical to the type from Oregon, USA, then the older name *S. calvatus* takes precedence over *H. glaucopus*. However, *S. calvatus* has, according to the protologue (Harrison 1964), clamps at the basidial bases while in *H. glaucopus* basidial bases and other septa are clampless. Thus, we find it less likely that these two species are synonyms.

We sequenced the holotypes of *Hydnellum glaucopus*, *H. illudens* and *H. lepidum*; an isotype of *Sarcodon regalis* and the neotype of *H. scabrosum* (see Table 1 for further details). The results show that *H. lepidum* and *S. regalis* are conspecific. They were initially described in the same publication (Maas Geesteranus 1975a) and so it would seem that although *Sarcodon lepidus* was presented first, both names have equal priority. However, although a holotype was designated for *S. lepidus*, this did not occur for *S. regalis* (or for *S. cyrneus*) and the name was not validly published. The oversight was soon corrected by the designation of a lectotype (correctable to holotype) and the name (and that of *S. cyrneus*) was validated in Maas Geesteranus (1975b). Hence *S. regalis* becomes a synonym of *Hydnellum lepidum*.

Hydnellum scabrosum was not supported in the present analyses. Its coherence should preferably be studied through an analysis including additional genetic regions. Such an analysis might also be useful in addressing the phylogenetic relationships within *Hydnellum* – an interesting and as yet unresolved topic which lay outside the scope of the current study.

Maas Geesteranus (1975a) reported the American species *Hydnellum underwoodii* from Europe and referred some Dutch collections to this name (as *Sarcodon*). Sequences from several American specimens identified as *S. underwoodii* were published by Baird *et al*. (2013). These sequences form a separate clade within section *Scabrosi* and any similar sequence has so far not been detected from Europe. We sequenced one Dutch specimen named *S. underwoodii* and it turned out to be *H. lepidum*. Whether true *H. underwoodii* is growing in Europe remains unclear.

Through this study future conservation prioritisation, planning and action will be underpinned by a more solid scientific foundation, particularly in central and northern European countries, the main focus of our sampling thus far. Needless to say, reports in the literature and in public databases using any of the names discussed here and not supported by sequence information, must be regarded with caution. When a voucher is available, it might be possible to revise the identification. However, all observations without a voucher, which are now being increasingly reported to biodiversity databases and further spread through meta-databases like GBIF, cannot be trusted and we warn against any uncritical usage of such data in checklist compilations and red-listing evaluations.

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

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