




Standard Paper

Umbilicaria ahtii – a new species of *Umbilicaria* subg. *Papillophora* from the vicinity of Helsinki with remarks on species of the *Umbilicaria vellea* group

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Abstract

Umbilicaria ahtii sp. nov. is described based on morphological and molecular characters. The new species resembles *Umbilicaria vellea* but the former has larger and submuriform ascospores, a darker lower surface, longer dark brown to black rhizomorphs, and lacks thalloconidia directly on the lower surface and basal part of the rhizomorphs. Phylogenetic analyses (ITS, mtLSU and *RPB2*) confirmed the distinctness of *U. ahtii* and indicated its sister relationship to *U. meizospora*. *Umbilicaria ahtii* is described from Finland and is currently known from several localities in Northern Europe (Svalbard, Norway, Finland, Kola Peninsula in Russia), Asia (Kodar Range, Siberia) and North America (Alaska). Within the *U. vellea* group, new molecular data confirmed *U. koidzumii* as a widespread, separate species sister to *U. cinereorufescens*. Diagnostic traits and variability of species, as well as their distribution patterns and nomenclature, are discussed.

Keywords: biogeography; lichen; Siberia; Svalbard; typification; *Umbilicaria cirrhosa*; *U. tylorhiza*

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Introduction

Species of *Umbilicaria* Hoffm. are predominantly saxicolous lichens, mostly found in regions of higher latitudes or altitudes worldwide (Frey 1936a, b; Llano 1950; Wei & Jiang 1993). *Umbilicaria* subg. *Papillophora* Davydov *et al.* is phylogenetically the most basal subgenus and includes species with a mostly Holarctic distribution, and European, East Asian and South American endemic elements (Davydov *et al.* 2017, 2020a, b). Two morphologically different species groups were segregated in the subgenus *Papillophora*, the *U. vellea* group and the *U. angulata* group. Species of the *U. vellea* group in this broad sense include well-known species, such as *U. vellea* (L.) Michx., *U. cinereorufescens* (Schaer.) Frey, *U. crustulosa* (Ach.) Lamy and *U. spodochoa* Hoffm.; they commonly possess rhizomorphs that may or may not bear multicellular thalloconidia, with different types of apothecia having 8-spored asci with simple or submuriform ascospores.

Umbilicaria vellea was described by Linnaeus (1753). Other species within the *U. vellea* group were described by lichenologists in the 18th and 19th centuries. Due to uneven knowledge at the time, many taxa were poorly understood and their species boundaries were debated (e.g. Hoffmann 1790, 1794; Acharius 1803; Merrill 1906; Hestmark 2007; Davydov *et al.* 2020a). Modern

concepts for many species of the *U. vellea* group were substantiated by Frey (1929, 1931, 1933, 1936a, b) who provided an artificial key and detailed descriptions that are still valuable. In particular, Frey (1929, 1931) recognized *U. cinereorufescens* as a distinct species. Poelt & Nash (1993) studied *U. vellea* and morphologically similar species and emphasized that *Umbilicaria* are particularly difficult to interpret because multiple individual thalli covering a range of ages must be collected to understand the full developmental sequence. Based on differences in the shape of rhizomorphs, Poelt & Nash (1993) described *U. americana* Poelt & T. H. Nash from North America, so far included within the concept of *U. vellea*. East Asian *U. orientalis* Davydov is another species in the group that resembles *U. vellea* but differs in terms of rhizomorphs and thalloconidia (Davydov *et al.* 2020b).

Although Poelt & Nash (1993) commented that there is no obvious reason to assume that more than one taxon exists within *Umbilicaria vellea* in Europe, we discuss morphological and molecular phylogenetic evidence to describe a new species, *U. ahtii* Davydov, from the *U. vellea* species complex. *Umbilicaria ahtii* has a fairly long history of understanding and informal acceptance. Back in 2003, during work on the *Umbilicariaceae* phylogeny (Davydov *et al.* 2017), ITS sequences assigned to *U. vellea* were obtained by ED. Sequences formed two clearly distinct clades: most of them ('*U. vellea*-1') appeared as a sister of *U. hirsuta* (Sw. ex Westr.) Ach., while the others ('*U. vellea*-2') clustered as a sister group to *U. cinereorufescens*. The same result was obtained after re-extracting DNA, increasing phylogenetic markers and including additional species. In the final publication

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(Davydov *et al.* 2017) based on ITS, mtLSU and *RPB2*, ‘*U. vellea*-1’ was found to cluster with *U. hirsuta*, and ‘*U. vellea*-2’ with *U. meizospora* (Harm.) Davydov & D. Masson, suggesting the presence of an undescribed species in Northern Europe. Examination of morphology revealed only minor differences in rhizomorphs and the colour of upper and lower surfaces, which are highly variable traits and not always discernible in scarce herbarium collections. To identify diagnostic features, extensive collections were studied in parallel with molecular phylogenetic verification of the results, which required fresh material. The authors searched for an older name and hypothesized that their putative new species belonged to either *U. tylorhiza* (Nyl.) Nyl. (Davydov 2017; Davydov *et al.* 2017) or *U. koidzumii* M. Satô (Davydov *et al.* 2020b). They also examined the types of *U. vellea*, *U. koidzumii*, *U. cinereorufescens* and the original material of *U. cirrhosa* Hoffm.

Although the putative new taxon was initially identified through molecular phylogenetic analysis, the first author later detected it in herbarium specimens. During his time at Helsinki University’s herbarium (H), ED discovered old specimens with distinct diagnostic traits that were collected in the vicinity of Helsinki in the 1930s. With the kind assistance of Professor Teuvo Ahti, we located this site and examined, in detail, a rock outcrop containing hundreds of specimens of this species. We have designated this collection as the type and named it as a new species in honour of Teuvo Ahti.

A final decision to describe the species as new could not be made until the status of *Umbilicaria koidzumii* was confirmed. YO attempted to collect this species in the *locus classicus* several times before succeeding. The obtained sequences and examined traits suggest that *U. koidzumii* is related to *U. cinereorufescens* and is distributed worldwide, while *U. cinereorufescens* s. str. may be endemic to Europe. As a result, the status and circumscription of two well-known species of the *U. vellea* group, namely *U. vellea* and *U. cinereorufescens*, are changing significantly. Although the data currently available are insufficient to develop a monograph for the entire group, we aim here to define the new species in relation to the *U. vellea* group and to discuss other potentially confusing taxa, such as *U. koidzumii*, *U. cinereorufescens* and *U. trabeculata* Frey & Poelt, while also resolving related nomenclature issues.

Materials and Methods

Sampling

Fresh material of the putative new species, *U. cinereorufescens* s. lat. and *U. vellea* was collected by ED. Specimens of *U. koidzumii* were collected by YO in the type locality in Japan. Type and other materials of the *U. vellea* group were examined from the herbaria ALTB, CHR, G, GZU, H, HMAS, KPABG, LE, LECB, M, MAG, MW, O, OSC, TNS and UHU, and the personal collections of S. V. Chesnokov, L. S. Konoreva, B. McCune, D. Masson and G. P. Urbanavicus. A high resolution stacked image of the rhizomorphs of the lectotype of *U. vellea* (LINN) was provided by Dr Mark Spencer (LINN). We used sequences obtained from GenBank exclusively from specimens we had previously studied morphologically, anatomically and chemically. Details of the material and GenBank Accession numbers are presented in Table 1. We included two distinct morphotypes of *U. cinereorufescens* in the analyses. The morphotype of ‘*U. cinereorufescens*-1’ collected in Norway corresponds with the type in having very

irregular, tuberoso to peg-like, often flattened rhizomorphs. In contrast, ‘*U. cinereorufescens*-2’ has predominantly peg-like, ball-tipped rhizomorphs, usually with additional black filiform rhizomorphs.

Morphology and anatomy

Morphological observations were carried out using a stereomicroscope (Zeiss Stemi 2000-C). Apothecia and thalli were hand-sectioned with a razor blade and observed in water mounts with a compound microscope (Zeiss Axio Lab.A1.). The images were captured using a Zeiss AxioCam ERC5s (resolution 5 Mpx) colour digital camera with the software ZEN 2012 (Carl Zeiss). Measurements were recorded to the nearest 0.5 μm . Measurements of ascospores and thalloconidia are presented as follows: (smallest value recorded) $(\bar{x} - \text{SD}) - \bar{x} - (\bar{x} + \text{SD})$ (–largest value recorded), where \bar{x} is the (arithmetic) sample mean, and SD the sample standard deviation. The two extreme values and the sample mean are given to the nearest 0.5 μm and n = the number of measurements made. Other measurements are presented as (extreme minimum) minimum–maximum (extreme maximum).

Chemical analyses

Lichen substances were studied by spot tests using potassium hydroxide solution (K), sodium hypochlorite solution (C), 1,4-*p*-phenylenediamine (PD), and by thin-layer chromatography (TLC) with solvent systems A, B’ and C following Orange *et al.* (2001). High performance liquid chromatography (HPLC) analysis was performed as described in Davydov *et al.* (2019).

DNA extraction, amplification and sequencing

Single thallus parts (*c.* 5 mm²) or 3–4 apothecia were carefully checked for fungal infections and thoroughly cleaned of extraneous matter. DNA extraction, amplification and sequencing followed the methods of Davydov & Yakovchenko (2017) and Ohmura *et al.* (2022). To test the phylogenetic relationships within the *Umbilicaria vellea* group, the internal transcribed spacer region of nuclear ribosomal DNA (ITS), the large subunit of the mitochondrial ribosomal DNA (mtLSU), and RNA polymerase II between six and seven conserved parts (*RPB2*) were amplified in a single reaction from DNA extracts. The primers used in this study are shown in Table 2. The program Geneious v. 6.0 (Biomatters Ltd, New Zealand) was used for assembling partial and complementary sequences.

Sequence alignment and phylogenetic analyses

New sequences of species of the *U. vellea* group were supplemented with sequences obtained during a study of *Umbilicariaceae* phylogeny (Davydov *et al.* 2017, 2020b; Davydov & Masson 2022), representing different subgenera with an emphasis on *Umbilicaria* subg. *Papillophora*; *Xylopsora friesii* (Ach.) Bendiksby & Timdal was used as the outgroup. This selection is based on the studies of Wedin *et al.* (2005), Bendiksby & Timdal (2013) and Davydov *et al.* (2017), in which *Xylopsora* Bendiksby & Timdal forms the sister clade to *Umbilicaria*. GenBank Accession numbers are provided in Table 1.

Three single-gene datasets containing the sequences listed in Table 1 were compiled and aligned using the MAFFT algorithm (Katoh *et al.* 2019). Introns in the mtLSU sequences were

Table 1. Voucher information and GenBank Accession numbers for the specimens used in the phylogenetic analyses. New sequences generated in this study are in bold.

Species	Source: collection location, collector and collection number, and herbarium	GenBank Accession number		
		ITS	mtLSU	RPB2
<i>Umbilicaria ahtii</i> 1 [as <i>U. vellea</i>]	Russia, Kola Peninsula, Laplandsky preserve, <i>I. N. Urbanavichene</i> 03-0106 (ALTB)	KY947801	KY947927	KY972630
<i>U. ahtii</i> 2 [as <i>U. vellea</i>]	Russia, Kola Peninsula, Velikii Isl., <i>I. S. Zhdanov</i> (ALTB-L196)	KY947831	KY947956	KY972660
<i>U. ahtii</i> 3	Russia, Murmansk Region, Lovozersky Distr., <i>A. V. Melekhin</i> Pu215 (ALTB-L5414)	PP849059	PP849092	PP855512
<i>U. ahtii</i> 4	Russia, Murmansk Region, Lovozersky Distr., <i>A. V. Melekhin</i> ki433 (ALTB)	PP849055	PP849088	
<i>U. ahtii</i> 5	Russia, Murmansk Region, Lovozersky Distr., <i>A. V. Melekhin</i> Pu263 (ALTB-L5418)	PP849056	PP849089	
<i>U. ahtii</i> 6	Svalbard, Tryghamna, <i>L. A. Konoreva</i> (ALTB-L7857)	PP849057	PP849090	
<i>U. ahtii</i> 7	Russia, Kandalaksha, <i>G. P. Urbanavichus</i> 05-0244 (ALTB-L5419)	PP849058	PP849091	
<i>U. ahtii</i> 8	USA, Alaska, Denali National Park, <i>P. Nelson</i> 08-520 (ALTB-L8101)	PP849062	PP849095	
<i>U. ahtii</i> 9	USA, Alaska, Denali National Park, <i>P. Nelson</i> 08-502 (ALTB-L8100)	PP849063	PP849096	
<i>U. ahtii</i> 10	Russia, Zabaikalye Territory, Kodar Range, <i>L. A. Konoreva</i> (ALTB-L5747)	PP849064	PP849098	
<i>U. ahtii</i> 11	Russia, Zabaikalye Territory, Kodar Range, <i>L. A. Konoreva</i> , 2016 (ALTB)	PP849065	PP849099	
<i>U. ahtii</i> 12	Finland, Uusimaa, Helsinki, Lankiniemi, <i>E. A. Davydov</i> 17830 (ALTB), isotype	PP849066	PP849101	
<i>U. ahtii</i> 13	Finland, Uusimaa, Helsinki, Lankiniemi, <i>E. A. Davydov</i> 17829 (ALTB), paratype	PP849067	PP849102	
<i>U. ahtii</i> 14	Finland, Uusimaa, Helsinki, Lankiniemi, <i>E. A. Davydov</i> 17830 (LE-L26006), holotype	PP849072	PP849105	
<i>U. ahtii</i> 15	Norway, Buskerud, Sigdal, <i>S. Rui & E. Timdal</i> 13263 (O-L194137)	PP849073	PP849107	
<i>U. ahtii</i> 16	Russia, Kola Peninsula, Laplandsky preserve, <i>I. N. Urbanavichene</i> (ALTB-L5163)	PP849049		
<i>U. ahtii</i> 17	Norway, Buskerud, Hol, <i>M. S. Dahl</i> et al. 16154 (O-L204939)		PP849106	
<i>U. ahtii</i> 18	Norway, Hordaland, Ullensvang, Dyrskar, <i>E. Timdal</i> 16178 (O-L204962) [OLICH-5733]		PP849112	
<i>U. americana</i>	U.S.A., Alaska, Katmai National Park, <i>J. K. Walton</i> 13054 (KATM-492)	MT649503	KY947968	KY972671
<i>U. angulata</i> Tuck.	USA, Oregon, Coos Co., <i>B. McCune</i> 30050 (OSC)	KY947834	KY947960	KY972663
<i>U. cinereorufescens</i> 1	Norway, Oppland, Sør-Fron, <i>R. Haugan</i> 10843 (O-L174420)	PP849074	PP849108	
<i>U. cinereorufescens</i> 2	Norway, Buskerud, Sigdal, <i>S. Rui & E. Timdal</i> 13262 (O-L194136)	PP849075	PP849109	
<i>U. cinereorufescens</i> 3	Norway, Nordland, Flakstad, <i>R. Haugan</i> 12265 (O-L190695)	PP849077	PP849110	
<i>U. cinereorufescens</i> 4	Norway, Viken, Sigdal, <i>E. Timdal</i> (O-L195830) [OLICH2202-15]	MK811655	PP864646	
<i>U. cinereorufescens</i> 5	Norway, Vestland, Ullensvang, Dyrskar, <i>E. Timdal</i> 16177 (O-L204961) [OLICH6034-19]		PP849111	
<i>U. cinereorufescens</i> 6	Norway, Innlandet, Øystre Slidre, <i>E. Timdal</i> 16255 (O-L201447) [OLICH6079-19]		PP849113	
<i>U. cinereorufescens</i> 7	Norway, Telemark, Tinn, Breidsetdalen, rim of Øvsetgjuvet, <i>S. Rui & E. Timdal</i> WG1-1405 (O-L200931)		PP849114	
<i>U. crustulosa</i> 1	Norway, Hordaland, Bergen, <i>T. Tønberg</i> 28870 (M-0083255)	KY948007	KY947918	KY972623
<i>U. crustulosa</i> 2	Spain, Madrid, Navacerrada, <i>A. Crespo</i> (MAF 10294)	KY947823	KY947947	KY972651
<i>U. deusta</i> (L.) Baumg.	Russia, Altai Mts, Tigiretsky Reserve, <i>E. A. Davydov</i> 5353 (ALTB)	KY947753	KY947897	KY972603
<i>U. freyi</i> Codogno et al. 1	Spain, Madrid, Navacerrada, <i>A. Pintad & A. Argueello</i> (MAF-10307)	KY947815	KY947938	KY972642
<i>U. freyi</i> 2	France, Haute-Corse, <i>D. M. Masson</i> 2B.3815 (ALTB)	KY948015	KY947979	KY972678
<i>U. grisea</i> Hoffm.	France, Haute-Corse, <i>D. M. Masson</i> 2B.3813 (ALTB)	KY948018	KY947986	KY972686
<i>U. hirsuta</i>	Spain, Madrid, Navacerrada, <i>A. Crespo</i> (MAF-10300)	KY947822	KY947946	KY972650

(Continued)

Table 1. (Continued)

Species	Source: collection location, collector and collection number, and herbarium	GenBank Accession number		
		ITS	mtLSU	RPB2
<i>U. hyperborea</i> (Ach.) Hoffm.	Russia, Karelia, A. A. Zavarzin (ALTB L148)	KY947998	KY947886	KY972596
<i>U. josiae</i>	France, Haute-Garonne, D. M. Masson 31.3650 (ALTB)	KY948013	KY947974	KY972676
<i>U. koidzumii</i> 1 [as <i>U. cinereorufescens</i>]	Russia, Buryatia, Baikalsky Reserve, G. P. Urbanavichus (ALTB-L5521)	KY947778	KY947913	KY972618
<i>U. koidzumii</i> 2 [as <i>U. cinereorufescens</i>]	Russia, Altai Mts, Ukok tableland, E. A. Davydov 651 (ALTB)	KY947766	KY947909	KY972613
<i>U. koidzumii</i> 3 [as <i>U. cinereorufescens</i>]	Russia, Buryatia, Baikalsky Reserve, G. P. Urbanavichus (ALTB-L5486)	KY947811	KY947934	KY972638
<i>U. koidzumii</i> 4 [as <i>U. cinereorufescens</i>]	USA, Alaska, Fairbanks North star Co., B. McCune 31407 (OSC)	KY947840	KY947967	KY972670
<i>U. koidzumii</i> 5 [as <i>U. cinereorufescens</i>]	Norway, Innlandet, Vang, Kelvesteinadn, E. Timdal (O-L201349)	MK812545	PP864645	
<i>U. koidzumii</i> 6	Russia, Altai Mts, Ukok tableland, E. A. Davydov 5275 (ALTB)	KY948002	KY947894	
<i>U. koidzumii</i> 7	Japan, Honshu, Shinano Prov., Mt. Kai-Komaga-take, Ina-city, Y. Ohmura 13926 (TNS)	PP849082		
<i>U. koidzumii</i> 8	Russia, the Caucasus, North Osetia, Tseisky Range, E. A. Davydov 21982 (hb. Davydov)	PP849054		
<i>U. koidzumii</i> 9	Mongolia, Altai Mts, Bayan-Ulegeisky aimak, E. A. Davydov 5283 (ALTB)	KY947765		
<i>U. koidzumii</i> 10	New Zealand, Otago, Old Man Range, D. J. Galloway 8095 (CHR-528377)	PP849061	PP849094	
<i>U. koidzumii</i> 11	New Zealand, Otago, Old Man Range, D. J. Galloway (CHR-628107)	PP849076	PP849115	
<i>U. koidzumii</i> 12	Japan, Honshu, Kai Prov., Sensui Pass, Minami-Alps-city, Y. Ohmura 13915 (TNS)	PP849080	PP849116	PP855514
<i>U. koidzumii</i> 13	Japan, Honshu, Kai Prov., Sensui Pass, Minami-Alps-city, Y. Ohmura 13921 (TNS)	PP849081	PP849117	PP855513
<i>U. koidzumii</i> 14	Japan, Honshu, Shinano Prov., Mt Kai-Komaga-take, Ina-city, Y. Ohmura 13932 (TNS)	PP849083	PP849118	PP855515
<i>U. koidzumii</i> 15	Japan, Honshu, Kai Prov., Sensui Pass, Minami-Alps-city, Y. Ohmura 13914 (TNS)	PP849079		
<i>U. leiocarpa</i> DC.	France, Hautes-Pyrenees, Sazos, D. M. Masson 65.3593 (ALTB)	KY947850	KY947980	KY972679
<i>U. loboperipherica</i> J. C. Wei et al. 1	China, Jilin, JL09103 (HMAS)	JQ739995		
<i>U. loboperipherica</i> 2	China (HMAS)	AF297671		
<i>U. meizospora</i> 1	France, Haute-Garonne, Oô, Neste d'Oô, D. M. Masson 31.3631 (ALTB)	OK491371	OK491221	OK514653
<i>U. meizospora</i> 2	France, Ariège, Mérens-les-Vals, étang de Comte, D. M. Masson 09.4205 (ALTB)	OK491372	OK491222	OK514654
<i>U. muehlenbergii</i> (Ach.) Tuck.	Russia, Primorye Territory, S. V. Smirnov (ALTB-L154)	KY947997	KY947885	KY972595
<i>U. orientalis</i> 1	Russia, Primorye Territory, E. A. Davydov 16633 & L. S. Yakovchenko (ALTB)	MT649509	MT679717	MT647274
<i>U. orientalis</i> 2	Russia, Buryatia, Baikalsky Reserve, I. N. Urbanavichene (ALTB-L5512)	MT649504	MT679713	MT647275
<i>U. pensylvanica</i> Hoffm.	Russia, Altai Mts, Tigireksky Reserve, E. A. Davydov 5310 (ALTB)	EU909462	KY947882	KY972594
<i>U. platyrhiza</i> Davydov [as <i>U. spodothroa</i>]	Turkey, Izmir, Yamanlar Dağ, V. John: Lich. Anatolici Exs. 171, V. John (H)	KY947760	KY947904	KY972608
<i>U. proboscidea</i> (L.) Schrad.	Russia, Altai Mts, Tigireksky Reserve, E. A. Davydov 7253 (ALTB)	KY947829	KY947953	KY972657
<i>U. pulvinaria</i> (Savicz) Frey	Russia, Sakhalin Isl., S. I. Tchabanenko (LE-L7943)	KY947735	KY947867	KY972582
<i>U. pustulata</i> (L.) Hoffm.	Finland, Uusimaa, T. Ahti & E. A. Davydov 5037 (ALTB)	EU909467	KY947893	KY972602
<i>U. rigida</i> Hoffm.	Norway, Møre og Romsdal, Dalsnibba, E. A. Davydov 5367 (ALTB)	KY947749	KY947892	KY972601
<i>U. semitensis</i> Tuck.	USA, Oregon, Coos Co., B. McCune 30048 (OSC)	KY947833	KY947959	KY972662

(Continued)

Table 1. (Continued)

Species	Source: collection location, collector and collection number, and herbarium	GenBank Accession number		
		ITS	mtLSU	RPB2
<i>U. spodochoa</i> (Hoffm.) DC. 1	Spain, Madrid, Navacerrada, A. Crespo (MAF 10297)	KY947824	KY947948	KY972652
<i>U. spodochoa</i> 2	France, Corse-du-Sud, D. M. Masson 2A.3739 (ALTB)	KY947853	KY947983	KY972682
<i>U. torrefacta</i> (Lightf.) Schrad. 1	Norway, Oppland Prov., E. A. Davydov 5352 (ALTB)	KY947799	KY947925	KY972628
<i>U. torrefacta</i> 2	Russia, Altai Mts., Katunsky range, E. A. Davydov 5314 (ALTB)	KY947746	KY947888	KY972598
<i>U. trabeculata</i> [as <i>U. tylorhiza</i>]	China, Yunnan prov., Dali Co., A. Aptroot 56888a (ALTB)	KY947805	KY947928	KY972631
<i>U. vellea</i> 1	Russia, Altai Mts, Seminsky range, E. A. Davydov 5305 (ALTB)	KY947995	KY947881	KY972593
<i>U. vellea</i> 2	Russia, Altai Mts, Seminsky range, E. A. Davydov 5469 (ALTB)	KY947797	KY947924	KY972627
<i>U. vellea</i> 3	Russia, Karachaevo-Cherkesia, Teberdinsky preserve, O. V. Blinkova 240700106 (ALTB)	KY947800	KY947926	KY972629
<i>U. vellea</i> 4	USA, Flathead Co., B. McCune 32390 (ALTB-L5889)	KY947835	KY947961	KY972664
<i>U. vellea</i> 5	Russia, Chukchi Peninsula, O. A. Kataeva (ALTB-L6962)	PP849052	PP849085	
<i>U. vellea</i> 6	Russia, Kamchatka Territory, Koryak Nature Reserve, D. Himelbrant Kor-Tal-05-2016 (LE-L15599)	PP849078	PP849086	
<i>U. vellea</i> 7	Russia, Kamchatka Territory, Koryak Nature Reserve, D. Himelbrant Kor-Tal-05-2016 (ALTB)	PP849053	PP849087	
<i>U. vellea</i> 8	Ethiopia, Amhara Region, North Gondar, Simien Mts, C. Printzen 12693 (FR)	PP849060	PP849093	
<i>U. vellea</i> 9	France, Ardeche, D. M. Masson 07.5198 (ALTB-L6557)	PP849068	PP849103	
<i>U. vellea</i> 10	France, Hautes-Pyrenees, 2013, D. M. Masson 65.4501 (ALTB-L6548)	PP849069	PP849104	
<i>U. vellea</i> 11	Norway, Telemark, Vinje, Vinjevatn, Bukkevalihylen, E. Timdal 13515 (O-L196275)	MK811710	PP864644	
<i>U. vellea</i> 12	Russia, Altai Mts, Tigiretsky range, E. A. Davydov 5453 (ALTB)	KY947791		KY972625
<i>U. vellea</i> 13	Russia, Altai Mts, Katunsky range, E. A. Davydov 5294 (ALTB)	KY947751		
<i>U. vellea</i> 14	France, Hautes-Garonne, D. M. Masson 31.5200 (ALTB-L6553)	PP849070		
<i>U. vellea</i> 15	France, Hautes-Pyrenees, D. M. Masson 65.4500 (ALTB-L6554)	PP849071		
<i>U. vellea</i> 16	North Macedonia, M. Kaltenböck 768 (GZU)	PP849050		
<i>U. vellea</i> 17	Russia, Yakutia, Ust'-Nera, A. P. Yatsyna (LE)	PP849051		
<i>U. vellea</i> 18	Russia, Kurile Isl., Paramushir, Chernoye Lake, A. K. Ezhkin (SAK)		PP849084	
<i>U. vellea</i> 19	USA, Colorado, Clear Creek Co., B. McCune 37257 (OSC)		PP849097	
<i>U. vellea</i> 20	USA, California, Siskiyou County, Lava Beds National Monument, B. McCune 32550 (OSC)		PP849100	
<i>Xylopsora friesii</i>	Russia, Murmansk Region, Pasvik Reserve, G. P. Urbanavichus (ALTB-L5425)	KY947740	KY947876	KY972589

manually removed from alignments. All *U. cinereorufescens* and *U. vellea* mtLSU sequences contained introns, whereas none of *U. ahtii* and seven of 12 *U. koidzumii* sequences contained introns at the same position. Before combining sequences into a joint ITS + mtLSU + RPB2 data matrix, the unambiguously alignable regions were used to calculate single-marker phylograms (not shown) using the online version of IQ-TREE (Nguyen *et al.* 2015; Trifinopoulos *et al.* 2016), and these were tested for conflicts among datasets. Since the cladograms were similar regarding well-supported ($BS \geq 70\%$) clades and therefore lacked conflicts, sequences were combined into one matrix consisting of 2030 sites and used for maximum likelihood and Bayesian analyses.

A heuristic search for the maximum likelihood (ML) bootstrap tree with simultaneous inference of the optimal partitioning

scheme and substitution models for each data partition was performed using the online version of IQ-TREE (Nguyen *et al.* 2015; Trifinopoulos *et al.* 2016), suggesting seven initial partitions (ITS1; 5.8S rDNA; ITS2; mtLSU; RPB2 1st, 2nd, and 3rd codon positions). Branch lengths were assumed to be equal for all partitions. Branch support was estimated with the ultrafast bootstrap algorithm (Minh *et al.* 2013) based on 1000 bootstrap replicates and using a maximum of 1000 iterations and a minimum correlation coefficient of 0.99 as a stopping rule.

To provide additional support for our phylogenetic reconstruction, we ran a Bayesian analysis. We used the Markov chain Monte Carlo (BMCMC) method (Larget & Simon 1999) implemented in MrBayes v. 3.2.3 (Ronquist *et al.* 2012) to infer phylogenetic trees, applying the partitioning scheme inferred

Table 2. Summary statistics, PCR settings and substitution models used for the different datasets.

Name	ITS	mtLSU (partial)	<i>RPB2</i>	ITS + mtLSU	ITS + mtLSU + <i>RPB2</i>
Regions	ITS1-5.8S-ITS2	ML3 – ML4	Between 6 and 7 conservative regions	–	–
PCR Settings					
Primers	ITS1F - 5' / ITS4 - 3' ITS1F - 5' / LR1 - 3' ITS1F - 5' / LR3 - 3'	ML3-A - 5' / ML4-A - 3'	RPB2-980F - 5' / fRPB2-7cR - 3' RPB2-5F - 5' / fRPB2-7cR - 3'	–	–
Denaturation	94 °C (2')	94 °C (2')	95 °C (2')	–	–
Amplification	35 cycles 94 °C (20'') 52 °C (1') 72 °C (2')	35 cycles 94 °C (20'') 52 °C (1') 72 °C (2')	35 cycles 94 °C (20'') 61 °C (1') 72 °C (2')	–	–
Extension	72 °C (15')	72 °C (15')	72 °C (15')	–	–
Datasets					
Alignment length	472	785	773	1257	2030
Polymorphic sites	158	125	255	273	553
Nucleotide diversity π	0.05328	0.02536	0.06408	0.04015	0.05590
Number of sequences (ingroup)	85	79	45	68	43
Substitution models					
IQ	ITS1: TIM2+F+G4 5.8S: K2P+I ITS2: TPM3u+F+I +G4	HKY+F+I+G4	pos1: TN+F+G4 pos2: HKY+F+I pos3: TPM2u+F+G4	As for separate markers	As for separate markers
MrBayes	ITS1, 2: GTR+G 5.8S: K80+I+G	HKY+I+G	pos1: HKY+G pos2, 3: K80+I+G	As for separate markers	As for separate markers

with IQ-TREE and slightly simplified substitution models inferred by PartitionFinder v. 1.1.1 (Lanfear *et al.* 2012), because most of the models inferred by IQ-TREE are not implemented in MrBayes. Three parallel analyses, each with six incrementally heated chains using the default heating factor of 0.2, were run for 100 million generations; every 200th generation was sampled until the average standard deviation (ASD) of split frequencies had dropped to 0.01. This was the case after 78 M generations. The first 50% of trees was discarded as burn-in and a 50% majority-rule consensus tree was calculated from the remaining trees of the three runs using the sumt command implemented in MrBayes v. 3.2.3.

Results

The phylogenetic study

For the phylogenetic analyses, we used a total of 208 sequences, 77 of which were obtained during this study and 131 in previous investigations (Davydov *et al.* 2017, 2020b; Davydov & Masson 2022) and deposited in GenBank (Table 1). To test the monophyly and phylogenetic relationships of the species, we used three markers as single gene matrices and in combined datasets. Summary statistics are shown in Table 2. ITS and mtLSU sequences were successfully obtained from a total of 18 specimens, including 15 specimens of *Umbilicaria ahtii* and three specimens of *U. koidzumii* from Japan. In addition, *RPB2* sequences were obtained from three specimens of each of the species, *U. ahtii* and *U. koidzumii*. Although the set of sequences is

incomplete with respect to the phylogenetic markers (Table 1), ITS or mtLSU markers were obtained for all specimens. The phylogenies based on ITS or the more conservative marker mtLSU (Supplementary Material Figs S1 & S2, available online) contained similar, well-supported lineages for separate species or their regional populations. The *RPB2* phylogram (Supplementary Material Fig. S3, available online) included only a small fraction of specimens, and the relationships in the backbone were not statistically supported. An ITS + mtLSU phylogram (Supplementary Material Fig. S4, available online), in which both phylogenetic markers were obtained for each specimen, had a similar topology to the ITS + mtLSU + *RPB2* phylogram, in which 1–3 phylogenetic markers were obtained for each specimen, and both phylogenies provided high support for most of the clades. Therefore, we present and discuss the ITS + mtLSU + *RPB2* phylogram (Fig. 1), which includes specimens from a wider geographical range. The combination of the phylogenies from the Bayesian 50% majority-rule consensus tree and the IQ-tree (Fig. 1) share the same topology.

Both *Umbilicaria ahtii* and *U. koidzumii* were grouped within *Umbilicaria* subg. *Papillophora*. All specimens of *U. ahtii* formed a well-supported clade for all single-marker (Supplementary Material Figs S1–S3) and combined phylogenies (Fig. 1, Supplementary Material Fig. S4). *Umbilicaria ahtii* was grouped as sister to *U. meizospora*, while the morphologically similar *U. vellea* was grouped as sister to *U. hirsuta* + *U. josiae* Frey. Sequences of *U. ahtii* were nearly identical and no geographical segregation was observed, except for two sequences from Alaska which formed a well-supported clade nested within the remaining sequences. *Umbilicaria vellea* from the northern Far East

(Chukotka, Koryakia and North Kurile) clustered as sister to the remaining *U. vellea*, but without support (76% BS; 0.7 PP).

Sequences of *Umbilicaria cinereorufescens* formed two well-supported groups (1 and 2; Fig. 1). Sequences of typical *U. koidzumii* from the *locus classicus* nested within the '*U. cinereorufescens*-2' clade. The ITS sequences of the Japanese material were identical, except for the fertile *U. koidzumii* 7 (Supplementary Material Fig. S1).

Morphology, anatomy and secondary chemistry

Upon careful examination and comparison of the sequenced material of *Umbilicaria vellea* and the putative new species, described below as *U. ahtii* (Fig. 2), we found that rhizinomorphs, apothecia and ascospores are diagnostic traits for these species (refer to Table 3, Figs 3 & 4). However, apothecia and ascospores are not useful for routine identification since apothecia develop infrequently and well-developed spores are rarely found.

Previous authors have adhered to a broad concept of *Umbilicaria cinereorufescens*, which included specimens with a black areolate lower surface and black thalloconidial rhizinomorphs of different shapes, including filiform and irregular, sometimes flattened, tuberoso to peg-like, short and long, often ball-tipped. The type material of *U. cinereorufescens* lacks filiform and long, ball-tipped rhizinomorphs. However, some other specimens from Europe, as well as the majority of investigated specimens from Asia and North America, do have them. Therefore, we assume that the varying shape of black rhizinomorphs is a characteristic trait of *U. cinereorufescens*. *Umbilicaria vellea* can be easily distinguished from all those specimens by its thin, beige-coloured, comparatively long rhizinomorphs, in addition to shorter, peg-like and black rhizinomorphs covered by thalloconidia. The present phylogenetic analyses revealed that *U. cinereorufescens* is represented by two clades, namely '*U. cinereorufescens*-1' and '*U. cinereorufescens*-2' (Fig. 1). All specimens of '*U. cinereorufescens*-1' were collected from various locations in Norway and included morphotypes corresponding to the type material of *U. cinereorufescens* (Fig. 5A & B). Specimens of '*U. cinereorufescens*-2' possess black filiform rhizinomorphs in addition to the predominate peg-like ball-tipped rhizinomorphs (Fig. 5F–I), which are sometimes segregated in tiers of shorter and longer lengths. Although '*U. cinereorufescens*-1' and '*U. cinereorufescens*-2' produce the same secondary compounds, such as gyrophoric, lecanoric and crustinic acids, there is a quantitative difference between them. *Umbilicaria* '*cinereorufescens*-1' consistently contains crustinic acid as a major compound, while '*U. cinereorufescens*-2' contains gyrophoric acid as a major compound, with crustinic acid sometimes present in trace amounts (Table 3).

The holotype of *Umbilicaria koidzumii* (Fig. 5C–E) does not quite fit the circumscription of *U. cinereorufescens* because, similar to *U. vellea* specimens, it has two types of rhizinomorphs: shorter and black with multicellular thalloconidia, and longer and pale. However, unlike *U. vellea* and similar to '*U. cinereorufescens*-2', the light-coloured rhizinomorphs often have balls of thalloconidia at the tips and the species also has submuriform ascospores. Of the five sequenced specimens collected around the type locality of *U. koidzumii*, two fully corresponded to the holotype (*U. koidzumii* 12 & 13). These two specimens had light and long rhizinomorphs with balls of thalloconidia at their tips. One specimen (*U. koidzumii* 7) was fertile. This fertile specimen, along with the two remaining specimens (*U. koidzumii* 14 & 15), fit our conception of *U. cinereorufescens* s. lat.

Therefore, we can observe both black and light-coloured ball-tipped rhizinomorphs in the same collections from Japan. The morphological variation of specimens with identical or very similar ITS, mtLSU and *RPB2* sequences allowed us to better morphologically circumscribe *U. koidzumii*. Therefore, it could be applied to the entire '*U. cinereorufescens*-2' clade since it contains sequences of specimens that share the same traits but differ from '*U. cinereorufescens*-1'. We have summarized the diagnostic traits of four species in Table 3. After considering anatomical, morphological, chemical and phylogenetic data, there is sufficient evidence to describe a new species and amend the circumscriptions of *U. cinereorufescens*, *U. koidzumii* and *U. vellea*.

Taxonomy

Umbilicaria ahtii Davydov sp. nov.

Mycobank No.: MB 854205

Resembles *Umbilicaria vellea* but with a darker lower surface, dark brown to black longer rhizinomorphs, and lacking thalloconidia directly on the lower surface and basal part of the rhizinomorphs. Multicellular thalloconidia develop exclusively on the tips and branches of short or long unbranched or branched rhizinomorphs. Ascospores are larger and submuriform.

Type: Finland, Uusimaa, Helsinki, Munkkiniemi, Lankiniemi near the bridge to Tarvo, 60°12'10.04"N, 24°51'07.98"E, elev. 5 m, rock outcrops covered by pine forest, W-exposed wet steep granite rock facing the sea bay, 27 October 2018, E. A. Davydov 17823 (LE L-26006—holotype; ALTB, FR, GZU, H, O, TNS—iso-types). GenBank Accession nos: PP849072, PP849105.

(Figs 2, 3, 4A & B)

Thallus monophyllous, frequently of medium size, 3–6(–18) cm diam. and 0.2–0.4 mm thick, umbilicate, rigid, undulating with broad folds, the margins first entire, later incised and often wrapped up or downwards; upper surface dull, minutely rimose to areolate, often pruinose; pale to dark grey, with a brown or violet tinge, senescent thalli getting brown, occasionally with rhizinomorphs protruding through cracks or splits; lower surface of juvenile thalli light brown, later entirely black or lighter towards the margins, smooth to rimose or finely areolate with abundant rhizinomorphs of several types in varied amounts; trabeculae emerging from the umbilicus often present and can also produce rhizinomorphs. Two main classes of rhizinomorphs occur, non-thalloconidial and thalloconidial; non-thalloconidial rhizinomorphs long, 1–2(–4) mm, grey-brown to black, tree-like branched (Fig. 3D), with one main thick axis being few or many times iso- or anisotomously branched. Thalloconidial rhizinomorphs are shorter and may be of several types: 1) pin-like, with a usually unbranched axis; 2) ball-tipped and branched, with branched axis 0.5–1 mm and balls of thalloconidia at tips (Fig. 3A); 3) branched rhizinomorphs with thalloconidial bundles (Fig. 3B & C). The thalloconidia never cover the lower surface or base of long rhizinomorphs, but always develop on branches. Vegetative propagules are usually absent. Exceptionally, schizidia (Fig. 2C) can develop under humid conditions. *Thalloconidia* present, developing exclusively on rhizinomorphs; multicellular with c. 10–50 cells, (15.0–)23.0–28.5–33.5(–42.5) × (10.0–)16.0–20.0–24.0(–30.0) μm (*n* = 60). *Upper cortex* paraplectenchatous, outer part brownish and 10–13 μm thick, inner part hyaline and

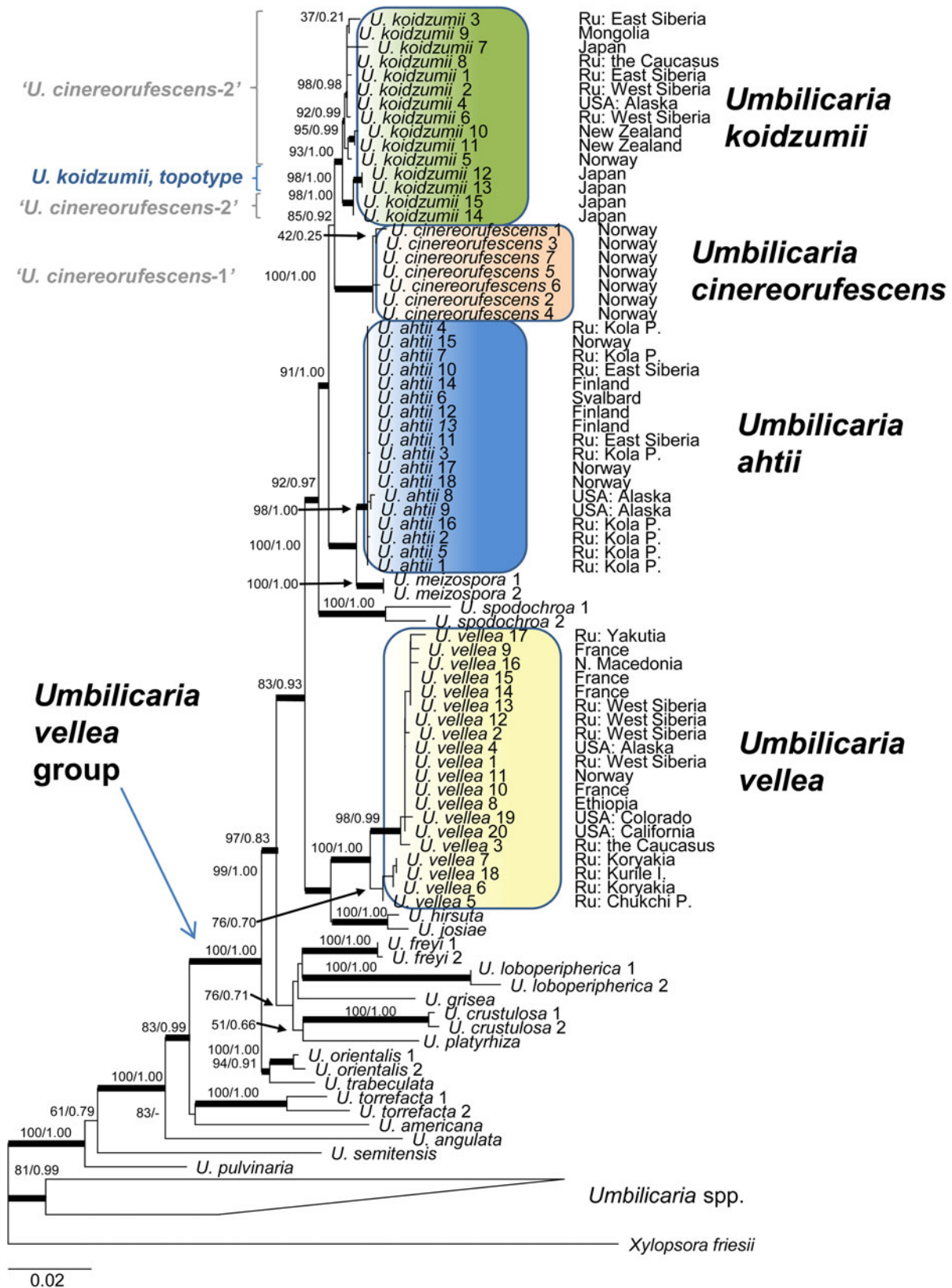


Figure 1. Phylogenetic relationships amongst *Umbilicaria* species, based on a maximum likelihood analysis (IQ) of ITS1-5.8S-ITS2, mtLSU and *RPB2*. Numbers at tree nodes indicate bootstrap values of ML (left) and BMCMC posterior probabilities (right). Thicker branches indicate when both the bootstrap value of ML is $\geq 70\%$ and the BMCMC posterior probability is ≥ 0.95 . Branch lengths represent the estimated number of substitutions per site assuming the respective models of substitution (Table 2). The basal branches of *Umbilicaria* are collapsed to reduce the overall figure size. ‘*U. cinereorufescens*-1’ and ‘*U. cinereorufescens*-2’ represent two distinct morphotypes of *U. cinereorufescens*, and sequences of typical *U. koidzumii* from the *locus classicus* are indicated. Ru = Russia, P = Peninsula. In colour online.

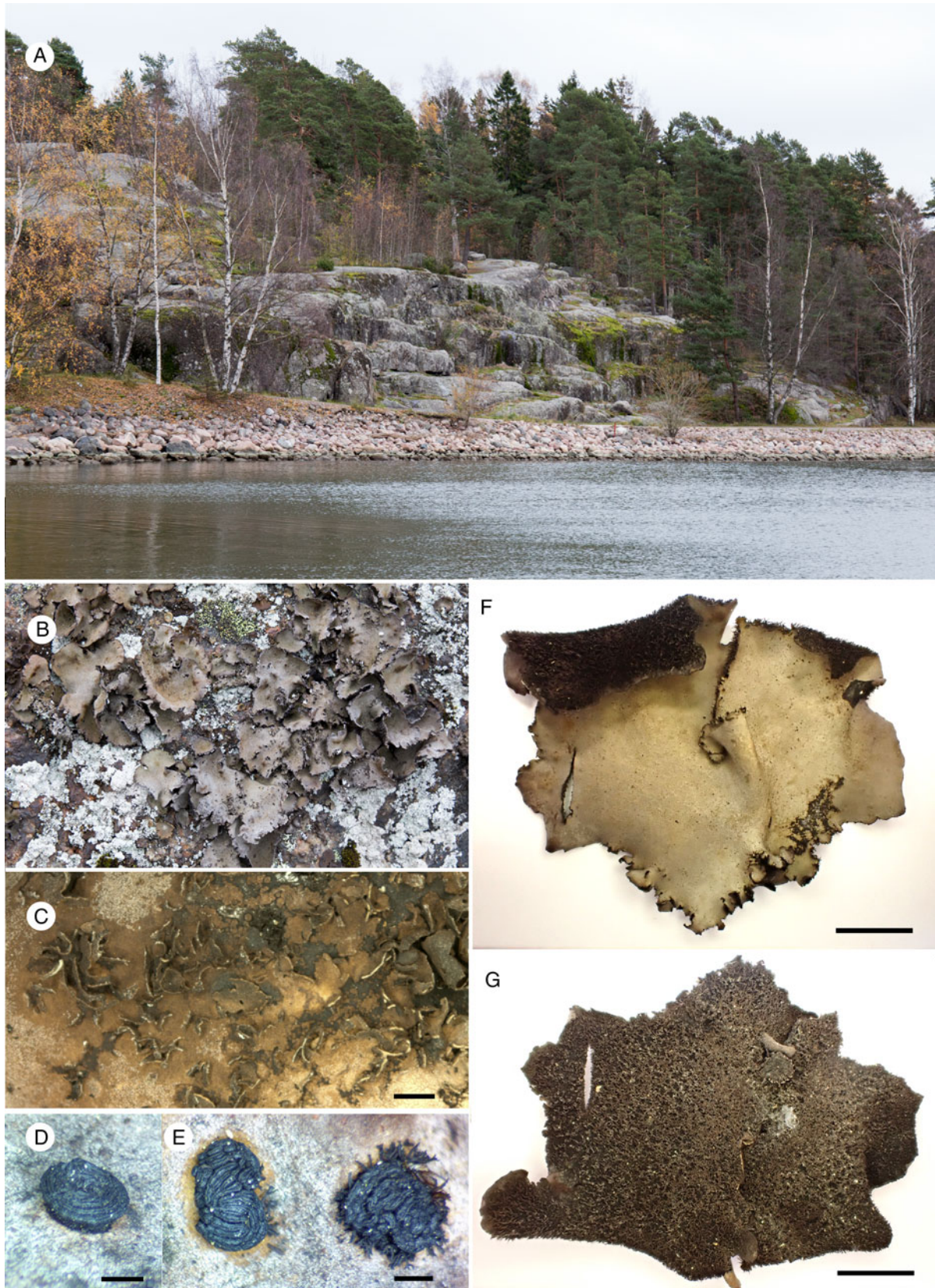


Figure 2. Habitat and morphology of *Umbilicaria ahtii*. A, type locality of *U. ahtii*: Helsinki, Lankiniemi near the bridge to Tarvo, rock outcrops covered by pine forest. B, general habit in the field (type locality). C, schizidia (develop occasionally, ALTB L5418). D & E, gyrodisc apothecia with a visible crack, a black lower cortex and a 'corona' of rhizinomorphs (ALTB L6939). F & G, general habit of the holotype (LE-L26006). F, upper side. G, lower side. Scales: C-E = 1 mm; F & G = 1 cm. In colour online.

Table 3. Diagnostic traits of selected species of *Umbilicaria vellea* group. M = major compound, m = minor compound, tr = trace.

Species/ character	<i>U. vellea</i>	<i>U. ahtii</i>	<i>U. cinereorufescens</i>	<i>U. koidzumii</i>
Lower surface	Remaining light for a long time but finally becoming blackish to deep black, smooth to rimose or finely areolate	Remaining light for a long time but finally becoming blackish to deep black, smooth to rimose or finely areolate	Soon black, roughly areolate	Soon black, roughly areolate
Longer rhizinomorphs without or with thalloconidia	Forked to strongly branched and slender, beige to greyish, basal part often thick and black due to thalloconidia, vermiform in appearance	Forked to strongly branched, grey-brown to black, thalloconidia never cover the surface of rhizinomorphs	Absent	Partly filiform, partly irregular, often ball-tipped, simple to branched, black, often derived from filaments, often flattened, bent and branching randomly, with branches of different lengths. Sometimes one branch is pointed at the end, and the other is flattened or carries a ball with thalloconidia
Shorter rhizinomorphs with thalloconidia	Tuberoso to peg-like, sometimes branched	Always with axes, branched with bundles of thalloconidia and/or peg-like, usually also branched	Short, black, very irregular, often strongly laterally flattened, wart-shaped, club-shaped, slightly indistinctly branched, in senescent thalli often derived from filaments	Predominantly ball-tipped, tuberoso to peg-like with short to long axis, simple to branched with balls of thalloconidia at tips
Thalloconidia	Multicellular, brown, (11)–28–(55) × (10)–23–(43) µm	Multicellular, brown, (15)–28–(43) × (10)–20–(30) µm	Multicellular, brown, (9)–25–(64) × (9)–18–(47) µm	Multicellular, brown, (10)–22–(43) × (10)–17–(27) µm
Ascospores	Simple, hyaline, 8–12 × 6–9 µm	Hyaline to brown, submuriform, 11–18 × 7–11 µm	Hyaline to brown, submuriform, 15–20 × 10–14 µm	Hyaline to brown, submuriform, 16–20 × 11–14 µm
Secondary metabolites	Gyrophoric (M), lecanoric (m), sometimes also umbilicatic (M, m)	Gyrophoric (M), lecanoric (m), sometimes also crustinic (tr)	Crustinic (M), gyrophoric (M), lecanoric (m)	Gyrophoric (M), lecanoric (m), crustinic (m)

20–30 µm thick; *epicortex* 5–10 µm thick; *algal layer* continuous, 100–120 µm thick, algae trebouxoid; *medulla* colourless, dense, 70–125 µm thick, arachnoid plectenchymatous of highly branched pachydermatous hyphae (of *Vellea*-type (Valladares & Sancho 1995)); *lower cortex* not clearly differentiated from medulla, scleroplectenchymatous, including a colourless inner layer *c.* 20–25 µm thick, and a brown outer layer 10–20 µm thick (Fig. 3E).

Apothecia rare, occurring at the periphery of thalli, 1–3 mm diam., sessile, gyrose, black; *apothecial margin* thin, *c.* 100–150 µm thick. Young apothecia flattened, sunken into depression in the thallus; mature apothecia adnate by a wide base to the lower cortex and separated from the other thallus layers by a crack, so the black surface of the lower cortex, and sometimes also a ‘corona’ of rhizinomorphs, is visible from above (Fig. 2D & E); flattened, overmature apothecia become convex, circular or angular; *epihymenium* brown, 12.5–17.5 µm thick; *hymenium* hyaline, 65–95 µm thick; *hypothecium* light brown, 45–60 µm thick; *excipulum* in inner part yellowish, in outer part dark brown; *paraphyses* septate, branched, 1.8 µm thick, sometimes slightly thickened at the tips, up to 1.8–2.0 µm; *asci* 8-spored; *ascospores* hyaline, simple to submuriform (11.0–)12.5–14.0–15.0(–17.5) × (6.5–)7.0–8.0–9.0(–10.5) µm (*n* = 20).

Pycnidia sometimes developing at the periphery of the thalli, 120–150 µm diam., with black prominent ostiole; wall brown, 10 µm thick; *pycnocidia* bacilliform, 3.5–4.5 × 1 µm.

Chemistry. Thallus K–, C+ red, KC+ red, Pd–, UV–; all specimens examined contain gyrophoric acid as a major compound and lecanoric acid as a minor compound, with crustinic acid sometimes occurring as a trace detectable by TLC. The holotype contains gyrophoric and lecanoric acids, and a trace of crustinic acid detectable only by HPLC.

Etymology. The species is named after the renowned lichenologist Teuvo Ahti, with huge gratitude for his kindness, responsiveness, care and help, and in recognition of his great contributions to lichenology.

Ecology. *Umbilicaria ahtii* grows mostly on steep siliceous rocks both near the sea and in the upper mountain belt at an elevation range of 5–1900 m in Fennoscandia and Alaska, and 1500–1900 m in South Siberia. It grows in damp places, often by the sea, lakes and rivers, and in shady places in forests.

Distribution. *Umbilicaria ahtii* is a Holarctic species currently known from a wide range of localities in Europe, Asia and North America, at latitudes from the High Arctic (Svalbard) to South Siberia.

Notes. *Umbilicaria ahtii* most resembles *U. vellea* although these are not sister species. This homoplasy can be explained by the same environmental influences on these species growing in

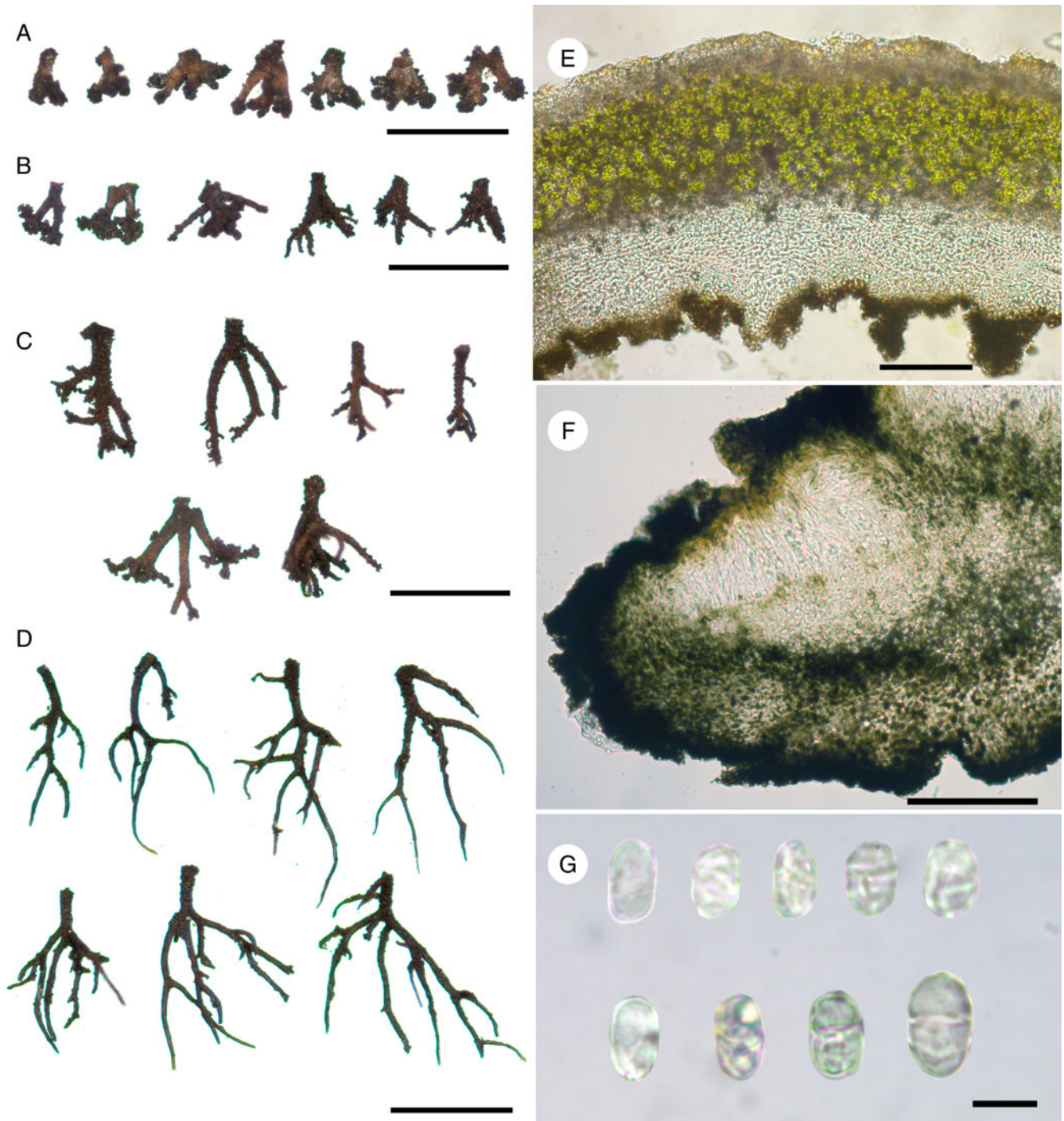


Figure 3. *Umbilicaria ahtii* (ALTB L5747). A–D, rhizomorphs. E, section of thallus. F, section of apothecium. G, simple and submuriform ascospores. Scales: A–D = 1 mm; E & F = 100 µm; G = 10 µm. In colour online.

similar conditions. The description and photographs in Poelt & Nash (1993) are of *U. vellea* s. str. *Umbilicaria ahtii* has a Holarctic distribution. After distinguishing *U. ahtii* and *U. koidzumii*, the true distribution of *U. vellea* should be revised.

The rhizomorph features are essential in distinguishing *U. ahtii* based on morphology. However, the separation of rhizomorphs into ‘non-thalloconidial’ and ‘thalloconidial’ is not absolute, because sometimes a small number of balls of thalloconidia may develop at some distal or basal branches of ‘non-thalloconidial’ rhizomorphs.

Branching of basically non-thalloconidial rhizomorphs is mainly at an acute angle (c. 45° to 60°) and not closely intertwined, giving the underside of the thallus a hairy appearance due to the many long \pm parallel branches. This type develops on juvenile thalli first. Branched rhizomorphs with thalloconidial bundles may be individual to well developed, covering almost the whole lower surface under the longer non-thalloconidial rhizomorphs. Also, branched rhizomorphs with thalloconidial bundles can be in two size classes on the same thallus, so that rhizomorphs segregate into three tiers: longer and middle-size

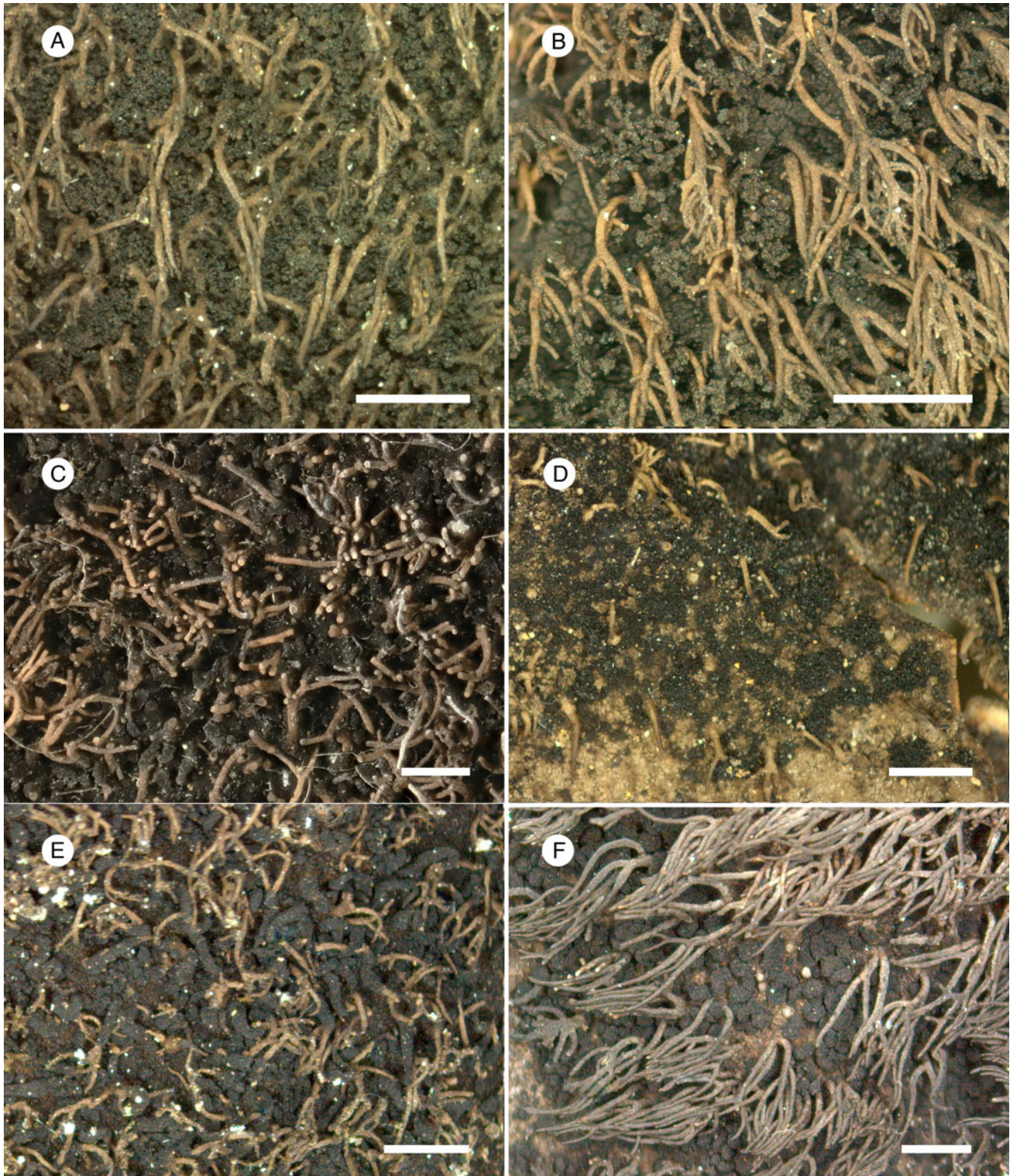


Figure 4. A & B, *Umbilicaria ahtii* (A, KPABG L4482; B, *Melekhin* ki433 (ALTB)), lower surface, longer light and shorter black, branched rhizomorphs with bundles of thalloconidia. C, *Lichen velleus* (LINN, lectotype), the lower surface with tuberoses and vermiform rhizomorphs covered by thalloconidia. D, *Umbilicaria vellea* (Davydov 16229; ALTB), light-coloured lower surface with clusters of black thalloconidia. E, *Umbilicaria vellea* (ALTB L6095), vermiform rhizomorphs with basal parts covered by cases of thalloconidia. F, *Umbilicaria vellea* (Davydov 6535; ALTB), light brown lower surface with longer light-coloured rhizomorphs and black tuberoses types with thalloconidia. Scales = 1 mm. In colour online.

branched and shorter pin-like. In addition, a secondary kind of thalloconidial rhizinomorph may be present: short, 0.2–0.4 mm long, radiating at the ends into thin branches bearing numerous thalloconidia, with a coral-like appearance. Over time, the axes may become indistinguishable due to the mass of thalloconidia.

Umbilicaria cinereorufescens (Schaer.) Frey

Hedwigia 71, 109 (1931).—*Umbilicaria vellea* γ *spadochroa* e. *cinereorufescens* Schaer., *Enum. Crit. Lich. Eur.*, 25 (1850).—*Gyrophora cinereorufescens* (Frey) Schol., *Nytt Mag. Naturvidensk.* 75, 28 (1934); type: [Switzerland] Grimsel, *Schaerer*, in *Lich. Helv. Exs.* no. 142 (G 53127!)—lectotype designated by Hestmark (2007).

The circumscription and species status of *Umbilicaria cinereorufescens* was proposed by Frey (1929, 1931) who examined herbarium material and collected specimens in the Alps, including from Grimsel, and from Dovre in Norway (Frey 1929). All our sequences of ‘*U. cinereorufescens*-1’ are from Norway and correspond to the lectotype and the description by Frey (1931). Regarding the rhizinomorphs, Frey (1931: 110) mentioned that ‘...fädige Rhizinen fehlen konstant.’ [filiform rhizines are constantly absent]. This trait seems to be diagnostic for *U. cinereorufescens* s. str. The distribution of *U. cinereorufescens* s. str. is poorly known due to previous misunderstandings. *Umbilicaria cinereorufescens* s. str. is known from the Alps and Scandinavia, and probably restricted to Europe or West Eurasia. The endemic status seems plausible in that West Eurasia is one of the centres of speciation and endemism in *Umbilicaria* subg. *Papillophora* (Frey 1933; Davydov 2022; Davydov & Masson 2022).

Umbilicaria cirrhosa Hoffm.

Descr. Adumb. Plant. Lich. 1(1), 9 (1790) as ‘*cirrosa*’; type: Icon.: *Descr. Adumb. Plant. Lich.* 1(1), 9 (1789) [1790]: Tab. II, figs 3 & 4.

Umbilicaria koidzumii Yasuda ex M. Satō

J. Jap. Bot. 11, 314 (1935); type: Japan, Honshu, Prov. Kai, Mt Komagatake, 27 July 1921, *H. Koidzumi* (TNS L119408—holotype; H—isotype!).

(Fig. 5C–E)

Umbilicaria koidzumii was described as a species related to *U. esculenta* (Miyoshi) Minks (Satō 1935) and was thought to be endemic to Japan (Ohmura & Kashiwadani 2018), based on the type specimens and several additional collections (TNS) identified by ED. The holotype of *Umbilicaria koidzumii* resembles *U. vellea* and *U. cinereorufescens* rather than *U. esculenta* as suggested by Satō (1935). The original description of *U. koidzumii* (Satō 1935) was based on senescent specimens. The combination of short pin-like and long ball-tipped branched rhizinomorphs led Davydov & Masson (2022) to suggest that *U. koidzumii* is probably conspecific with ‘*U. cf. koidzumii* from Kola Peninsula’ (= *U. ahtii*). The presence of light-coloured rhizinomorphs is a rare and probably atavistic trait in *U. koidzumii*; it has been observed in large, probably senescent specimens from Japan and New Zealand.

According to the current molecular phylogenetic data, *U. koidzumii* is not an endemic species of Japan; the species is distributed

in the Holarctic (Europe, Asia and North America) and in the Southern Hemisphere (New Zealand). Sequence data suggest that *U. koidzumii* also occurs in South America. We have tested sequences of *U. vellea* and *U. cinereorufescens* from GenBank but have not included them in the phylogram because we have not examined the corresponding specimens. Sequences of both *U. cinereorufescens* (GenBank Accession numbers HM161503 and HM161511) and *U. vellea* (HM161490) from equatorial South America clustered within *U. koidzumii*. The identification as *U. vellea* (Hestmark 2016) suggests that the specimen probably also has slender rhizinomorphs, as we have mentioned for specimens from Japan and New Zealand.

Umbilicaria trabeculata is another species which may be related to *U. koidzumii*. In describing *Umbilicaria trabeculata*, Poelt (1977) emphasized the unusual nature of its rhizinomorphs as ‘strongly warty in appearance ..., often twisted in a wavy manner, ... occasionally [with] the compacted ends come together to form a coarse-blackish second surface.’ Hestmark (1990) had not studied the type but suggested that it might be a synonym of *U. cinereorufescens*, which also has identical multicellular thalloconidia. Poelt & Nash (1993) accepted *U. trabeculata* as a separate species and Wei & Jiang (1993) synonymized it with *U. tylorhiza* from the Kola Peninsula. This concept was followed by Davydov *et al.* (2017), who named a specimen from Yunnan as *U. tylorhiza*. It is noteworthy that Poelt & Nash (1993) mentioned that the original description of *U. trabeculata* from the Himalayas (Poelt 1977) was based on rather sparse material, but examination of additional material from Asia, Africa and North America changed Poelt’s opinion on the diagnostic characters of *U. trabeculata*, which should include ‘partly filiform, partly irregular, often ball-tipped rhizinomorphs’. This trait fully corresponds to our current concept of *U. koidzumii*. Most of the specimens identified by Poelt as *U. trabeculata* from GZU were re-identified by the first author as *U. cinereorufescens* (s. lat.) or ‘*U. vellea*-2’, the former actually belonging to *U. koidzumii*. *Umbilicaria trabeculata* differs from both *U. cinereorufescens* and *U. koidzumii* mainly by the characteristics of the rhizinomorphs, but this trait is variable and more specimens with a range of morphologies are needed for it to be conclusive. At present we do not have enough material to conclude whether *U. trabeculata* is a separate species or not.

Umbilicaria tylorhiza (Nyl.) Nyl.

Flora, Regensburg 52, 389 (1869).—*Umbilicaria vellea* (L.) Ach. [subsp.?] *tylorhiza* Nyl., *Not. Sällsk. Fauna et Fl. Fenn. Förh.*, *Ny Ser.* 8, 122 (1866).—*Gyrophora tylorhiza* (Nyl.) Nyl. in Hue, *Rev. Bot.* 5, 14 (1887) [1886–87]; type: [Russia, Murmansk Region], Lapponia orientalis, Kantalahti, 1861, *N. I. Fellman* (H-NYL 31524 = H 9510903—lectotype designated here!, MycoBank Typification no.: MBT 10020878; H 9503606—isolectotype!).

Molecular phylogenetic data support a Holarctic distribution of *U. vellea* (Fig. 1, Table 1), while the presence of the species in the Southern Hemisphere requires further investigation. A worldwide revision of the *Umbilicaria vellea* and *U. cinereorufescens* groups is needed before we can confidently characterize the distribution and ecology of the species.

Umbilicaria vellea (L.) Michx.

Fl. Boreali-Americ. (Paris) 2, 323 (1803), nom. illegit., ICN (Shenzhen Code) Art. 53.1.—*Lichen velleus* L., *Sp. Pl.* 2, 1150

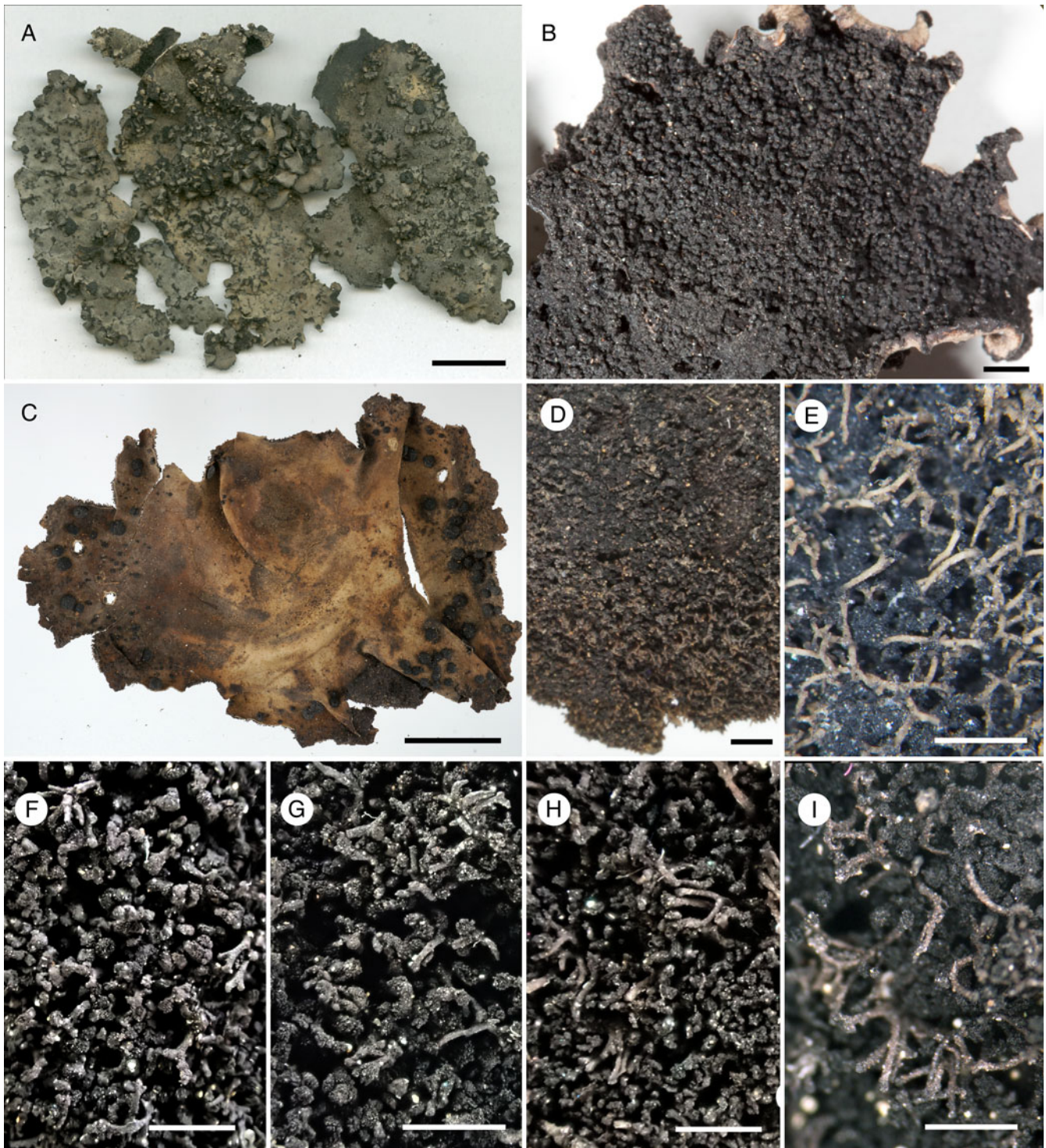


Figure 5. A & B, lectotype of *Umbilicaria cinereorufescens* (G 53127). A, upper side. B, lower side with black irregular tuberoso rhizomorphs covered by thalloconidia. C–E, holotype of *Umbilicaria koidzumii* (TNS L119408). C, upper side. D, lower side with two types of rhizomorphs. E, lower side with longer light and shorter black ball-tipped rhizomorphs. F–I, lower side of *Umbilicaria koidzumii* with black ball-tipped rhizomorphs. F, Alaska, USA (McCune 31407). G, Altai, Russia (Davydov 651). H, New Zealand (Galloway 8095). I, Japan (Ohmura 13921). Scales: A & C = 1 cm; B & D–I = 1 mm. In colour online.

(1753).—*Gyrophora vellea* (L.) Ach., *Methodus, Sectio prior* (Stockholmiae), 109 (1803); type: “*L[ichen] velleus*” (LINN-HL 1273-199 (high resolution digital photograph!, Fig. 4C), lower left specimen—lectotype, designated here, MycoBank Typification no.: MBT 10020613).

Nomenclatural notes

Lichen velleus. Howe (1912: 201) designated the entire sheet LINN-HL 1273-199, annotated by Linnaeus, as the type (lectotype) of *Lichen velleus* L. Since the sheet contains three specimens,

the lectotype was restricted to the right-hand (largest) specimen by Jørgensen *et al.* (1994: 364), who did not explain that choice. We do not consider this choice optimal, since this specimen is glued to the sheet of paper and we can see only its upper surface, which lacks apothecia and looks like many species of the *U. vellea* group. However, diagnostic traits (i.e. rhizinomorphs and thalloconidia) can be examined on the only specimen that is glued upside down, so that both wrapped edges of the upper surface and lower surface are available for examination. This specimen is therefore designated as the lectotype. The high-resolution digital photograph of the lower surface showed characteristic light-coloured, longer rhizinomorphs as well as tuberoso and vermiform types, covered by thalloconidia (Fig. 4C).

***Umbilicaria cirrhosa*.** The figures of *Umbilicaria cirrhosa* in Hoffmann (1790) or in Dillenius (1768) lack details of the rhizinomorphs which could help to adequately identify species of the *U. vellea* group in its modern concept. The only specimen of *U. cirrhosa* was traced in Hoffmann's General Herbarium (Fig. 6C–F). The specimen at MW belongs to the personal collection of Hoffmann, which was purchased from him by Moscow University (Hoffmann 1825; Sokoloff *et al.* 2002). This specimen was certainly examined by Hoffmann. The characteristics of this specimen do match well with the original description, but it evidently also belongs to *U. vellea*. The label reads '*cirrhosa*', whereas the protologue reads '*cirrosa*' (Hoffmann 1790: 9). Vainio (1888) examined the Hoffmann's Herbarium specimen in MW and identified it as '*Gyrophora spodochoa* (Ehrh.) Ach.', but it clearly belongs to *U. vellea* in its modern concept (Fig. 6C).

***Umbilicaria tylorhiza*.** Nylander (1866) cited the collection 'Kantalahti (N. I. Fellman 1861)' in the protologue. Two duplicate specimens were traced in H herbarium (H 9510903 and H 9503606); the first, having the label written in Nylander's handwriting and including a positive C reaction mark (H-NYL 31524), was cited as 'holotype' by Wei & Jiang (1993) and designated here as the lectotype of the name *U. tylorhiza*. The first author examined both specimens several times and finally came to the conclusion that it is a senescent specimen of *U. vellea*. This is supported by the following features: the brown, finely rimose lower surface and the presence of slender rhizinomorphs (some of which are broken off) in addition to the capitate rhizinomorphs which are common to many species. The predominance of capitate thalloconidial rhizinomorphs and the degradation of the slender ones suggest that this senescent specimen probably grew in moist conditions. Thalloconidia may develop around the base of simple slender rhizinomorphs, as is characteristic for *U. vellea* but not for other species of the *U. vellea* group with similar multicellular thalloconidia, (i.e. *U. ahtii*, *U. cinereorufescens*, *U. koidzumii*, and *U. trabeculata*), which also, in contrast to *U. vellea*, have a lower surface that soon turns dark and rough areolate. Extensive material of both *U. ahtii* and *U. vellea* from Kantalahti has been examined at KPABG, and we have also obtained sequences of both species from the *locus classicus* of *U. tylorhiza*.

***Umbilicaria vellea*.** A species of *Umbilicaria* with the specific epithet '*vellea*' was first introduced by Hoffmann (1794). He referred the specimen '*Lichen polyrhizus* Lightf. Scot. 864' from *Flora Scotica* by Lightfoot (1777) to *Umbilicaria vellea*. The species description provided by Hoffmann is inadequate to distinguish between the species of *Umbilicaria* in their current circumscription. However, the figures (Tabula XXVI no. 3)

made from Ehrhart's specimens from Uppsala clearly belong to *U. polyrhizos* (L.) Stenh. in the modern sense. The polyphyllous thallus, brown upper surface, entirely black lower surface, and especially the apothecia with radial gyri (i.e. of actinodisc type (Scholander 1934)) are diagnostic traits for *U. polyrhizos*. In the protologue of *U. vellea*, Hoffmann (1794) also referred to Linnaeus' *Lichen velleus*, but with a question mark, indicating that he was not sure whether *L. velleus* belonged to *U. vellea* or not. We have recognized the specimen of *U. vellea* in the lichen collection of Hoffmann in MW; specimen no. 8603 in Hoffmann's Herbarium in MW belongs to *U. polyrhizos* and could be a candidate for the lectotype of the name *U. vellea* Hoffm.

Umbilicaria vellea Hoffm. is, therefore, a synonym of *U. polyrhizos*. Combinations of *U. vellea* with *Lichen velleus* L. as basionym proposed by subsequent authors are later homonyms and therefore illegitimate under ICN (Shenzhen Code) Art. 53.1. At present, the legitimate name for the species which we currently refer to as '*U. vellea*' is *Umbilicaria cirrhosa* Hoffm.

In order to achieve nomenclatural stability, we propose to conserve the well-known but homonymous name *Umbilicaria vellea* (L.) Michx., historically applied to a widespread lichen species known at least since Linnaeus (1753), against *Umbilicaria vellea* Hoffm. Such a proposal is in preparation.

Discussion

Phylogenetic position

The phylogenetic position of *Umbilicaria ahtii* outside of *U. vellea* was initially assumed based on previous molecular phylogenetic analyses (Davydov *et al.* 2017; Davydov & Masson 2022). *Umbilicaria ahtii* belongs to the *U. vellea* group and phenotypically fully corresponds to this group by having a medium to large, rigid grey thallus with a smooth to areolate, never pustulate or reticulate upper thallus surface, a lower surface with trabeculae emerging from the umbilicus, the lower surface and rhizinomorphs being characteristically papillose or areolate, and simple to submuriform ascospores.

Umbilicaria ahtii clusters as sister to *U. meizospora*. Both species have apothecia of very similar appearance, and the senescent thalli of *U. ahtii* resemble *U. meizospora* in the brown upper surface and black lower surface with black rhizinomorphs giving a hairy appearance. *Umbilicaria meizospora* and *U. ahtii* are another example of divergence by alternation of the reproduction mode, as shown for many groups of lichens including *Umbilicaria* (Poelt 1970; Hestmark 1990; Buschbom & Mueller 2006; Davydov *et al.* 2017). *Umbilicaria meizospora* reproduces sexually and *U. ahtii* mostly asexually. Both species have very clear diagnostic traits and are well defined and distinct in appearance. Sexually reproducing *U. meizospora* is remarkably restricted in distribution and is endemic to south-western Europe (Davydov & Masson 2022).

Our results suggested two alternatives for the taxonomic treatment of *Umbilicaria koidzumii* within *U. cinereorufescens* s. lat.: either synonymize *U. koidzumii* with the previously described *U. cinereorufescens*, or distinguish *U. cinereorufescens* s. str. and *U. koidzumii* as an independent species, thereby identifying all specimens of '*U. cinereorufescens*-2' as *U. koidzumii*. We chose the latter option because: 1) diagnostic traits were observed in each species; 2) the genetic distance between the clades is relatively large, possibly indicating a somewhat distant relationship between the species, especially considering that statistical support for the '*U. cinereorufescens*-1' + '*U. cinereorufescens*-2' clade is relatively low (85% BS; 0.92 PP).

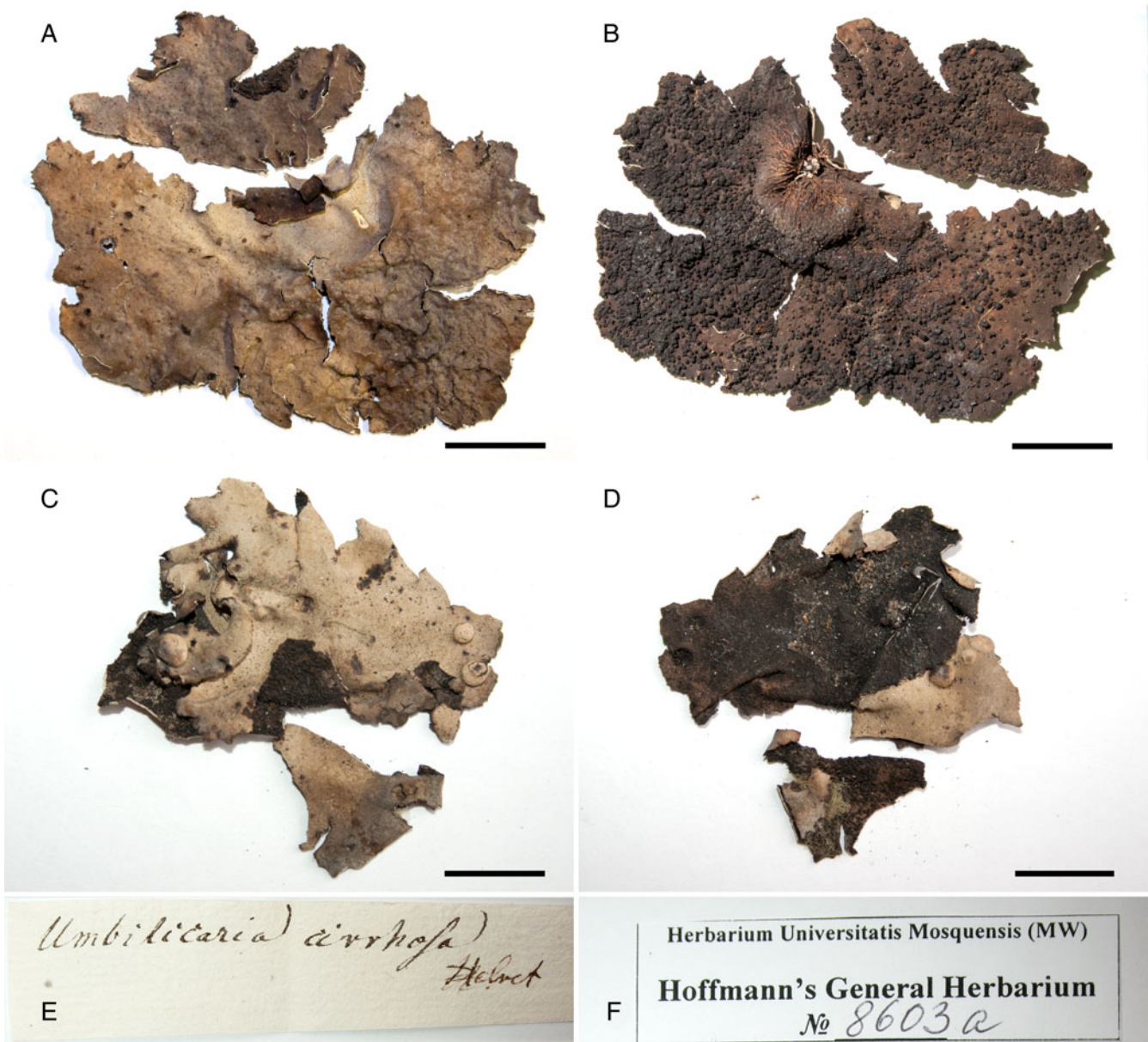


Figure 6. A & B, islectotype of *Umbilicaria tylorhiza* (H 9503606). A, upper side. B, lower side. C–F, *Umbilicaria cirrhosa* (MW-Hoffm 8603a). C, upper side. D, lower side. E, label written in Hoffmann's handwriting. F, label from MW. Scales: A–D = 1 cm. In colour online.

Umbilicaria vellea is represented by two major clades in the present phylogeny with a clear geographical pattern. We were unable to find any morphological differences between the north-west Asian specimens and those from other parts of the *U. vellea* range. This segregation may reflect a geographical isolation of north-west Asian populations or it may indicate another unrecognized species within *U. vellea*. Since no diagnostic traits were found and the north-west Asian clade lacked statistical support, we concluded that it does not require a taxonomic rank.

Diagnostic traits

All species discussed possess rhizomorphs and thalloconidia and are rarely fertile. The size and septation of thalloconidia have been shown to be highly species-specific in some cases

(Poelt 1977; Hasenhüttl & Poelt 1978; Hestmark 1990; Krzevicka 2010; Davydov *et al.* 2020b). However, this is not the case in the *Umbilicaria vellea* and *U. cinereorufescens* groups, in which all species show multicellular thalloconidia of similar size, with a mean between $22\text{--}28 \times 17\text{--}23 \mu\text{m}$. The variation in maximum size could be explained by the different number of measurements between species, since we used only our own measurements of thalloconidia for *U. ahtii* and *U. koidzumii*, but for *U. cinereorufescens* and *U. vellea* we also used literature data (Hestmark 1990; Poelt & Nash 1993). However, rhizomorphs and distribution patterns of thalloconidia on rhizomorphs are variable and diagnostic (Table 3). Small, non-septate hyaline ascospores are diagnostic for *U. vellea*. Mature spores of *U. ahtii*, *U. cinereorufescens* and *U. koidzumii* are submuriform. So far, we have observed only hyaline ascospores in *U. ahtii*.

However, we believe they may be brown when mature, like the mature submuriform spores seen in other *Umbilicaria* species. Although the apothecia of all the species mentioned are similarly gyrose, *U. ahtii* stands out in that its apothecia are very similar in appearance to those of *U. meizospora*, the phylogenetically closest species. Mature apothecia of both species are attached to the lower cortex by a wide base and separated from the other thallus layers by a crack, so that the black surface of the lower cortex is visible from above (Fig. 2D & E; Frey 1933: 264, fig. 36). However, apothecia and ascospores are not useful diagnostic traits for routine identification of the *U. vellea* group because they develop too rarely.


All four species discussed contain gyrophoric and lecanoric acids as secondary metabolites, as revealed by TLC. *Umbilicaria cinereorufescens* s. str. stands out with crustinic acid as the major compound. This chemical feature appears to be rare in the genus *Umbilicaria* and is shared, as far as is known, only by

U. meizospora (Davydov & Masson 2022) and one chemotype of *U. crustulosa* (Posner *et al.* 1992; Narui *et al.* 1996; Serina *et al.* 1996). This result is in agreement with Posner *et al.* (1992) and Narui *et al.* (1996) who used European and Himalayan material of *U. cinereorufescens* for HPLC analyses. It is noteworthy that the major compound of the sister species *U. koidzumii* is gyrophoric acid, while crustinic acid is also detectable by TLC, although always as a minor compound. Posner *et al.* (1992) reported hiascic acid (minor) for the isotype of *U. koidzumii* in addition to gyrophoric (major) and lecanoric (minor) acids, and exactly the same pattern was shown for the *U. trabeculata* isotype. Similar to *U. cinereorufescens*, *U. meizospora* contains crustinic acid as the major compound and the sister species *U. ahtii* contains only a trace of crustinic acid detectable by HPLC and sometimes by TLC. *Umbilicaria vellea* sometimes contains umbilicic acid in addition to gyrophoric and lecanoric acids (Posner *et al.* 1992; Narui *et al.* 1996; Serina *et al.* 1996).

Key to species of the *Umbilicaria vellea* group with thalloconidia

- 1 1–2(–6)-celled thalloconidia develop on lower surface and rhizinomorphs **U. orientalis**
6–10 to 30–50-celled thalloconidia develop on rhizinomorphs 2
- 2(1) Rhizinomorphs of mature specimens vary in size and type and are often segregated in tiers: 1) simple to branched filiform rhizinomorphs without or occasionally with thalloconidia, and 2) thalloconidial rhizinomorphs tuberoso to peg-like, branched and ball-tipped, or with thalloconidia produced in bundles 3
Rhizinomorphs only thalloconidial, short, tuberoso to knob-like or irregular, never filiform 5
- 3(2) Peg-like ball-tipped rhizinomorphs predominate (Fig. 5E–I), sometimes segregated in tiers; shorter and longer, black filiform rhizinomorphs usually develop in addition and grow in irregular directions, often from filaments (Fig. 5C–I) **U. koidzumii**
Peg-like ball-tipped rhizinomorphs rare; rhizinomorphs arranged in two layers; shorter ones bearing thalloconidia and longer ones simple to branched, growing perpendicular to lower surface 4
- 4(3) Longer rhizinomorphs pale, shorter rhizinomorphs tuberoso (Fig. 4F) to peg-like; the bases of simple rhizinomorphs often covered with thalloconidia and worm-like (Fig. 4E) **U. vellea**
Longer rhizinomorphs dark (Fig. 3D), shorter rhizinomorphs branched with bundles of thalloconidia (Figs 3A–C, 4A & B) and/or peg-like and usually also branched, always with axes, never tuberoso or worm-like **U. ahtii** (Fig. 2)
- 5(2) Rhizinomorphs abundant, very irregular, tuberoso to peg-like, often flattened **U. cinereorufescens** (Fig. 5A & B)
Rhizinomorphs scarce, separate, short and knob-like **U. trabeculata**

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