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Research article

Myriospora molybdina comb. nov. and the identity of *Acarospora hysgina*

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The nomenclature and taxonomy of *Acarospora molybdina* is revised using morphological and molecular data. The new combination *Myriospora molybdina* is proposed and *Acarospora hysgina* is recognized as a distinct species while *A. brunneola* is reduced to synonymy with *A. hysgina*. In its new circumscription *M. molybdina* is an arctic species, in Scandinavia only occurring in northernmost Norway. Further localities are reported from Greenland, Russia, Svalbard and the USA (Alaska). *Acarospora hysgina* is the correct name for a species distributed along the west coast of Sweden and Norway, formerly thought to belong to *A. molybdina*. Localities are also reported from Canada (New Brunswick), Greenland and the USA (Maine). The following names are lectotypified: *Acarospora brunneola*, *A. molybdina* var. *confusa*, *Lecanora ereutica* β *microcyclos*, *Parmelia ereutica*, *P. hysgina* and *P. molybdina*.

Keywords: Acarosporaceae, beta-tubulin, ITS, Lecanoromycetes, lichens, mrSSU, phylogeny

Introduction

Acarospora A.Massal. is a large genus of crustose lichenized fungi occurring on all continents. They are characterized by multi-spored asci (mostly containing >100 small, simple, colorless spores) and apothecia commonly being immersed in the thallus. The growth form is usually crustose areolate to squamulose but some species are placodioid, featuring prominently developed and elongated marginal lobes. Among the latter is *Acarospora molybdina* (Wahlenb.) Trevis., a large species growing on seashore rocks, in Fennoscandia known along the coastline of Norway and the westcoast of Sweden (Magnusson 1924, 1929, Westberg et al. 2021).

The taxonomy and nomenclature of *A. molybdina* s. lat. has a complicated history involving several names at both specific and infraspecific ranks. The species was first collected by Wahlenberg in Finnmark, Norway, and described as *Parmelia molybdina* Wahlenb. in Acharius (1803). Subsequently, Magnusson, in his Scandinavian monograph (Magnusson 1924), used a broad concept of the species but later split off two additional species. The first was *A. wahlenbergii* H.Magn. which Magnusson (1929) introduced for montane populations in Sweden and Norway with a C+ red thallus. A few years later, *A. intricata* H.Magn. was described from a single locality in the Alps (Magnusson 1936). Timdal (1984) clarified the morphological and chemical distinctions among these three species, and *A. intricata* was later placed in the monotypic genus *Timdalia* Hafellner (Hafellner and Türk 2001). Some of the material that Magnusson had first included in *A. molybdina* (1924) and then in *A. wahlenbergii* (1929) is now included in *T. intricata*.

To complicate matters further, both Wahlenberg and Magnusson described additional taxa in the *A. molybdina* complex. Wahlenberg (in Acharius 1803) described *Parmelia ereutica* Wahlenb. and *P. hysgina* Wahlenb. based on material from northern Norway. Later, he placed *P. ereutica* under *P. molybdina* (as *Lichen molybdinus* β *ereuticus* (Wahlenb.) Wahlenb.) but kept *hysgina* as a distinct species, *Lichen hysginus* (Wahlenb.) Wahlenb. (Wahlenberg 1812). Magnusson (1924) tentatively accepted *Acarospora hysgina* (Wahlenb.) H.Magn. as a distinct species on Wahlenberg's authority as the original collections in UPS are scanty and partly destroyed (apparently by herbivores), while recognizing the taxon *ereutica* as a form of *A. molybdina* (*A. molybdina* f. *ereutica* (Wahlenb.) H.Magn.). Fries (1860), who studied the species in the field, was of the opinion that *A. hysgina* was only a young form of *A. molybdina* and Santesson (in litt.) agreed and treated the name as a synonym of *A. molybdina* in his checklist (Santesson 1984, 1993, Santesson et al. 2004).

Magnusson (1924) described *A. brunneola* H.Magn. based on a few collections made by Norman in Troms in northern Norway, a species supposedly distinguished by its red-brown color and short marginal lobes. This species is still included in the current checklist of Fennoscandia (Westberg et al. 2021) but is only known from the original collections. Magnusson compared this species to *A. molybdina* f. *microcyclos* (Ach.) H.Magn. a name originally suggested by Acharius (1810) as a form of *Lecanora ereutica* (Wahlenb.) Ach. Magnusson did not, however, compare *A. brunneola* with *A. molybdina* var. *confusa* H.Magn. which he described for the Swedish populations of *A. molybdina* and also reported from a few localities in Norway (Magnusson 1924). *Acarospora molybdina* var. *confusa* has for a long time been recognized in the regional checklists and is distributed from the northern part of the Swedish west coast north to Nord-Trøndelag in Norway, whereas *A. molybdina* var. *molybdina* is regarded as confined to northernmost Norway (Santesson 1984, 1993, Santesson et al. 2004, Westberg 2021). Roux et al. (2019) recognized *A. brunneola* and *A. hysgina* as distinct species and divided *A. molybdina* into three forms based on thallus and lobe size (f. *molybdina*, f. *microcyclos* and f. *confusa*).

During an international workshop in Varanger, Norway 2014, we had the opportunity to study rich populations of *A. molybdina* at several localitites along the coast. Excluding the today well-established, montane species *A. wahlenbergii* and *T. intricata*, which are both chemically and habitually distinct, our observations in the field and on herbarium material indicated that there are two distinct lobate, coastal taxa in Sweden and Norway. In this paper we investigate the identity of these entities using morphological data as well as DNA sequence data from four markers.

Material and methods

Morphological studies

Material from O, S and UPS was studied including type material of all relevant taxa mentioned above. Specimens were initially studied under a dissecting microscope. Measurements of finer anatomical structures (e.g. ascospores and paraphyses) were made under a light microscope on material mounted in water, using an oil-immersion lens, with a precision of 0.5 μm. Only well-developed ascospores lying outside the asci were measured. To examine color reactions of pigments, we used a 10% solution of KOH (abbreviated K), and a 4–5% solution of common commercial bleach (abbreviated C).

DNA extraction, amplification and sequencing

DNA was extracted from recently collected material or from dried herbarium specimens (Table 1). Total DNA was extracted using the Qiagen DNEasy Plant Minikit, according to the manufacturer's instructions. Selected markers for this study were the internal transcribed spacer complete repeat (ITS) and the large subunit of the nuclear ribosomal DNA (nrLSU), the small subunit of the mitochondrial ribosomal DNA (mrSSU), and the coding sequence of the β-tubulin gene (BT). PCR-amplification, purification and sequencing was performed using the same primers and methods as in Westberg et al. (2015).

Taxon sampling

We assembled a dataset based on the four markers including newly sequenced material of *A. molybdina* s. lat. and representative samples from several groups in Acarosporaceae downloaded from Genbank (Table 1). *Pycnora sorophora* was used as outgroup.

Sequence alignment and partitioning scheme

We estimated separate alignments for the non-protein-coding markers (mrSSU, ITS, and LSU) using PASTA (Mirarab et al. 2015), with the mask option activated, MAFFT (algorithm L-INS-i) as the aligner, OPAL for the pairwise merging, and FastTree as the tree estimator, with GTR+G as the model for molecular evolution. PASTA's iterative method results in an optimized alignment, negating the need for additional filtering of ambiguous regions. The ITS and LSU sequences, amplified simultaneously using the primers ITS1F and LR3 (Westberg et al. 2015), were initially aligned together and later split into separate alignment files. For the protein-coding

Table 1. Sequences newly produced (in bold) or downloaded from Genbank.

Species	Isolate	Voucher	ITS+LSU	mtSSU	Beta-tub.
Acarospora atrata	WE16	Sweden, Halland, Arup L02737 (LD 1256597)	LN810760	LN810885	LN810652
Acarospora badiofusca	WE05	Sweden, Östergötland, Nordin 5552 (UPS L-124833)	LN810762	LN810887	LN810654
Acarospora cervina	SAR144	Switzerland, Valais, Westberg 10-172 (S F177758)	LN810764	LN810889	LN810656
Acarospora fuscata	SAR120	Sweden, Gotland, Westberg SAR120 (LD 2057584)	LN810766	LN810891	LN810658
Acarospora glaucocarpa	WE23	Sweden, Öland, Westberg s.n. (LD 1972513)	LN810769	LN810894	LN810661
Acarospora heufleriana	SAR166	Switzerland, Valais, Westberg 10-174 (S F177764)	LN810774	LN810899	LN810666
Acarospora hysgina	CO119	Norway, Troms, Wedin 7225 (UPS L-1078535)	AY853352	AY853304	—
Acarospora hysgina	SAR121	Sweden, Bohuslän, Westberg & Westberg SAR121 (LD 2060592)	LN810783	LN810908	LN810675
Acarospora hysgina	SAR329	Norway, Finnmark, Westberg VAR111 (S F278294)	**OR236204**	**OR236216**	**OR285161**
Acarospora impressula	SAR33	Norway, Oslo, Westberg 08-107 (S F121708)	LN810776	LN810901	LN810668
Acarospora insolata	WE06	Sweden, Bohuslän, Westberg 06-022 (LD 2057648)	LN810777	LN810902	LN810669
Acarospora moenium	SAR93	Sweden, Västmanland, Westberg 09-066 (S F138363)	LN810781	LN810906	LN810673
Acarospora nodulosa	SAR146	Spain, Madrid, Westberg 10-215 (S F177732)	LN810789	LN810914	LN810681
Acarospora obpallens	SAR163	USA, California, Knudsen 9325 (S F256015)	LN810790	LN810915	LN810682
Acarospora placodiiformis	SAR145	Spain, Madrid, Westberg 10-211 (S F177733)	LN810795	LN810920	LN810687
Acarospora privigna	SAR71	Norway, Rogaland, Westberg 08-134 (S F123693)	LN810818	LN810943	LN810709
Acarospora rosulata	SAR34	Norway, Oppland, Westberg 08-193 (S F315173)	LN810797	LN810922	LN810689
Acarospora rugulosa	SAR172	Norway, Telemark, Westberg 08-119 (S F123671)	LN810798	LN810923	LN810690
Acarospora schleicheri	SAR222	USA, Arizona, Sweat & Yansky KGS1196 (UPS L-162697)	LN810801	LN810926	LN810693
Acarospora septentrionalis	SAR60	Norway, Sogn og Fjordane, Westberg 08-148 (S F132535)	LN836018	LN836022	LN836020
Acarospora sinopica	MW20	Sweden, Härjedalen, Wedin 6617 (UPS L-1078537)	DQ374148	DQ374120	EU870753
Acarospora socialis	SAR165	USA, California, Knudsen 9392 (S F256016)	LN810802	LN810927	LN810694
Acarospora squamulosa	SAR109	Sweden, Uppland, Westberg 09-222 (S F139588)	LN810793	LN810918	LN810685
Acarospora subfuscescens	SAR72	Norway, Oppland, Westberg 08-281 (S F122560)	LN810830	LN810956	LN810719
Acarospora umbilicata	CO238	Sweden, Västergötland, Tibell 23532 (UPS L-136981)	LN810808	LN810933	LN810700
Acarospora wahlenbergii	SAR91	Sweden, Härjedalen, Westberg SAR91 (S F312211)	LN810809	LN810934	LN810701
Acarospora wahlenbergii	SAR227	Sweden, Torne lappmark, Westberg P115 (S F312436)	LN810810	LN810935	LN810702
Glypholecia scabra	SAR128	Norway, Oppland, Westberg 08-232 (S F315174)	LN810811	LN810936	LN810703
Myriospora dilatata	WE02	Sweden, Lycksele lappmark, Nordin 5507 (UPS L-124304)	EU870660+LN810871	EU870712	EU870770
Myriospora dilatata	WE39	Sweden, Torne lappmark, Baloch SW116 (S F114109, holotype)	EU870656+LN810872	EU870708	EU870766
Myriospora molybdina	SAR326	Norway, Finnmark, Westberg VAR092 (S F278293)	**OR236205**	**OR236217**	**OR285162**
Myriospora molybdina	SAR330	Norway, Finnmark, Westberg VAR080 (S F278291)	**OR236206**	**OR236218**	—
Myriospora molybdina	SAR331	Norway, Finnmark, Westberg VAR046 (S F278198)	**OR236207**	**OR236219**	**OR285163**
Myriospora myochroa	WE12	Sweden, Bohuslän, Westberg 06-051 (LD 1448172)	EU870678+LN810873	EU870729	EU870788
Myriospora myochroa	WE20	Finland, Lapponia inarensis, Westberg LIN-159 (LD 1450032)	EU870669+LN810874	EU870721	EU870780
Myriospora rhagadiza	WE04	Sweden, Bohuslän, Westberg 06-040 (LD 1449312)	EU870647+LN810875	EU870699	EU870757
Myriospora rhagadiza	WE08	Sweden, Bohuslän, Westberg 06-034 (LD 1449252)	EU870646+LN810876	EU870698	EU870756
Myriospora rufescens	A42	Sweden, Härjedalen, Wedin 6616 (UPS L-1078539)	EU870690+MF095736	EU870742	EU870804
Myriospora rufescens	MW21	Sweden, Härjedalen, Wedin 6615 (UPS L-1078540)	AY853354	AY853306	EU870803
Myriospora scabrida	SAR195	Sweden, Härjedalen, Westberg 07-009g (LD 1508765)	MF074117	MF074123	MF074129
Myriospora scabrida	WE03	Sweden, Härjedalen, Santesson 33077a (UPS L-529787)	LN810812	LN810937	LN810704
Myriospora signyensis	MW123	Antarctica, Signy Island, Purvis & Maltman OWPS2_8 (BM)	MF074120	MF074126	MF074132
Myriospora signyensis	MW141	Antarctica, Signy Island, Smith 8668a (AAS)	MF074121	MF074128	MF074133
Myriospora smaragdula	A36	Sweden, Hälsingland, Ågren 384 (UPS L-098484)	EU870686+LN810878	EU870738	EU870798
Myriospora smaragdula	A37	Sweden, Härjedalen, Wedin 6620 (UPS L-1078538)	EU870688+LN810879	EU870740	EU870800
Myriospora tangerina	WE28	Sweden, Lycksele lappmark, Wedin 6873 (UPS L-1078536)	EU870683+LN810880	EU870735	EU870795

(Continued)

Table 1. Continued.

Species	Isolate	Voucher	ITS + LSU	mtSSU	Beta-tub.
Pleopsidium chlorophanum	MW57	Sweden, Torne lappmark, Nordin 4439 (UPS L-076485)	EU870691 + LN810881	EU870743	EU870805
Pleopsidium flavum	MW58	Austria, Steiermark, Obermayer 7790 (UPS L-105590)	AY853385	AY853336	EU870806
Pycnora sorophora	CO15	Sweden, Härjedalen, Hermansson 7903a (UPS L-111613)	FJ959357 + AY853387	AY853338	LN810757
Sarcogyne algoviae	SAR37	Norway, Oppland, Westberg 08-276 (S F122564)	LN810849	LN810975	LN810738
Sarcogyne clavus	SAR02	Austria, Steiermark, Obermayer 09129 (GZU 49-2002)	LN810852	LN810978	LN810741
Sarcogyne distinguenda	SAR42	Sweden, Jämtland, Westberg 08-305 (S F120452)	LN810854	LN810979	LN810743
Sarcogyne hypophaea	SAR198	Sweden, Uppland, Westberg SAR198 (S F312434)	LN810856	LN810981	LN810745
Sarcogyne regularis	SAR39	Norway, Oslo, Westberg 08-102 (S F121703)	LN810860	LN810985	LN810749
Timdalia intricata	SAR92	Sweden, Härjedalen, Westberg SAR92 (LD 2060784)	LN810866	LN810991	LN810755
Timdalia intricata	SAR226	Sweden, Torne lappmark, Westberg s.n. (S F312430)	LN810867	LN810992	LN810756
Trimmatothelopsis rhizobola	WE15	Sweden, Lule lappmark, Westberg 2994 (LD 1206046)	EU870640 + LN810868	EU870692	EU870745
Trimmatothelopsis terricola	SAR94	USA, California, Knudsen 11216 & Sagar (S F256012)	LN810806	LN810931	LN810698

gene BT, we estimated an alignment using MAFFT with the algorithm E-INS-i (Katoh et al. 2019), subsequently removing identified noncoding introns.

Potential incongruences among markers were examined through individual maximum likelihood analyses using IQ-TREE 2.0.7 (Minh et al. 2020), with 500 non-parametric bootstrap replicates (BS). Single-marker trees resulting from these analyses were then juxtaposed to identify any conflicts (defined as conflicting clades with > 75% BS); none were found, prompting the concatenation of the four alignments.

We assessed the division of the concatenated alignment into partitions using ModelFinder as implemented in IQTREE2 (Kalyaanamoorthy et al. 2017). We restricted the estimation to models included in MrBayes ver. 3.2.7a, used BIC for model selection, and assessed the division of the concatenated alignment into eight partitions: mrSSU, LSU, ITS1, 5.8S, ITS2, and independent 1st, 2nd and 3rd codon positions for the protein-coding gene BT.

The best model fit was achieved when the eight partitions were reduced to five (with corresponding substitution model): 1) ITS1 + ITS2; SYM + I + G4 (SYM + I + G in MrBayes), 2) 5.8S + mrSSU; GTR + F + I + G4 (GTR + I + G), 3) BT 1st codon position + LSU; GTR + F + I + G4 (GTR + I + G), 4) BT 2nd codon position; JC + I + G4 (JC + I + G), and 5) BT 3rd codon position; GTR + F + G4 (GTR + G).

Phylogenetic analysis

Using MrBayes ver. 3.2.7a (Ronquist et al. 2012), we conducted phylogenetic analyses on the partitioned, concatenated alignments, utilizing the molecular evolution models and partitioning scheme from ModelFinder. Substitution rates and state frequencies were assigned flat Dirichlet priors, while an exponential 1) distribution was used for the gamma shape parameter, and uniform distributions were employed for invariant sites and topology. Given a total tree length of approximately 1.8 in maximum likelihood test runs, we adjusted the branch length prior to a compound Dirichlet prior ($\alpha = 1$, $\beta = 0.55$). We carried out two runs of four Markov chain Monte Carlo (MCMC) chains, with three heated and one cold chain, setting the temperature for heated chains at 0.20. Sampling occurred every 100th generation, stopping once convergence was reached, indicated by an average split frequencies deviation below 0.004. 25% of trees were discarded as burn-in, and a posterior probability above 0.95 was considered as high support.

We also executed maximum likelihood analyses of the concatenated alignment with IQ-TREE 2.0.7, maintaining the same partitioning scheme and molecular evolution models as in the Bayesian analysis. Branch support was evaluated with 500 nonparametric bootstrap replicates, with a bootstrap value over 85% regarded as high support.

Results

The final alignment had 58 terminals and 2599 columns, of which 647 were parsimony-informative. The Bayesian analysis halted after 360 000 generations, resulting in a posterior of 7202 samples.

Specimens of *A. molybdina* s. lat. form two separate monophyletic clades within the Acarosporaceae (Fig. 1). The position of both clades received strong support, the first within *Myriospora* Uloth (posterior probability [PP] = 1, bootstrap [BS] = 90) as sister to *M. tangerina* (M.Westb. & Wedin) K.Knudsen & Arcadia (PP = 1, BS = 87) and the other within *Acarospora* (PP = 1, BS = 100) as sister to *A. wahlenbergii* (PP = 1, BS = 99). The former is identified as *M. molybdina* and the latter as *A. hysgina* (Fig. 1).

Discussion

Our study confirms the presence of two distinct lobate species of *Acarospora* s. lat. distributed along the Scandinavian coastline. One species occurs from the northern part of the Swedish west coast and up along the Norwegian coast reaching eastern Finnmark, whereas the second is an arctic species that in the Nordic countries is restricted to northernmost Norway. Below we propose the new combination *Myriospora molybdina* for the arctic species while the other is identified as *A. hysgina*. From the morphological studies we conclude that the remaining taxa mentioned in the introduction (*brunneola*, *ereutica*, *molybdina* var. *microcyclos* and *molybdina* var. *confusa*) should all be viewed as synonyms to *A. hysgina*. Recognizing the position of *molybdina* in *Myriospora* also explains the contradictory phylogenetic positions of *A. molybdina* within *Acarospora* s. str. in the phylogenetic analysis of Westberg et al. (2015, that specimen belongs to *A. hysgina*), compared to that of Miadlikowska et al. (2014), where it was found to be a close relative to *Myriospora smaragdula* (Wahlenb.) Uloth.

The genus *Myriospora* was earlier known as the *Acarospora smaragdula* group. Westberg et al. (2011) investigated the affinities of this group and proposed the new genus *Silobia* M.Westb. & Wedin to which they assigned seven species. Roux and Navarro-Rosinés (2011) argued that the valid name for this group should be *Trimmatothelopsis* Zschacke, a name today used for a different group of species within the Acarosporaceae (Gueidan et al. 2014, Knudsen and Lendemer 2016, Roux et al. 2016), while Arcadia and Knudsen (2012) found that the older name *Myriospora* was available for the *A. smaragdula* group. Since then, an additional five species have been added to *Myriospora* and with the addition of *M. molybdina* the current number of species in the genus is 13 (Arcadia and Knudsen 2012, Knudsen and Bungartz 2014, Purvis et al. 2018, Knudsen et al. 2021, Mishra et al. 2021).

In summary we conclude that the early concept of *A. molybdina* in Magnusson (1924) comprises four distinct species in three different genera: *Acarospora hysgina*, *A. wahlenbergii*, *M. molybdina* and *Timdalia intricata*. An additional southern hemisphere species, *A. macrocyclos* Vain. (Magnusson 1929), is not evaluated here. Vainio (1903) suggested that it could be a form of *M. molybdina*, but Magnusson (1929) could not reach a conclusion due to a lack of material.

Taxonomy

Acarospora hysgina **(Wahlenb.) H.Magn. (Magnusson 1924, p. 46)**

Parmelia hysgina Wahlenb. (in Acharius 1803, p. 48). *Lichen hysginus* (Wahlenb.) Wahlenb. (Wahlenberg 1812, p. 419). – Type: Norway, Finnmark: Alta, ad Alten prope Kaafjord. 27 May 1802, Wahlenberg (lectotype: UPS L-049306, designated here, MBT 10014126; isolectotype: UPS L-049305).

Parmelia ereutica Wahlenb. (in Acharius 1803, p. 43). *Acarospora molybdina* f. *ereutica* (Wahlenb.) H.Magn. (Magnusson 1924, p. 42). – Type: Norway, Finnmark: Alta, Brattholmen sinus Altenfjord. 29 May 1802, [Wahlenberg] (lectotype: UPS L-137857, designated here, MBT 10014085).

Lecanora ereutica β *microcyclos* Ach. (Acharius 1810, p. 431). *Acarospora molybdina* f. *microcyclos* (Ach.) H.Magn. (Magnusson 1924, p. 43). – Type: Norway, Finnmark: Alta, in montis juxta Båsekop Altensis, 27 Apr. 1802, [Wahlenberg] (lectotype: UPS L-137863, designated here, MBT 10014127).

Acarospora brunneola Norman ex H.Magn. (Magnusson 1924, p. 44). *Acarospora molybdina* var. *brunneola* (H.Magn.) Clauzade and Cl. Roux (Clauzade et al. 1981, p. 78). – Type: In insula Tromsø ad Ladenæsset. [undated] J.M. Norman (lectotype: O L-10328, designated here, MBT 10014083).

Acarospora molybdina var. *confusa* H.Magn. (Magnusson 1924, p. 43). – Type: Sweden, Bohuslän: Grötåns holme, 1918, A. H. Magnusson [Malme, Lich. Suec. exs. No. 746] (lectotype: UPS L-109335, designated here, MBT 10014084).

Nomenclature

Parmelia ereutica and *P. hysgina* were both described in the same work (Acharius 1803) and in our opinion represent the same species. As far as we know, no author has previously synonymized one of these names with the other but *P. hysgina* has by different authors been recognized as a distinct species (Magnusson 1924, 1929, Roux et al. 2019), whereas the epithet *ereutica* has not been used at species level since Acharius (1810). We see no reason to not use the name *A. hysgina*. Hafellner and Spribille (2016) argued that the authorship to *Parmelia elaeina*, also described in Acharius (1803) in a similar way to *P. ereutica* and *P. hysgina*, should be Wahlenb. ex Ach., and not Wahlenb. in Ach. (ICN Art. 46.5). However, Jörgensen (2020) showed that the introduction in Acharius (1803) makes it clear that Wahlenberg must be attributed the authorship. We agree with this and assign the author to *P. ereutica* and *P. hysgina* as Wahlenb. in Ach.

In UPS, there are two specimens of *Parmelia hysgina* that clearly originate from the same gathering. One is from Wahlenberg's herbarium and with a label written in Latin

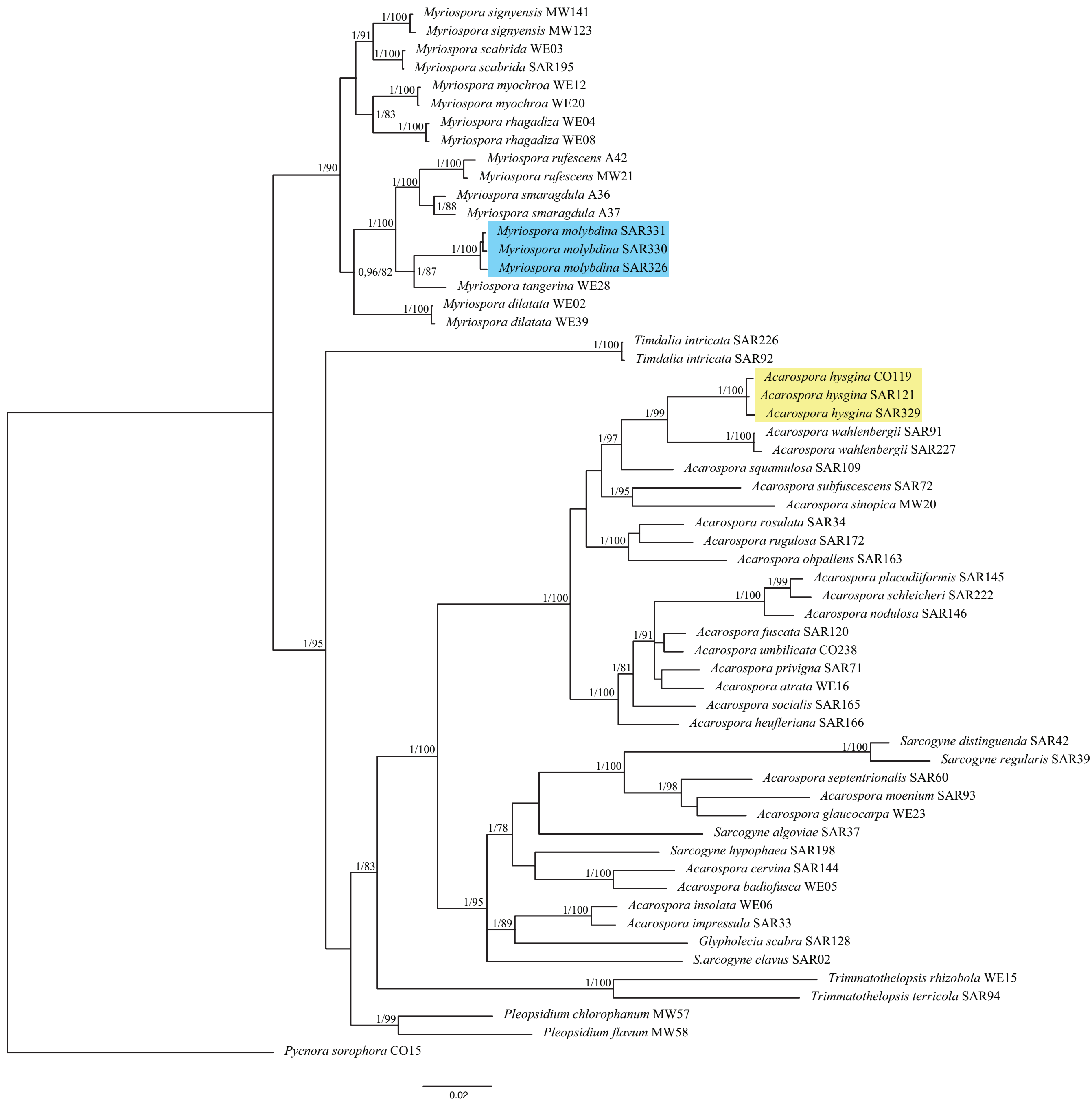

Figure 1. Majority-rule consensus tree based on Bayesian MCMC analysis of combined mrSSU, ITS, nrLSU and β-tubulin data, showing the phylogenetic positions of *Acarospora hysgina* (yellow) and *Myriospora molybdina* (blue). Bootstrap support values are from a separate maximum likelyhood analysis performed on the same data set. Branch support is given as posterior probability (PP)/bootstrap support(BS) for nodes with >0.95 PP and >75% BS.

in his own hand. It contains a few lobes that are small and damaged but nevertheless possible to identify. A much larger specimen with ca 20 thalli, of which some are damaged, has a label written in Swedish by Th. M. Fries and we choose this specimen as the lectotype.

Illustrations

Figure 2A–D.

Description

Thallus lobate, orbicular and distinctly rosette-like, rarely more than 10 mm in diam., or often of scattered lobes not forming distinct rosettes, indeterminate in size, up to 200 µm thick, its upper surface mostly dark brown but variable, sometimes medium brown or green brown or reddish brown, matt, usually minutely wrinkled when dry; lobes only distinct for at most 3 mm, 0.2–0.4 mm wide, mostly flattened and widening to up to 0.5 mm at the margin. Upper cortex thin and indistinctly delimited from the algal layer, to 15 µm thick, a thin, colorless epicortical layer is usually present, up to 3 µm thick; green algae evenly distributed below the cortex; medulla colorless; lower cortex lacking. *Apothecia* common, rounded, at first immersed in the lobes but later elevated above the thallus; thalline margin persistent, smooth, a proper margin is often visible as a thin ring around the disc; disc dark brown to black, smooth, concave to flat, 0.2–0.7 mm wide. Hymenium disc-shaped and not narrowing at the surface (compare *M. molybdina*), I+ greenish blue, (75–)100–125(–145) µm tall, the uppermost part reddish brown; paraphyses 1.5–2.0 µm wide in midhymenium, sparsely branched and anastomosing; hypothecium I+ dark blue, colorless, to 40 µm thick; proper exciple prosoplechtenchymatous, below the hymenium ca 10 µm wide, becoming wider and fan-shaped towards the surface with a distinct latitudinal direction, to 150 µm wide at the surface. Asci clavate, with several hundreds of spores; ascospores narrowly ellipsoid to short bacilliform, 3.0–4.5 × 1.0–1.5 µm. *Pycnidia* common and usually numerous, visible as minute dark pits on the marginal lobes, single-chambered (one pycnidum measured to 80 × 150 µm); conidia narrowly ellipsoid to fusiform, ca 2 × 1 µm.

Chemistry

Spot tests: K–, KC–, C–, UV–.

Distribution and habitat

Acarospora hysgina grows on coastal, granitic rocks, always within a few meters from the sea. Unlike *M. molybdina,* it has no preference for nitrogen enriched sites. In Varanger we never saw the two species growing together but one mixed specimen was found in the herbarium. *Acarospora hysgina* reaches much further south than *M. molybdina*; in Scandinavia occuring from the northern parts of the Swedish

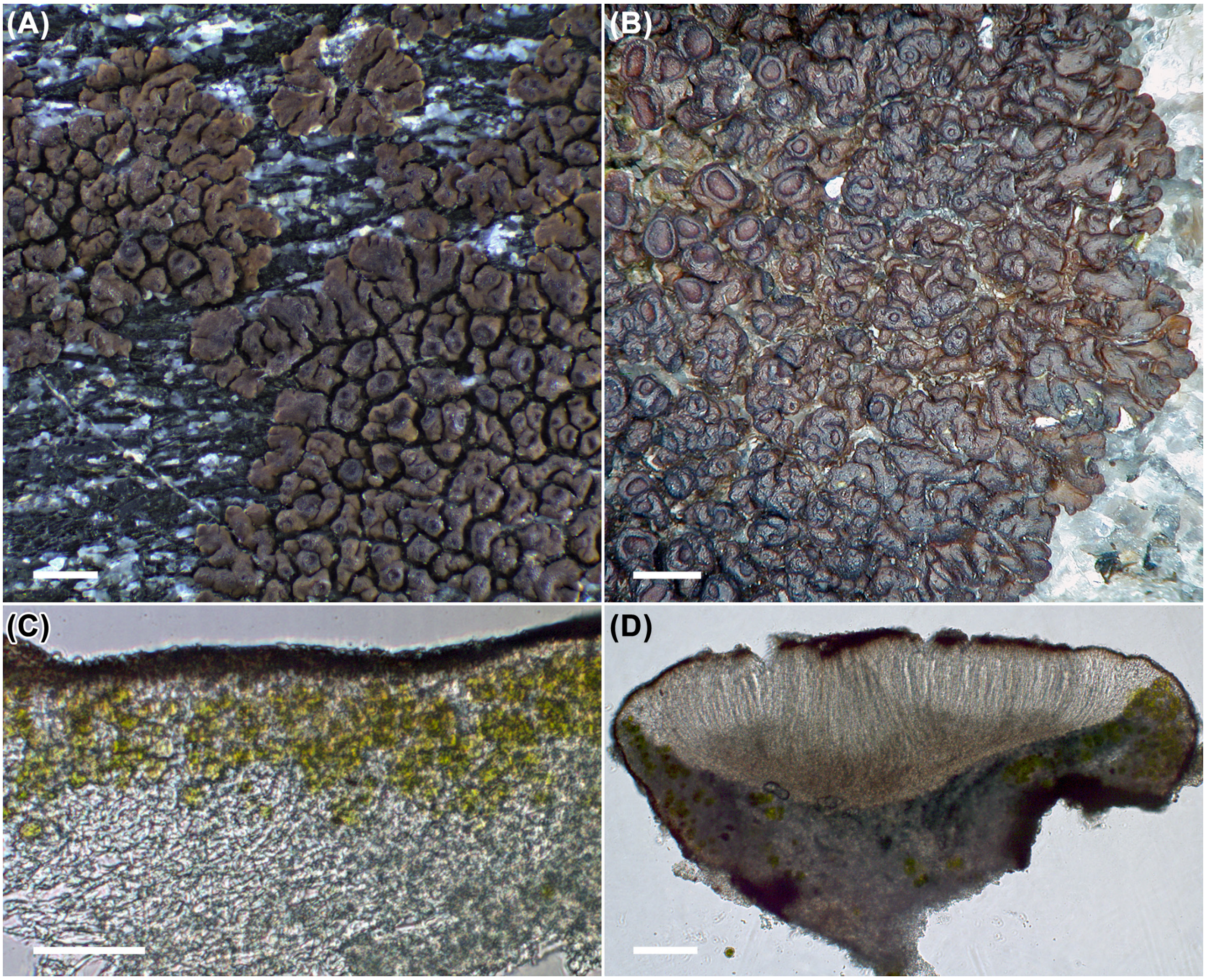

Figure 2. *Acarospora hysgina*. (A) (UPS L-515049), (B) (S F278294), (C) section of thallus showing an evenly distributed algal layer (S F278294), (D) section of apothecium showing an expanded disc-shaped hymenium (S F278294). Bars: (A)–(B) = 1 mm, (C) = 50 µm, (D) = 100 µm.

west coast all the way up to the Varanger Peninsula. There is also a report accompanied by a photo from the east coast of Sweden (Ångermanland, Artportalen 2023, Mikael Hagström pers. comm.) which appears to be correct, but no specimen has been collected from the east coast. From outside Scandinavia we have so far seen a few specimens from Greenland and the east coast of North America.

Remarks

There are many morphological and anatomical differences between *A. hysgina* and *M. molybdina*. *Acarospora hysgina* is usually easily recognized by its smaller size with short, flattened and thinner lobes and an evenly colored thallus. In section, the lower hymenium and the continuous algal layer are among the obvious differences. The thallus color is variable, mostly dark brown but it ranges from medium brown, green brown to red brown. The large variation in color, lobe shape and length as well as thallus development, to a considerable degree explains the number of synonyms we attach to this species. Small, adpressed, dark forms of *M. molybdina* can be somewhat difficult to distinguish from *A. hysgina* at first glance. Such specimens may also have an uncharacteristically low hymenium but the general habitus with long lobes with a matt and nodular surface and a smooth texture, gives them a clearly different impression than *A. hysgina*.

Selected specimens examined

Greenland, Godhavn, 11–12 June 1871, T. M. Fries (S F93186); Maligiaq, 7 July 1871, T. M. Fries (S F93403). Norway, Akershus, Oslo, Naesoddtangen, 15 Oct. 1871, N. G. Moe (UPS L-518564); Telemark, Bamble, Rognstranda, 59.00737°N, 9.70335°E, 9 June 2008, M. Westberg (S F123657); Vest-Agder, Kristiansand, eastern shore, 22 July 1939, A. H. Magnusson 16687 (UPS L-137840); Sogn og Fjordane, Lyster, Skjolden, östra fjordstranden ett stycke söder om hamnen, 27 July 1947, G. Degelius (UPS L-048340); Sør-Trøndelag, Stadsbygd, Bekkaneset (E of Röbergneset), 30 July 1961, R. Santesson 14288 (UPS L-118263); Nordland, Öifjord vid färjestället mitt emot Narvik, 15 Aug. 1933, G. E. Du Rietz (UPS L-559208); Troms, Storfjord, Røykesneset, seashore cliffs N of Skibotn, 69.4°N 20.25°E, elev. 2 m, 6 Aug. 2003, A. Nordin 5645 (UPS L-130902); Finnmark, Alta, Bossekop, 13 Aug. 1968, R. Santesson 20093c (UPS L-137865); Berlevåg, Kongsfjorden, between Kongsfjord and Kobkrokhögda, 2 Aug. 1966, L. Tibell 2784 (UPS L-137879); Hammerfest, 14 July 1864, T. M. Fries (UPS L-137849); Sør-Varanger, Balgami, 69.97807°N 29.58055°E, elev. 5–10 m, 4 July 2014, M. Westberg VAR111 (S F278294, UPS L-921593). Sweden, Västergötland, Lerum par., Aspenäs, 19 May 1936, A. Frisendahl (UPS L-515066); Bohuslän, Lycke, Nordön, strandblock i NO-delen av ön, 26 June 1956, S. W. Sundell 675 (S F91671, UPS L-515061); Forshälla, St. Hasselön, on the shore, 26 July 1930, Magnusson 12530 (S F91689). United States, Maine, [Knox Co.], Penobscot Bay District, Rockport, Jamesons Point. bird-summit in the (upper?) hygrohaline belt, 9 Aug. 1926, G.E. Du Rietz and G. Du Rietz 16:4 (UPS L-195991); Salisbury Cove, on rocks close to the sea, sometimes inundated, 29 July 1922, C.G. Plitt 16 (UPS L-195992).

Exsiccates

Krypt. exs. (Vindob.) No. 2957 (UPS L-679513); Lich. East. N. Amer. Exs. No. 442 (UPS L-584728, S F215791); Malme, Lich. Suec. Exs. No. 746 (UPS L-109335).

Myriospora molybdina (Wahlenb.) M.Westb. comb. nov.

MycoBank: MB 849454.

Basionym: *Parmelia molybdina* Wahlenb. (in Acharius 1803, p. 42). *Lecanora molybdina* (Wahlenb.) Ach. (Acharius 1810, p. 430). *Lichen molybdinus* (Wahlenb.) Wahlenb. (Wahlenberg 1812, p. 418). *Acarospora molybdina* (Wahlenb.) Trevis. (Trevisan 1853, p. 262). – Type: Norway, Finnmark: Kjelviig juxta Nordkap, 22 June 1802, G. Wahlenberg (lectotype: UPS L-137856, designated here, MBT 10014081).

Illustrations

Figure 3A–D.

Description

Thallus crustose, rosette-like or irregularly spreading, 1–10 cm wide (up to 50 cm wide according to Magnusson 1929), areolate centrally, elongately lobate at the margin, pale brown to grey brown to dark brown or almost black, sometimes pale grey to almost white in parts, occasionally with a rusty red color, smooth to strongly nodulose; lobes long and narrow, often clearly distinguishable for up to ca 1 cm, 0.25–0.50 mm wide, widening and up to 1.0 mm wide (occasionally up to 1.5 mm) at the margin, sometimes flattened but mostly thick, up to at least 700 µm thick; cortex paraplechtenchymatous with small cells (lumina 2–4 µm), or above medullary bundles (below) prosoplechtenchymatous with irregularily arranged hyphae with elongated cells, in uppermost part reddish brown to dark brown, often with a thin (up to 10 µm), colorless epicortical layer; green algae clumped between thick bundles of medullary hyphae, these up to 60 µm across; medulla colorless; lower cortex lacking. *Apothecia* common and usually numerous, arising in rounded to globular nodules on the lobes; proper margin occasionally visible from the outside; disc concolorous with the thallus, smooth, at first punctiform, in older apothecia somewhat widening, up to 0.4 mm wide. Hymenium subglobose with a narrow disc compared to its midhymenium diameter, colorless, I+ greenish blue, (150–)160–230 µm tall, the upper 10–15 µm reddish brown; hypothecium colorless, I+ dark blue, ca 50 µm thick in the centre; proper exciple colorless, I–, below the hymenium 20–30 µm thick, towards the surface widening to ca 100 µm across, formed by narrow, elongated cells often without a distinct latitudinal direction; paraphyses 1.0–1.5 µm in midhymenium, their tips slightly widened, to 3 µm wide, with dark brown caps. Asci

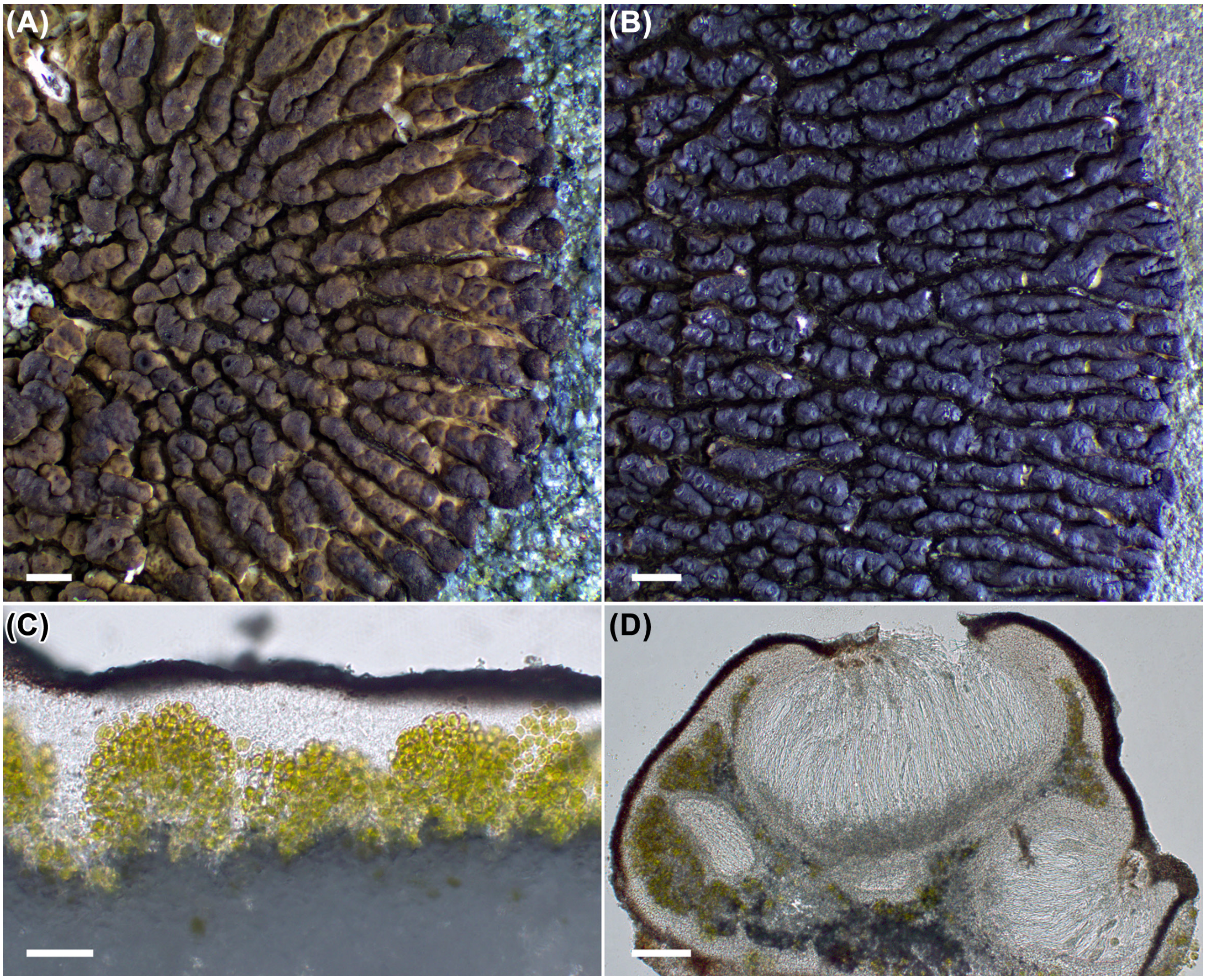

Figure 3. *Myriospora molybdina*. (A) (UPS L-118262), (B) (S F298293), (C) section of thallus showing a clumped algal layer penetrated by bundles of fungal hyphae (S F298293), (D) section of apothecium showing the globose hymenium (S F298293). Bars: (A)–(B) = 1 mm, (C) = 50 µm, (D) = 100 µm.

clavate, with several hundreds of spores; ascospores narrowly ellipsoid to short bacilliform, 3–4 × 1.0–1.5 µm. *Pycnidia* common, nearly invisible on the thallus surface, single-chambered (one pycnidium measured to measuring 120 × 200 µm); conidia narrowly ellipsoid to fusiform, ca 2.0–2.5 × 1 µm.

Chemistry

Spot tests: K–, KC–, C–, UV–.

Distribution and habitat

This species grows on nutrient enriched, coastal rocks. Other characteristic species growing in the same habitat in Varanger include e.g. *Candelariella arctica* (Körb.) R.Sant., *Myriolecis straminea* (Ach.) Śliwa et al. and *Rinodina balanina* (Wahlenb.) Vain. Unlike *A. hysgina*, we have found *M. molybdina* a couple of times 100–200 meters inland from the coast. We have so far not seen any specimen collected south of Finnmark and it seems to be restricted to northernmost Norway in Scandinavia. It is an arctic species, probably with a circumpolar distribution. Here we confirm it also from Greenland, Russia, Svalbard and the United States of America (Alaska).

Remarks

On closer examination, *M. molybdina* is a typical *Myriospora* species. It shares morphological features with *M. smaragdula*, including a algal layer interrupted by thick bundles of medullary hyphae, a tall hymenium that is almost globose in section with a narrow disc and a general '*Myriospora*'-appearance with a matt thallus surface (Westberg et al. 2021). There are numerous differences between *M. molybdina* and *A. hysgina*, but small, dark, adpressed forms of the former (in UPS usually annotated as var. *microcyclos*) with an unusually low hymenium may be somewhat difficult to identify (discussion under *A. hysgina*).

Selected specimens examined

Greenland, Sartoq, 19 June 1871, T. M. Fries (UPS L-195993); Nuqssuaq Peninsula, 30 Oct. 1949, P. Gelting 12425b (UPS L-726760); Godhavn, 13 June 1871, T. M. Fries (S F93187); Blåfjell, 18 June 1871, T. M. Fries (S F93392). Norway, Finnmark: Alta, Bosekop, 2 Aug. 1931, G. Degelius (UPS L-048334); Berlevåg, Vadsø, Stora Vadsøa, elev. 20 m, 20 July 1966, L. Tibell 2588 (UPS L-137874); Båtsfjord, ca 1 km NW of Finnvik (ca 4.5 km S of Hamningber), 70.48°N 30.62°E, 30 July 1966, R. Moberg 588 (UPS L-021277); [Gamvik,] Langfjorden, Goalsevuoppe, 29 July 1857, T. M. Fries (UPS L-137850, L-137858, S F91725); Kjelvik, Magerøy, Kamøyvaer, berget vid byn, elev. 10–20 m, 14 July 1959, G. Degelius (UPS L-048338); Nesseby, Fugleberget, 2–3 km E of Mortensnes, 4 Aug. 1966, R. Santesson 19080a (UPS L-137859); Vadsø, Komagnes, 70.20642°N 30.46812°E, elev. 1–5 m, 3 July 2014, M. Westberg VAR092 (S F278293, UPS L-921587), Vadsø, Store Ekkerøya, 70.07048N 30.10787°E, elev. 10 m, 3 July 2014, M. Westberg VAR080 (S F278291); Vadsø, SW of Kvalnesetes batteri, S of road E75, 70.20648°N 30.46955°E, elev. 15 m, on calcareous rocks close to the shore, 3 July 2014, M. Svensson 2929 (UPS L-1076511); Vadsø, 13 Aug. 1857, T. M. Fries (UPS L-137852, S F29348); Vardø, Skagodden, by the lighthouse, 70.40448°N 31.07040°E, 1 July 2014, M. Westberg VAR046 (S F27898); Vardø, 1864, Fries (S F92349, UPS L-137854). Russia, Novaya Zemlya, Sol Bay, Mashigin, 25 Aug. 1921, B. Lynge (UPS L-515079, L-726756); Veselago Island, 29 Aug. 1921, Lynge (S F93184); Sibiria Arctica, Insula Minin, 11 Aug. 1878, E. Almquist (S F93173, F93174); Pitlekaj, 1878–1879, E. Almquist (S F93178); Lapp. ponojensis, ad promontorium Orlow, 28 May 1889, A. O. Kihlman (S F93183); Sibiria septentrionalis, Sakha, Ryrkajpia, 12–18 Sept. 1878, E. Almquist (S F93175). Svalbard, Reinholmen, Recherche Bay, 16 July 1926, B. Lynge (UPS L-048341); Smeerenberg, 1861, A. J. Malmgren (UPS L-710563); Rypön, 1861, Malmgren (UPS L-710564); Kobbeberg, 1861, A. J. Malmgren (UPS L-710565); Fosters öar, 1861, A. J. Malmgren (UPS L-710566), Moffen, 23 June 1931, Scholander (S F93155). United States, Alaska, Insula St. Lawrence in freto Bering, 63.5°N, 171.5°W, 31 July–2 Aug. 1879, E. Almquist (S F93182).

Exsiccates

Fries, Lich. Scand. Rar. Critic. Exs. No. 32, (S F92341); Havaas, Lich. Exs. Norveg. No. 306 (UPS L-136855); Lich. Groenl. Exs. No. 647 (UPS L-087724).

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Author contributions

Martin Westberg: Conceptualization (lead); Data curation (lead); Funding acquisition (equal); Investigation (lead); Methodology (lead); Project administration (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Mats Wedin:** Data curation (supporting); Funding acquisition (equal); Investigation (supporting); Methodology (supporting); Project administration (supporting); Writing – original draft (supporting); Writing – review and editing (equal). **Måns Svensson:** Formal analysis (lead); Investigation (supporting); Methodology (supporting); Visualization (supporting); Writing – original draft (supporting); Writing – review and editing (equal).

Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.m63xsj48m (Svensson et al. 2024).

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