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Phenotypic and phylogenetic evidence reveals the position of *Parmelia skultii* in a new monotypic genus *Arneparmelia* within *Parmeliaceae*

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Abstract. The new monotypic genus *Arneparmelia* is introduced on the basis of phylogenetic and phenotypic evidence. The new combination, *A. skultii*, is proposed. Phylogenetic analyses using nuITS, nuLSU, mtSSU, and *mcm7* markers place the new genus close to *Parmelia* and *Notoparmelia*, although relationships among these genera remain incompletely resolved. The distinction between these three lineages as separate genera is also reflected in their morphological, chemical and geographical differences. *Arneparmelia* is characterized by a foliose, dark brown to black thallus with a black, stiff rim around the lobes, the upper surface covered by a bluish-white to lilac pruina and with silver, marginal or rarely laminal pseudocyphellae and by the presence of norstictic acid in high concentrations. The thalli of most species belonging to *Parmelia* and *Notoparmelia* exhibit a range of grey shades. The presence of a black margin is rarely observed and is found in only a few *Parmelia* species, and it is always absent in *Notoparmelia*. The pruina is always absent in *Notoparmelia*, and, when it is present in *Parmelia* species, its color is white. The presence of norstictic acid is rare and it is never present in high concentration in *Parmelia* and the substance is absent in *Notoparmelia*. The distribution of *Arneparmelia* is predominantly Arctic-Alpine. Species of the genus *Parmelia* are widely distributed, but *Notoparmelia* occurs in the Southern Hemisphere.

Key words: arctic species, *Ascomycota*, integrative taxonomy, new combination, new genus, parmelioid lichens

Introduction

Traditional methods of classifying lichens were based on their morphological and anatomical features, such as the size and type of spores or the type of vegetative propagules or thallus morphology. Later, chemical methods, especially thin-layer chromatography, became widely used in lichenology, and nowadays molecular methods are indispensable in the taxonomy and systematics of this group of fungi (Lücking et al. 2021). The use of phylogenetic evidence has contributed to the increase in the number of lichen species, as well as to the identification of cryptic or semicryptic species (e.g., Molina et al. 2004, 2011a, b; Hodkinson & Lendemer 2011; Lendemer 2011; Kraichak et al. 2015; Onuţ-Brännström et al. 2017, 2018; Magain et al. 2023). According to the most recent estimates, the number of known lichen species is above 19,000 (Lücking et al. 2017), and increasing as several species are described each year, especially from tropical regions.

Parmeliaceae is one of the largest families of lichen-forming fungi, containing almost 2,800 species grouped in ~80 genera (Crespo et al. 2010; Buarung et al. 2015; Lücking et al. 2017; Kraichak et al. 2018; Kirika et al. 2022; Chesnokov et al. 2023) and is divided into several clades based on multiple species phylogeny. Nine of these clades form a parmelioid group (Thell et al. 2004, 2012; Crespo et al. 2010), including the *Parmelia* clade, which contains the genus *Parmelia* Ach. (Crespo et al. 2010). This genus was introduced by Acharius in 1803 (Acharius 1803, 1810) and its taxonomic classification and circumscription have been repeatedly discussed (e.g., Crespo et al. 2010; Thell et al. 2012; Ferencova et al. 2014). As presently circumscribed, it is primarily characterized by foliose thallus, elongate to effigurate pseudocyphellae, which are usually laminal or more rarely marginal, the presence of atranorin in the upper cortex, common production of salazinic acid as a medullary secondary substance, dark and rhizinate lower surface and simple, furcate to squarrose rhizines (Molina et al. 2004, 2011a, b; Thell et al. 2008, 2011; Ossowska et al. 2019, 2026).

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Over the past twenty-four years, since the publication of the first species of *Parmelia* distinguished on the basis of molecular studies (Feuerer & Thell 2002), the advances in molecular methods have contributed much to the taxonomy of the genus. Ten new *Parmelia* species have been recognized, including some cryptic taxa (Feuerer & Thell 2002; Molina et al. 2004, 2011a, b, 2017; Divakar et al. 2005; Crespo et al. 2020; Dong et al. 2025). At the same time, some species have been excluded from *Parmelia* s.str. and segregated as separate genera, *Nipponoparmelia* K. Moon, Y. Ohmura & Kashiw., and *Notoparmelia* A. Crespo, Ferencova & Divakar (Kurokawa 1994; Crespo et al. 2010; Ferencova et al. 2014). At present 40 species are included in *Parmelia* s.str. (Divakar et al. 2015; Crespo et al. 2020; Dong et al. 2025). Most of these have an established phylogenetic position (e.g., Molina et al. 2004, 2017; Corsie et al. 2019; Ossowska et al. 2019), but some still require more study (Molina et al. 2004, 2017; Lumbsch et al. 2011; Ossowska et al. 2018; Ossowska 2023). This includes *Parmelia skultii* Hale, which was first recognized by Skult (1985) as *P. omphalodes* subsp. *glacialis* Skult. He distinguished it from *P. omphalodes* s.str. (L.) Ach. based on morphological and chemical differences, including the presence of norstictic acid, bluish-white to lilac pruina, and a black rim around lobe margins (Skult 1985). Later, Hale (1987) considered these differences to be significant enough to recognize this taxon at the species level, and he named it after H. Skult.

The phylogenetic position of *P. skultii* within *Parmeliaceae* is still puzzling, although attempts were made to verify its phylogenetic position by Thell et al. (2004). In this work, they noted that the sequence of *P. skultii* (GenBank no. AY251456) formed a separate clade, sister to *Parmelina tiliacea* (Hoffm.) Hale. However, the authors' analysis was based exclusively on one or two nuITS rDNA sequences (the second sequence was deposited in GenBank by Thell in 2008) obtained from two specimens from Canada and Greenland and those results showed that the use of this marker is limited in establishing the position of *P. skultii* within *Parmeliaceae*.

During our research, we obtained new sequences of *P. skultii*, which together with those previously deposited in GenBank, helped us to determine its position among other parmelioid genera within the family *Parmeliaceae*. The aims of our work are: (1) to assess the taxonomic position of the new lineage within parmelioid lichens, and (2) to analyze the phenotypic characters (morphological, chemical) and distribution of specimens grouped in the new lineage in comparison to closely related genera.

Materials and methods

Taxon sampling, morphology and chemistry

In total, twenty-seven *Parmelia skultii* specimens deposited in B, CANL, H, LECB, MSC, TUR, and UBC were used for the study. Morphology was examined under Nikon SMZ800N stereomicroscope and ZEISS Discovery.V12 stereomicroscope. Secondary lichen compounds were identified using thin-layer chromatography (TLC) with solvents A and C according to Orange et al. (2001). The sample of *Cladonia symphycarpa* (Ehrh. ex Schrad.) Fr. (UGDA L-9477) was used as a reference to properly identify norstictic acid. Detailed information on all analyzed specimens is presented in Supplementary Data Table S1.

DNA extraction, PCR amplification and sequencing

DNA was extracted using a modified CTAB method (Guzow-Krzemińska & Węgrzyn 2000) or E.Z.N.A.® HP Plant DNA Kit Omega Bio-tek. Four fungal markers were analyzed, i.e. nuITS rDNA, mtSSU rDNA, nuLSU rDNA, and *mcm7* gene. Additionally, nuITS rDNA region and rbcL from the green algal partner were amplified from one sample (LECB specimen collected by D.E. Himelbrant 14 & I.S. Stepanchikova). The PCR conditions and primers used in this study are presented in Table S2. PCRs were performed in a volume of 25 µl using StartWarm HS-PCR Mix (A&A Biotechnology) or MyFi DNA Polymerase (Bioline) following manufacturers' protocols. 2 µl of genomic DNA was used for amplification.

In order to determine DNA fragment lengths after PCR 1% agarose gels stained with SimplySafe (Eurx) dye were used. Afterwards, PCR products were purified using Clean-Up Concentrator or Gel-out Concentrator (A&A Biotechnology). The sequencing was performed by Macrogen Europe (The Netherlands; https://www.macrogen-europe.com/), using amplification primers. The newly obtained sequences were deposited in GenBank, and their accession numbers are listed in Tables 1 and S1.

Sequence alignment and phylogenetic analyses

The newly generated sequences were compared to the sequences available in GenBank (http://www.ncbi.nlm.nih.gov/BLAST/) using BLASTn search (Altschul et al. 1990). For the phylogenetic analyses, we used representatives of *Parmeliaceae* (see also Blanco et al. 2004; Divakar et al. 2012, 2015; Molina et al. 2017; Ossowska et al. 2019; Crespo et al. 2020; Hurtado et al. 2020) and *Protoparmelia badia* (Hoffm.) Hafellner was used as outgroup (Crespo et al. 2010; Thell et al. 2012). The independent alignments for each marker were generated in Seaview software (Galtier et al. 1996; Gouy et al. 2010) employing the Muscle option. Then, selection of unambiguously aligned positions was performed using Gblocks 0.91b (Castresana 2000) employing less stringent conditions. Single-locus matrices consisted of 61 sequences for nuITS, 53 sequences for mtSSU, 51 sequences for nuLSU, and 49 sequences for *mcm7*. The best ML trees were inferred for each locus using IQ-TREE with 1,000 ultrafast bootstrap replicates as implemented in the IQ-TREE web server (Nguyen et al. 2015; Chernomor et al. 2016; Kalyaanamoorthy et al. 2017; Hoang et al. 2018). Two concatenated datasets were prepared. The first dataset with representatives of 26 parmelioid genera consisted of 62 terminals (individuals) and 2,587 positions and the second dataset with representatives of *Parmelia* clade consisted of 20 terminals and 2,674 sites. The concatenated datasets were subjected to IQ-TREE analysis to find best-fitting nucleotide substitution models for each partition (Nguyen

Table 1. Species used in the phylogenetic analyses with their GenBank accession numbers. New sequences are marked in bold.

Genus	Species	Voucher	nuITS	nuLSU	mtSSU	*mcm7*
Arneparmelia Ossowska, Kukwa & Guzow-Krzem.	*Arneparmelia skultii* 1	LD	FJ425881	–	–	–
	Arneparmelia skultii 2	Westberg 1808 (LD)	AY251456	–	–	–
	Arneparmelia skultii 3	Himelbrant 14 & Stepanchikova (LECB)	**OR500512**	**OR498900**	**OR498899**	**OR500714**
	Arneparmelia skultii 4	Hansen, Lich. Groenl. Exs. No. 1034, MSC-97936	**OR500513**	–	–	**OR500716**
	Arneparmelia skultii 5	TUR-69499	–	–	–	**OR500715**
	Arneparmelia skultii 6	TUR-69500	**OR500514**	**–**	**–**	**–**
Austroparmelina A.Crespo, Divakar & Elix	*Austroparmelina endoleuca* (Taylor) A. Crespo et al.	Herb. Elix 38802	GU183185	GU183178	GU183192	JX974673
	Austroparmelina pseuodrelicina (Jatta) A.Crespo et al.	MAF-Lich 16115	GU183188	GU183181	GU183195	JX974676
Bulbothrix Hale	*Bulbothrix isidiza* (Nyl.) Hale	MAF-Lich 15511	GQ919262	GQ919237	GQ919210	KY859588
	Bulbothrix apophysta (Hale & Kurok.) Hale	Lücking 16650b, F	DQ279481	EU562670	DQ287788	GQ272392
Canoparmelia Elix & Hale	*Canoparmelia concrescens* (Vain.) Elix & Hale	MAF-Lich 15547	GU994543	GU994585	KR995317	KR995552
	Canoparmelia nairobiensis (J. Steiner & Zahlbr.) Elix & Hale	MAF-Lich 15544	GU994545	GU994587	KR995318	KR995553
Cetrelia W.L. Culb. & C.F. Culb.	*Cetrelia cetrarioides* (Duby) W.L. Culb. & C.F. Culb.	MAF-Lich 15552	JN943844	GU994591	GU994636	KR995562
	Cetrelia olivetorum (Nyl.) W.L. Culb. & C.F. Culb.	MAF-Lich 15507	JN943843	GU994593	KR995321	KR995563
Emodomelanelia Divakar & A. Crespo	*Emodomelanelia masonii* (Essl. & Poelt) Divakar & A. Crespo	MAF-Lich 15515	GU994549	GU994595	GU994640	JX974682
Flavoparmelia Hale	*Flavoparmelia caperata* (L.) Hale	MAF-Lich 10175	AY586561	AY584834	AY586585	KR995579
	Flavoparmelia soredians (Nyl.) Hale	MAF-Lich 10176	AY586562	AY584835	AY586586	JX974684
Flavopunctelia (Krog) Hale	*Flavopunctelia flaventior* (Stirt.) Hale	MAF-Lich 6046	AY581060	JN939611	AF351164	–
	Flavopunctelia soredica (Nyl.) Hale	MAF-Lich 17771	KR995280	GU994600	KR995327	KR995584
Hypotrachyna (Vain.) Hale	*Hypotrachyna cryptochlora* (Vain.) D. Hawksw. & A. Crespo	MAF-Lich 10398	DQ279535	–	DQ287845	–
	Hypotrachyna dubitans (Sipman) Divakar et al.	MAF-Lich 15621	GQ919270	GQ919246	GQ919218	GQ272427
	Hypotrachyna minarum (Vain.) Krog & Swinscow	MAF-Lich 13968	DQ279539	–	DQ287849	–
	Hypotrachyna endochlora (Leight.) Hale	MAF-Lich 10379	DQ279496	JN939614	DQ287805	KR995593
Melanelixia O. Blanco et al.	*Melanelixia californica* A. Crespo & Divakar	MAF-Lich 15559	EU761210	KR995406	EU761227	KR995612
	Melanelixia fuliginosa (Fr. ex Duby) O. Blanco et al.	MAF-Lich 10223 (10219)	AY611089	AY607801	AY611146	JX974686
Melanohalea O. Blanco et al.	*Melanohalea elegantula* (Zahlbr.) O. Blanco et al.	MAF-Lich 10231	AY611094	AY607806	AY611151	JX974693
	Melanohalea exasperatula (Nyl.) O. Blanco et al.	Esslinger 16554	AY611119	AY607833	AY611175	JX974696
Myelochroa (Asahina) Elix & Hale	*Myelochroa metarevoluta* (Asahina) Elix & Hale	MAF-Lich 10208	AY611102	AY607814	AY611159	KR995624
	Myelochroa irrugans (Nyl.) Elix & Hale	MAF-Lich 10207	AY611103	AY607815	AY611160	JX974708
Nesolechia A. Massal.	*Nesolechia oxyspora* (Tul.) A. Massal.	Fröberg 10/08/03, UPS	DQ980020	DQ923669	DQ923642	–
Nipponoparmelia K. Moon et al.	*Nipponoparmelia laevior* (Nyl.) K.H. Moon, Y. Ohmura & Kashiw.	MAF-Lich 19605	KR995296	GU994614	GU994660	KR995628
	Nipponoparmelia ricasolioides (Nyl.) A. Crespo & Divakar	MAF-Lich 15527	GU994569	GU994616	GU994661	KR995629
Notoparmelia A. Crespo et al.	*Notoparmelia crambidiocarpa* (Zahlbr.) A. Crespo et al.	MAF-Lich 19608	GU994571	KR995419	GU994665	KR995631
	Notoparmelia cunninghamii (Crombie) A. Crespo et al.	MAF-Lich 19607	GU994572	KR995420	GU994666	KR995632

Table 1. Continued.

Genus	Species	Voucher	nuITS	nuLSU	mtSSU	*mcm7*
Parmelia Ach.	*Parmelia barrenoae* Divakar et al.	MAF-Lich 17773	KR995303	JN939626	KR995361	KR995642
	Parmelia discordans Nyl.	MAF-Lich 10232	AY583212	EF042918	DQ287841	KR995643
	Parmelia encryptata A. Crespo et al.	MAF-Lich 15422	EU788036	–	–	KT625531
	Parmelia ernstiae Feuerer & A. Thell	MAF-Lich 20000	KT625495	–	–	KT625536
	Parmelia omphalodes (L.) Ach.	S:F-252763	MN412797	–	–	–
	Parmelia pinnatifida Kurok.	MAF-Lich 7272	AY036988	–	AY611161	–
	Parmelia saxatilis (L.) Ach.	Wedin 5051, BM	AF058037	AY300849	AF351172	JX974709
	Parmelia serrana A. Crespo et al.	MAF-Lich 9756	AY295109	AY578948	AY582319	JX974710
	Parmelia submontana Nádv. ex Hale	PH2	MT066087	MT086745	MT068517	–
	Parmelia sulcata Taylor	MAF-Lich 10159	AY579454	JN939625	KR995362	KR995645
Parmelina Hale	*Parmelina quercina* (Willd.) Hale	MAF-Lich 13947	DQ273844	DQ268542	DQ268562	–
	Parmelina pastillifera (Harm.) Hale	MAF-Lich 6058	AY611104	AY607817	EU562697	KR995646
Parmelinella Elix & Hale	*Parmelinella wallichiana* (Taylor) Elix & Hale	MAF-Lich 7653	AY611106	AY607819	AY611165	KR995647
Parmelinopsis Elix & Hale	*Parmeliopsis hyperopta* (Ach.) Vain.	MAF-Lich 10181	AY611109	AY607823	AY611167	JX974711
Parmotrema A. Massal.	*Parmotrema subtinctorium* (Zahlbr.) Hale	GUH 02-000696	AY586558	AY584830	AY586582	JX974713
	Parmotrema reticulatum (Taylor) M. Choisy	MAF-Lich 10164	AY586577	AY584848	AY586599	JX974712
Pleurosticta Petr.	*Pleurosticta acetabulum* (Neck.) Elix & Lumbsch	MAF-Lich 9914	AY581087	AY578953	AY582323	–
Protoparmelia M. Choisy	*Protoparmelia badia* (Hoffm.) Hafellner	Printzen FR-0217382	KY066258	KP796297	KP822427	JN009752
Pseudoparmelia Lynge	*Pseudoparmelia cyphellata* Lynge	Nash 46672, WIS	KM657272	KM657291	KM567311	KY859607
	Pseudoparmelia uleana (Müll. Arg.) Elix & T.H. Nash	Seavey 1386, LSU	KM657276	KM657295	KM657315	KY859608
Punctelia Krog	*Punctelia borreri* (Sm.) Krog	MAF-Lich 9919	AY581088	AY578954	AY582324	–
	Punctelia rudecta (Ach.) Krog	MAF-Lich 7661	AY586573	AY584844	AY586596	KR995674
Relicina (Hale & Kurok.) Hale	*Relicina sydneyensis* (Gyeln.) Hale	Lumbsch 19179a	GU994581	GU994630	GU994675	JX974714
	Relicina intertexta (Mont. & Bosch) Kirika, Divakar & Lumbsch	Lumbsch 19756g	KM657283	KM657301	KM657323	KR995678
Remototrachyna Divakar & A. Crespo	*Remototrachyna crenata* (Kurok.) Divakar & A. Crespo	MAF-Lich 10377	DQ279495	EU562683	DQ287804	JX974715
	Remototrachyna infirma (Kurok.) Divakar & A. Crespo	MAF-Lich 10210	AY785271	AY785264	AY785278	KR995684
Xanthoparmelia (Vain.) Hale	*Xanthoparmelia isidiovagans* O. Blanco, A. Crespo et al.	MAF-Lich 9956	AY581094	AY578960	AY582330	JX974718
	Xanthoparmelia tinctina (Maheu & A. Gillet) Hale	BCN-13862	AY581110	AY578978	AY582345	JX974720

et al. 2015; Chernomor et al. 2016; Kalyaanamoorthy et al. 2017; Hoang et al. 2018). The following nucleotide substitution models for the four predefined subsets in the large dataset were selected: HKY+F+R3 for mtSSU rDNA, SYM+I+G4 for nuITS rDNA, K2P+R3 for *mcm7*, and SYM+R3 for nuLSU rDNA marker. For the *Parmelia* clade dataset the following models were selected: HKY+F+I for mtSSU rDNA, TNe+I for both nuITS rDNA and nuLSU rDNA, K2P+I for *mcm7* marker. The search for maximum likelihood tree was performed in IQ-TREE and followed with 100 bootstrap replicates (Nguyen et al. 2015; Chernomor et al. 2016; Kalyaanamoorthy et al. 2017; Hoang et al. 2018).

Bayesian analysis was carried out using a Markov Chain Monte Carlo (MCMC) method, in MrBayes v. 3.2.6 (Huelsenbeck & Ronquist 2001; Ronquist & Huelsenbeck 2003) on the CIPRES Web Portal (Miller et al. 2010). Two parallel MCMC runs were performed, each using four independent chains and ten million generations, sampling every 1,000th tree. The resulting log files were analyzed using Tracer 1.7.2 (Rambaut et al. 2018). Posterior probabilities (PP) were determined by calculating a majority-rule consensus tree after discarding the initial 25% trees of each chain as the burn-in. The convergence of the chains was confirmed by the convergent diagnostic of the Potential Scale Reduction Factor (PSRF), which approached 1 and the 'average standard deviation of split frequencies' was <0.01 (Ronquist et al. 2005).

Phylogenetic trees were visualized using FigTree v. 1.4.3 (Rambaut 2009) and further modified in Inkscape (https://inkscape.org/). Bootstrap support (BS values ≥70) and PP values (values ≥0.95) are given near the branches on the phylogenetic tree.

Results

Phylogenetic analyses

Three new nuITS rDNA, one nuLSU rDNA, three *mcm7*, and one mtSSU rDNA sequences were generated from four specimens of *Parmelia skultii* during this study (Table 1 & S1). These were aligned with reference sequences from GenBank representing 26 parmelioid genera according to the literature data (Crespo et al. 2010; Divakar et al. 2012, 2015, 2017; Thell et al. 2012; Buarung et al. 2015).

The phylogenetic reconstruction (Fig. 1) shows that all the species used in our phylogeny are arranged into several clades, previously defined by Crespo et al. (2010), Thell et al. (2012), and Divakar et al. (2012, 2015, 2017). Five clades are represented by monogeneric and well-supported lineages: *Cetrelia*, *Hypotrachyna*, *Nipponoparmelia*, *Parmeliopsis*, and *Xanthoparmelia* (Fig. 1). The *Parmelina* clade contains *Bulbothrix*, *Myelochroa*, *Parmelina*, *Parmelinella*, and *Remototrachyna*, while *Emodomelanelia*, *Melanelixia*, *Melanohalea*, and *Pleurosticta* are clustered together in the *Melanohalea* clade sensu Crespo et al. (2010). The *Parmotrema* clade is another multi-generic clade which splits into three lineages: (1) *Austroparmelina*, *Flavoparmelia* and *Parmotrema*, (2) *Flavopunctelia*, *Nesolechia* and *Punctelia*, and (3) *Canoparmelia*, which is basal to other genera.

In our analyses, species belonging to the *Parmelia* clade sensu Crespo et al. (2010) are divided into two clades. The first one consists of well-supported lineages of *Parmelia* s.str., *P. skultii* and *Notoparmelia*, however, their relationship is poorly supported. Moreover, *Relicina* Hale and *Pseudoparmelia* form a separate highly supported clade.

The sequences retrieved from specimens of *Parmelia skultii* form a separate and strongly supported group (PP 1 and BS 100), which is closely related, but with no clear relationships with two other genera, *Parmelia* and *Notoparmelia* (both strongly supported: PP 1 and BS 100; Fig. 1).

Due to the weak resolution of the clade comprising *Parmelia*, *P. skultii* and *Notoparmelia* (this clade was only weakly supported in maximum likelihood analysis: BS 71), we decided to construct a second phylogenetic tree (nuITS rDNA, nuLSU rDNA, *mcm7* and mtSSU rDNA markers), but restricted to these three groups of species, and with two *Pseudoparmelia* sequences as the outgroup. Consequently, the support values for the clade grouping these three lineages increased on the resulting tree (Fig. 2; PP 1, BS 100). Specimens of *P. skultii* are grouped into a highly-supported clade (PP 1, BS 100) that is sister to *Parmelia*, however, their relationship is supported only in Bayesian analysis (PP 0.99, unsupported in ML analysis with BS<70). *Notoparmelia* is highly supported (PP 1, BS 100) and closely related to *Parmelia* spp. These results indicate that *P. skultii* represent a new genus within the family *Parmeliaceae*, described here as *Arneparmelia*.

We sequenced two DNA fragments of the photobiont from a single sample of *Arneparmelia skultii*. The nuITS rDNA (OR498901) based on BLAST analysis matches *Trebouxia* sp. clade IV (GenBank no. KJ754244; Muggia et al. 2014) and the chloroplast rbcL (OR500717) matches *Trebouxia* OTU A29 (GenBank no. KR914368; Leavitt et al. 2015).

Morphology and secondary chemistry

The lineage containing specimens of *Parmelia skultii* differs from closely related genera (i.e., *Parmelia* s.str. and *Notoparmelia*) by the following features: (1) the presence of norstictic acid in high concentrations (very rarely observed in trace to minor amounts in *Parmelia* s.str., and absent in *Notoparmelia*); (2) mostly marginal and elongate silver pseudocyphellae (laminal or rarely marginal and white in *Parmelia* s.str., and mostly marginal and white in *Notoparmelia*); (3) a black, stiff rim around lobes (present only in a few species of *Parmelia* s.str. and absent in *Notoparmelia*); (4) a dark, brown to black thallus (grey or rarely brown in *Parmelia* s.str., and grey in *Notoparmelia*); (5) a bluish-white to lilac pruina in the middle part of lobes (pruina is white in *Parmelia* s.str., and thalli can be strongly pruinose to epruinose, and in *Notoparmelia* thalli are epruinose); (6) Arctic-alpine distribution (*Parmelia* s.str. is widely distributed, and *Notoparmelia* is predominantly found in Australia and New Zealand). A summary of the differences between *Arneparmelia*, *Parmelia* s.str., and *Notoparmelia*, as well as other genera from the *Parmelia* clade is provided in Table 2, with detailed comments in the discussion section.

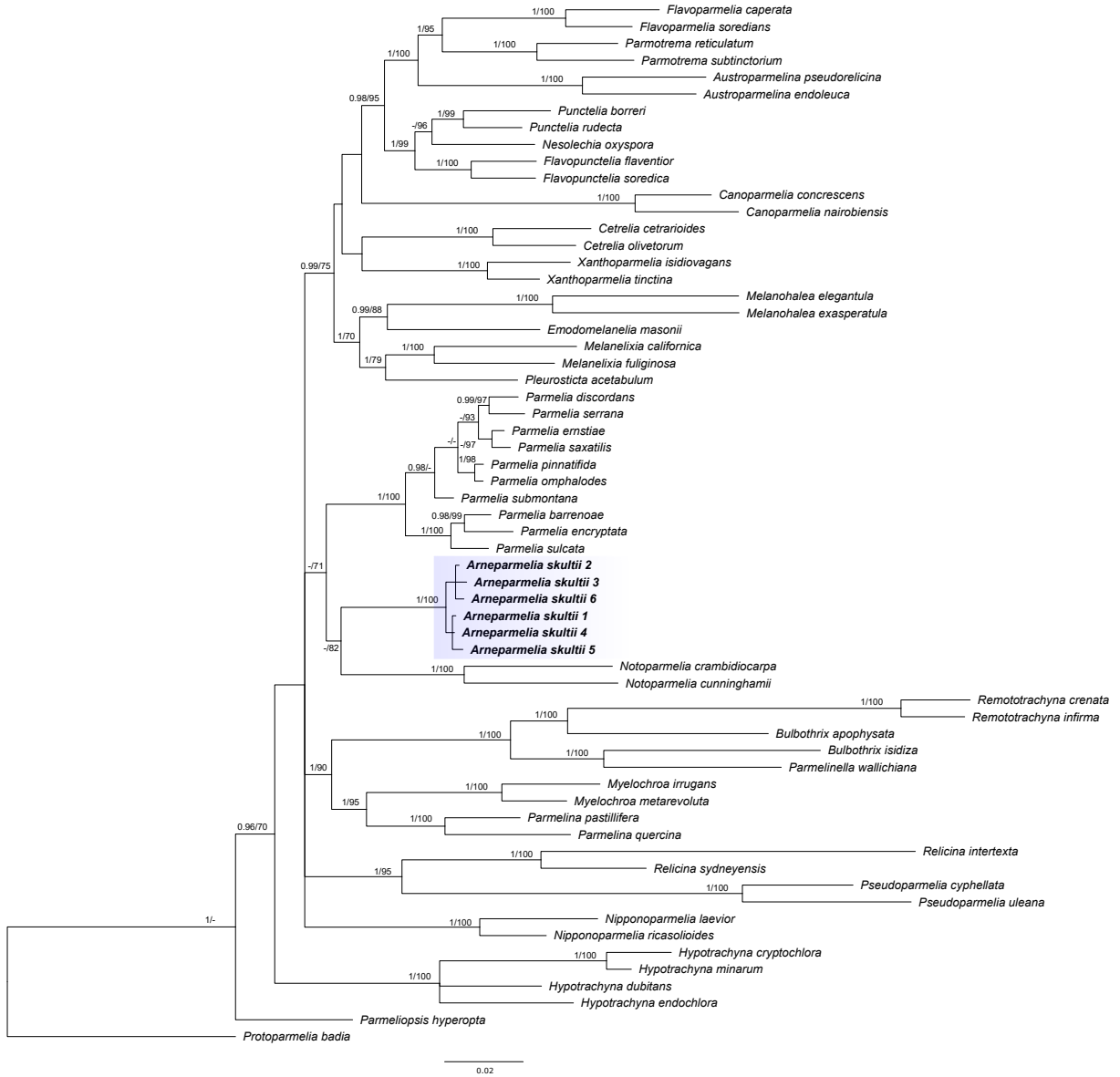

Figure 1. Bayesian phylogenetic tree for selected representatives of *Parmeliaceae* based on the concatenated nuITS rDNA, nuLSU rDNA, *mcm7* and mtSSU rDNA markers. Numbers near nodes indicate Bayesian posterior probabilities (values ≥ 0.95) and IQ-TREE bootstrap support values (BS values ≥ 70). *Arneparmelia* is marked in bold in the pale purple box. *Protoparmelia badia* was used as an outgroup.

Taxonomy

Arneparmelia Ossowska, Kukwa & Guzow-Krzem., gen. nov.

MycoBank MB 849841

Diagnosis. Characterized by a dark brown to black thallus with a black, stiff rim around the margins, very often with bluish-white to lilac pruina, silver marginal or rarely laminal pseudocyphellae, and the presence of norstictic acid in high concentration equal to salazinic acid.

Etymology. Named in honor of the outstanding lichenologist Arne Thell, for his contributions to the taxonomy of *Parmeliaceae*.

Notes. As this is a monotypic genus, the description below constitutes the generic description. A combined phylogenetic and phenotypic approach, incorporating morphological, chemical, and ecological evidence, permits the separation of *P. skultii* from *Parmelia* s.str. and *Notoparmelia*, and its recognition as the new genus, *Arneparmelia*. This is formally defined below and is accompanied by a new combination of *A. skultii*, which is designated as the type species of the genus.

Type species. *Arneparmelia skultii* (Hale) Ossowska, Kukwa & Guzow-Krzem .

Arneparmelia skultii (Hale) Ossowska, Kukwa & Guzow-Krzem., comb. nov. (Fig. 3)

MycoBank MB 849842

Basionym: *Parmelia skultii* Hale, Smithson. Contr. Bot. 66: 43. 1987.

Type: Canada, Northwest Territories, District of Franklin, Prince Patrick Island, Mould Bay, on damp polygon soil, south-facing slope, 24.VII.1952, S.D. MacDonald s.n. (holotype: CANL 136565, specimen not seen, but a good-quality photograph of specimen determined by H. Skult and M. Hale from US has been seen: https://www.gbif.org/occurrence/1804413113).

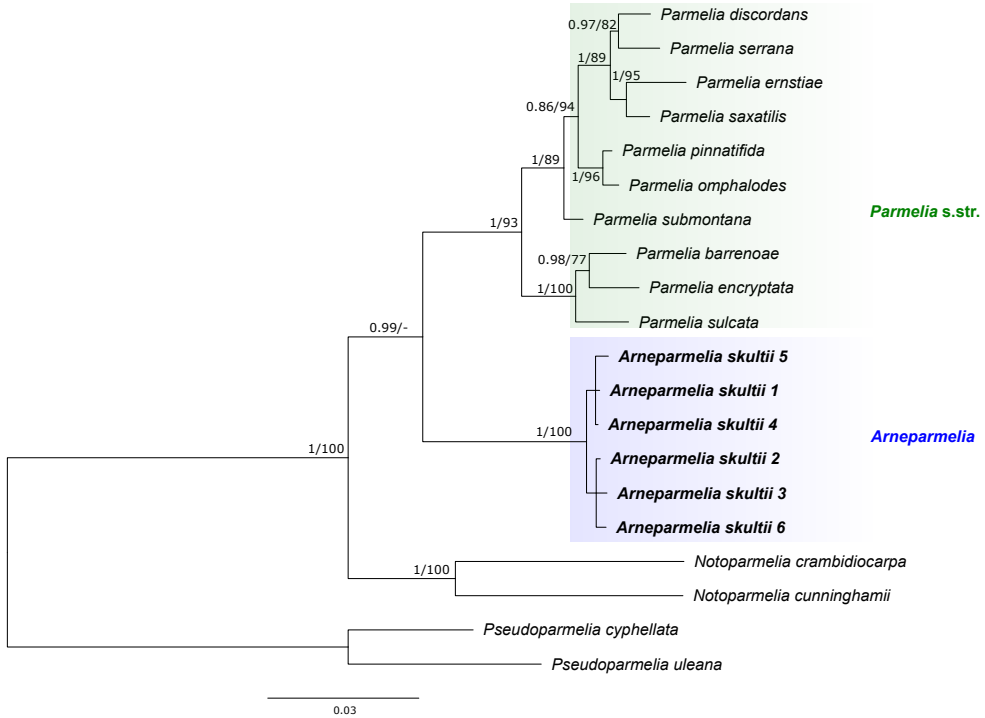

Figure 2. Bayesian phylogenetic tree for representatives of *Parmelia* clade based on the concatenated nuITS rDNA, nuLSU rDNA, *mcm7* and mtSSU rDNA markers. Numbers near nodes indicate Bayesian posterior probabilities (values ≥ 0.95) and IQ-TREE bootstrap support values (BS values ≥ 70). Genus *Arneparmelia* is marked in bold in the blue box and *Parmelia* s.str. in green box. *Pseudoparmelia cyphellata* and *P. uleana* were used as outgroup taxa.

Table 2. Differences in phenotype and distribution between *Arneparmelia* and other related and/or similar genera with references.

Traits	*Arneparmelia*	*Notoparmelia*	*Nipponoparmelia*	*Parmelia* s.str.	*Pseudoparmelia*	*Relicina*
pseudocyphellae	elongate, marginal or rarely effigurate, laminal, silver	elongate to effigurate, marginal or rarely laminal, white	punctiform to rarely elongate, marginal, white	elongate to effigurate, marginal and laminal, white	absent	
thallus color	dark, brown to black	greenish grey to grey-green	grey to grey-brown	grey to green-grey or grey-brown	yellow-green	
black, stiff rim	present	absent		sometimes present[a]	absent	
pruina	present, bluish-white to lilac	absent		present, white	absent	
vegetative propagules	absent	absent to present, in the form of isidia or soredia	absent to present, in the form of isidia	absent to present, in the form of isidia, sorsidia or soredia	absent to present, in the form of isidia	absent to present, in the form of isidia
rhizines	simple to furcate	squarrose	simple to furcate	simple to furcate or squarrose	simple	simple to furcate
norstictic acid	present (major)	absent		rarely[b]	absent	in some species[c]
distribution	Arctic	Australia and New Zealand, N & S America, S Africa	Asia	Asia, Africa, Europe, N & S America	Neotropics, S Africa	Asia, Africa, Europe, S America, Australia
references	this study	Ferencova et al. 2014	Crespo et al. 2010	Hale 1987; Thell et al. 2008; Crespo et al. 2010; Ossowska et al. 2018	Buaruang et al. 2015	Hale 1974; Kirika et al. 2017

[a] present in a few specimens of *P. omphalodes* and *P. discordans*; [b] present in *P. submutata* Hue; [c] present in *Relicina abstrusa* (Vain.) Hale, *R. limbata* (Laurer) Hale, *R. subabstrusa* (Gyeln.) Hale, *R. sydneyensis* (Gyeln.) Hale.

≡ *Parmelia omphalodes* subsp. *glacialis* Skult, Ann. Bot. Fenn. 22(3): 201. 1985.

Description. Thallus orbicular to irregular, up to 10 cm in diam; lobes sublinear, up to 8 mm wide (Fig. 3A–D), imbricate and crowded, with small, round laciniae (Fig. 3C); upper surface dark, brown to black with a black and stiff rim around the margins (Fig. 3B, D), smooth to minutely rugose, with bluish-white to lilac pruina (Fig. 3A, B) in the central part of the lobes, or with single pruina crystals (Fig. 3C). Pseudocyphellae marginal or rarely laminal (Fig. 3A, D) and then not connected to marginal ones, silver, elongated to rarely rounded. Vegetative propagules absent. Lower surface brown to black; rhizines sparse to moderately abundant, simple to furcate, black. Apothecia absent (see also Skult 1985; Hale 1987; Thell et al. 2011).

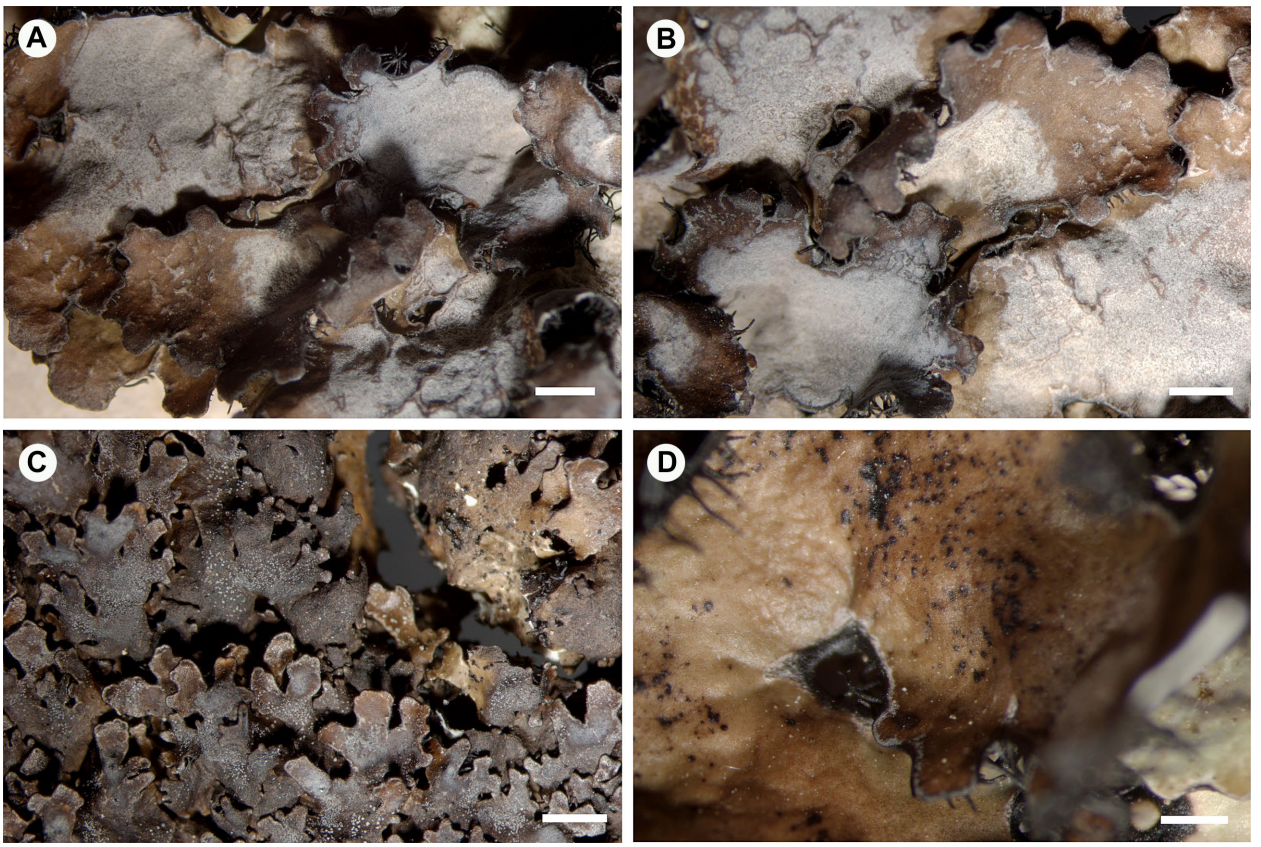

Figure 3. Morphology of *Arneparmelia skultii*. A–D – upper surface covered with bluish-white to lilac pruina; A–C – lobes sublinear; B, D – black, stiff rim along the lobe margins; C – laciniae; A, B, D – pseudocyphellae marginal and laminal (A, B, D – LECB; C – UBC L–38141). Scales = 1 mm.

Chemistry. Atranorin, salazinic, and norstictic acids as major substances were detected in all studied specimens, with minor or trace amounts of connorstictic (one specimen), and protolichesterinic (two specimens) acids. According to literature data the species can also produce fumarprotocetraric, protocetraric, and stictic acids (Skult 1985; Thell et al. 2011).

Ecology and distribution. *Arneparmelia skultii* usually grows on terricolous and saxicolous mosses. So far, it has been reported from the Northern Hemisphere: Canada (British Columbia province and Nunavut territory), Greenland, Svalbard, Sweden, Russia (Chukotka, Novaya Zemlya, Siberia, Kamchatka, Arkhangel'sk regions, Yakutia) and USA (Alaska, Montana) (Skult 1985; Hale 1987; Zhurbenko et al. 2005; McCune 2007; Hansen 2009; Thell et al. 2011; Chesnokov et al. 2025; see also below and Supplementary Data Table S1 for studied specimens).

Notes. The GBIF database contains two specimens that have been designated as the holotype of *A. skultii*: one from the CANL collection (collected by S.D. MacDonald, CANL 136565) and one from the US (collected by G. Llano 299a). In the latter case, the specimen bears a note by M.E. Hale stating 'Holotype'. However, this is likely an error, as the protologue of *A. skultii* (Hale 1987) states that the holotype is the specimen from CANL (see https://www.gbif.org/taxon/RBJ39). Although Hale (1987) cited the specimen from CANL as the holotype, two figures in the same publication (Figs 7a and 22c) bear a note stating that they were taken from the holotype deposited the US herbarium, rather than in the CANL herbarium. This must be treated as an editorial error.

Selected specimens examined (specimens used for DNA extraction). GREENLAND. Constable Bugt., 83°34′N, 32°01′E, in *Cassiope tetragona* heath, 13 Aug 2007, E.S. Hansen s.n. (Hansen, Lich. Groenl. Exs. No. 1034; MSC 97936). RUSSIA. Siberia, Taimyr, 73°30′N, 82°20′E, coast of the Cara Sea, mouth of Uboinaia river, on drift wood, 14 Aug. 1990, M.P. Zhurbenko (TUR 69500); 73°00′N, 81°00′E, mouth of Rogozinka river, in rocky outcrop by the river bank, terricolous, 14 Jul. 1990, M.P. Zhurbenko (TUR 69499); Kamchatka Territory, Aleut District, Commander Islands, Bering Island: S part, top of the NW spur of the mountain 518.2 between Kislaya (Nepropuskovaya) and Lisinskaya bays, alt. 360 m, 54°52′24.3″N, 166°33′30.4″E, layered crumbling outlier on the spur ridge surrounded by gravel tundra with small patches of vegetation, terricolous, 09 Aug. 2021, D.E. Himelbrant 14 & I.S. Stepanchikova (LECB).

Discussion

The classification of *Parmelia skultii* has been debated by various authors over the years. The discrepancies between *P. skultii* and other *Parmelia* species, and particularly the phylogenetic tree presented by Thell et al. (2004), can be identified as pivotal, as these authors indicated that sequences of the species (GenBank no. AY251456) represented a clade distinct from *Parmelia*. Nevertheless, Thell et al. (2004) did not propose any taxonomic novelty for *P. skultii* at that time, which may have been due to the limited number of specimens available for that study. The results presented here are based on a more

comprehensive sampling and an extended methodology. Taking into consideration phylogenetic results supported by the analysis of chemical and morphological characters and ecological differences, we propose a new genus for this species, which is named here as *Arneparmelia*.

The genus *Arneparmelia* is nested within the *Parmelia* clade, but the support of the clade is low and the relationships to *Notoparmelia* and *Parmelia* are poorly resolved. Despite the close relationship between these genera, the new genus exhibits several morphological, chemical and distribution differences (see Table 2), which preclude its placement within the genera *Parmelia* or *Notoparmelia*. In the light of the prevailing data, our conclusion is that *Arneparmelia* should henceforth be recognized as a new monotypic genus. Notwithstanding, it is worth note that a number of additional species have been described within the genus *Parmelia*, including, e.g., *P. submutata* and *P. neodiscordans* Hale. The phylogenetic position of these species still needs to be verified (to date, these species have not been sequenced, or only one or two sequences have been deposited in GenBank). For instance, *P. submutata*, similarly to *A. skultii*, produces norstictic acid and lacks propagules (Hale 1987), thus indicating its close relation to *A. skultii*. However, this hypothesis requires further investigation. On the other hand, the establishment of monotypic genera within *Parmeliaceae* is not unique to this family, as several such genera have been recently established within the family (Chesnokov et al. 2023).

One of the most important diagnostic characters in *Parmelia* and similar genera is the shape and placement of pseudocyphellae. Its usefulness has been confirmed by molecular data (Crespo et al. 2010; Thell et al. 2012; Ossowska et al. 2019). Hale (1987) divided pseudocyphellae in *Parmelia* s.lat. into three groups, based on differences in their distribution and shape. Following Hale (1987) and our current knowledge, pseudocyphellae can be: (1) elongate or effigurate, laminal and sometimes marginal (most species of *Parmelia* s.str.), (2) elongate, marginal and rarely laminal (*Arneparmelia*, *Notoparmelia*, and *P. pinnatifida* and some other *Parmelia* species with not yet confirmed phylogenetic position), and (3) punctate, circular, at the lobe edge (*Nipponoparmelia*). It should be noted that in *P. pinnatifida*, especially in older lobes, laminal pseudocyphellae may develop, but they are always connected to the marginal pseudocyphellae (Ossowska et al. 2019). On the other hand, laminal pseudocyphellae in *Arneparmelia* are rare and are not connected with the marginal ones, similarly as in *Notoparmelia*, in which pseudocyphellae are often fused to form a rim around the lobes (Ferencova et al. 2014). Furthermore, the color of the pseudocyphellae is also different; they are white in *Notoparmelia* and *Parmelia* s.str., whereas in *Arneparmelia* they are silver (Skult 1985; Hale 1987; Ferencova et al. 2014).

The presence of specific pruina, the black, stiff rim around the lobes, the dark color of the upper surface of thallus and the lack of vegetative propagules are other characters for *Arneparmelia* (Skult 1985; Hale 1987). In the new genus, the pruina is bluish-white to lilac and located in the central part of the lobes. In *Parmelia* s.str., the pruina is white and the lobe ends are usually pruinose (Ossowska et al. 2018), while in *Notoparmelia* lobes are epruinose (Ferencova et al. 2014). Ossowska et al. (2018) pointed out that specimens of *Parmelia* can be epruinose to strongly pruinose; however, the presence or absence of pruina have no diagnostic value in the species taxonomy (Ossowska et al. 2018; Corsie et al. 2019; Haugan & Timdal 2019), in contrast to other lichen genera, e.g., *Dermatocarpon* Eschw., *Hypogymnia* (Nyl.) Nyl. or *Psora* Hoffm. (Timdal 1984; Heiðmarsson 1996; Wie & Wie 2012; Guttová et al. 2014) and presumably also in *Arneparmelia* as its color and placement separate it from morphologically similar *Notoparmelia* and *Parmelia* s.str. Several hypotheses have been proposed for the presence of pruina in lichens (Wadsten & Moberg 1985; Heiðmarsson 1996; Giordani et al. 2003). In the case of *Arneparmelia skultii*, Skult (1985) suggested that it may be an adaptative strategy related to its arctic distribution and is likely to reflect sunlight, thus protecting the photobiont.

An interesting feature in the new genus is the presence of a black, stiff rim along the lobe margins, which may have a supporting function for the thallus (Skult 1985), and such rim is absent in similar genera and sometimes only a narrow black line of lower cortex is visible along lobes in *Parmelia omphalodes* group (figures in Ossowska et al. 2019). The color of the upper surface in *Arneparmelia* is brown to black, while in the genus *Parmelia* it is grey to green-grey or brown (Hale 1987; Thell et al. 2011), and in *Notoparmelia* whitish to mineral grey or greenish-grey to grey-green (Hale 1987; Ferencova et al. 2014).

The photobiont may also potentially support the distinction between *Arneparmelia* and *Parmelia* s.str. According to literature, photobionts in *Parmelia* taxa belong to *Trebouxia* clade S (in the *P. saxatilis* group) or clade I (mainly in the *P. sulcata* group) (Ossowska et al. 2019, 2024; Moya et al. 2021), which is different from the strain found in *A. skultii*. It is noteworthy that all three species in the *P. omphalodes* group (*P. discordans*, *P. omphalodes*, and *P. pinnatifida*), which exhibit morphological and chemical similarities to *A. skultii*, form lichen associations with OTU S (Ossowska et al. 2019). In our sample of *A. skultii*, a *Trebouxia* photobiont belonging to clade A (*T. arboricola*/*gigantea* group) lineage A29 was identified. This specific photobiont has previously been detected in *Tephromela atra* (Huds.) Hafellner s.lat. and *Montanelia predisjuncta* (Essl.) Divakar, A. Crespo, Wedin & Essl. (Muggia et al. 2014, 2020; Leavitt et al. 2015), it was known to occur in the Northern Hemisphere (Ruprecht et al. 2022), but it was recently reported also from *Hypotrachyna nigrociliata* from Bolivia (Kosecka et al. 2022). The limited number of photobiont sequences obtained in this study precludes any meaningful discussion of this taxon's preference for the *Trebouxia* lineage or its specificity and selectivity. However, with regard to the differences between *Parmelia* and *Arneparmelia*, it would be worthwhile to revisit this topic once a better sampling has been obtained.

Uncertainties in the identification of samples of *Arneparmelia skultii* based on morphological features can be resolved by chemical analysis. This species produces atranorin, salazinic and norstictic acids (the last two in equal concentrations) as the main secondary metabolites (Skult 1985; Thell et al. 2011), thus the substances are similar to those found in other similar genera (e.g., Hale 1987; Molina et al. 2004, 2017; Thell et al. 2008, 2017; Ferencova et al. 2014; Ossowska et al. 2018, 2019, 2026; Corsie et al. 2019; Tsurykau et al. 2019; Castellani et al. 2021). However, the presence of norstictic acid in high concentration equal to the concentration of salazinic acid distinguishes it easily from species of *Parmelia* s.str. as it is absent or can be found only in trace to minor concentrations in some specimens of *P. submutata* and *P. omphalodes* (Hale 1987). *Notoparmelia* and also *Nipponoparmelia* lack this substance (Hale 1987; Molina et al. 2004, 2017; Thell et al. 2008, 2017; Ferencova et al. 2014; Ossowska et al. 2018, 2019, 2026; Corsie et al. 2019; Crespo et al. 2020).

A significant divergence between the new genus and both, *Notoparmelia* and *Parmelia* s.str., is evident in their distribution and geographical range. *Arneparmelia* occurs only in the cold regions of the Northern Hemisphere (e.g., Skult 1985; Hale 1987; McCune 2007; Hansen 2009; Thell et al. 2011). It may therefore be defined as an Arctic-alpine species. In contrast, the genus *Notoparmelia* is geographically restricted to the Southern Hemisphere, with a primary distribution in Australia and New Zealand (Crespo et al. 2010; Ferencova et al. 2014). Of these, *Parmelia* s.str. has the widest geographic range and is distributed in the boreal-temperate zone of the Northern Hemisphere (Hale 1987; Crespo et al. 2010).

The newly described genus *Arneparmelia* is another supraspecific taxon within the family *Parmeliaceae*, that like *Nipponoparmelia* and *Notoparmelia* (Crespo et al. 2010; Ferencova et al. 2014), is separated from *Parmelia* s.str. based on phenotypic characters supported by molecular evidence. In the case of *Nipponoparmelia*, the decision to separate was more straightforward, as Hale (1987) had already divided the species of *Parmelia* s.lat. into three groups based on the structure of pseudocyphellae. Moreover, he classified the taxa currently included in *Nipponoparmelia* as a group with lateral, effigurate pseudocyphellae. Subsequently, Kurokawa (1994) transferred them to the subgenus *Nipponoparmelia*. Ultimately, as they constituted a distinct and novel clade within the phylogeny of *Parmeliaceae*, it was resolved to designate *Nipponoparmelia* as a genus (Crespo et al. 2010). In contrast, the situation is more complex with *Notoparmelia* and *Arneparmelia*, as both are grouped in separate clades, yet seem to be closely related to *Parmelia* s.str. This topology suggests that both could be classified as subgenera within *Parmelia*. However, their relationships are poorly supported. Also, we believe that such treatment would result in taxonomic chaos, as it would then be necessary to reduce *Notoparmelia* to the rank of subgenus within *Parmelia*. In such a scenario, it would also be reasonable to consider dividing *Parmelia* into two subgenera related to *P. saxatilis*, and *P. sulcata* groups, as indicated by the length of the branches on the phylogenetic tree, as well as some morphological and chemical differences between these clades. A study by Ferencova et al. (2014) revealed important discrepancies in the anatomical structure of the taxa that were subsequently categorized as *Notoparmelia*, in comparison to *Parmelia* s.str. Accordingly, the authors deemed these observations to be sufficiently important to justify the introduction of a new genus. We have conducted similar analyses and provided evidence to support the recognition of *Arneparmelia* at the genus rank. In conclusion, the new genus, *Arneparmelia*, differs from the *Parmelia* species in terms of both morphological and chemical characteristics; its distribution is Arctic-alpine, and it forms a distinct lineage within *Parmeliaceae*. Our data also suggests that the *Parmelia* clade should be redefined to include only *Arneparmelia*, *Parmelia* s.str., *Notoparmelia*, while *Relicina* and *Pseudoparmelia* should be treated as a separate clade. Furthermore, the absence of pseudocyphellae in *Relicina* and *Pseudoparmelia*, and the presence of a pored epicortex (Hale 1974; Buaruang et al. 2015; Kirika et al. 2017) provide additional support for this proposal.

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Supplementary electronic materials

Table S1. List of all *Arneparmelia skultii* specimens used in this study with TLC plate number, chemistry and GenBank accession numbers. Download file

Table S2. The PCR conditions used in this study to amplify the nuITS rDNA, mtSSU rDNA, nuLSU rDNA regions, *mcm7* gene and the chloroplast rbcL gene with references. Download file

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