



Lithothamnion* (Hapalidiales, Rhodophyta) in the changing Arctic and Subarctic: DNA sequencing of type and recent specimens provides a systematics foundation

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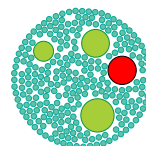
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Lithothamnion (Hapalidiales, Rhodophyta) in the changing Arctic and Subarctic: DNA sequencing of type and recent specimens provides a systematics foundation*

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ABSTRACT

Coralline red algae in the non-geniculate genera *Clathromorphum*, *Phymatolithon* and *Lithothamnion* are important benthic ecosystem engineers in the photic zone of the Arctic and Subarctic. In these regions, the systematics and biogeography of *Clathromorphum* and *Phymatolithon* have mostly been resolved whereas *Lithothamnion* has not, until now. Seventy-three specific and infraspecific names were given to Arctic and Subarctic *Lithothamnion* specimens in the late 19th and early 20th century by Frans R. Kjellman and Mikael H. Foslie. DNA sequences from 36 type specimens, five historical specimens, and an extensive sampling of recent collections resulted in the recognition of four Arctic and Subarctic *Lithothamnion* species, *L. glaciale*, *L. lemoineae*, *L. soriferum* and *L. tophiforme*. Three genes were sequenced, two plastid-encoded, *rbcL* and *psbA*, and the mitochondrial encoded COI-5P; *rbcL* and COI-5P segregated *L. glaciale* from *L. tophiforme* but *psbA* did not. Partial *rbcL* sequences obtained from type collections enabled us to correctly apply the earliest available names and to correctly place the remainder in synonymy. We were unable to sequence another 22 type specimens, but all of these are more recent names than those that are now applied. It is difficult to identify these species solely on morpho-anatomy as they can all occur as encrusting corallines or as maerl (rhodoliths). We demonstrate the importance of sequencing historical type specimens by showing that the recently proposed North-east Atlantic *L. erinaceum* is a synonym of one of the earliest published Arctic species of *Lithothamnion*, *L. soriferum*, itself incorrectly placed in synonymy under *L. tophiforme* based on morpho-anatomy. Based on sequenced specimens, we update the distributions and ecology of these species.

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Introduction

Coralline algae are important ecosystems engineers worldwide through the formation of extensive and bio-diverse cover on hard substrata and as unattached maerl (rhodoliths, Freiwald & Henrich, 1994; Foster, 2001; Amado-Filho *et al.*, 2010; Riosmena-Rodriguez *et al.*,

2017). Approximately one-third of the total continental carbonate production takes place in temperate and polar coastal waters with a significant amount coming from coralline algae (Nelson, 2009). In cold-water habitats, coralline algae can live for hundreds of years (Freiwald & Henrich, 1994; Halfar *et al.*, 2013; Adey

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et al., 2015a), providing habitats for other seaweeds (Peña *et al.*, 2014a) and for many epibenthic and cryptic macrofauna (Gagnon *et al.*, 2012; Teichert, 2014). Over the past two decades, surveys have shown that rhodolith beds are widespread in the NE Pacific (Robinson *et al.*, 2017), NW Atlantic (Gagnon *et al.*, 2012; Copeland *et al.*, 2013; Adey *et al.*, 2015a), Labrador Sea and Western Greenland (Jørgensbye & Halfar, 2017; Schoenrock *et al.*, 2018a, b) and the Arctic (Teichert *et al.*, 2012, 2014); this habitat is clearly much more abundant in Arctic environments than was previously assumed.

Adey & Steneck (2001) identified as Arctic those marine habitats ranging in temperature from $\leq 5^{\circ}\text{C}$ in summer to $\sim -1.5^{\circ}\text{C}$ in winter, and as subarctic, those experiencing $5\text{--}15^{\circ}\text{C}$ in summer and -1.5 to $+1^{\circ}\text{C}$ in winter. This characterization also applies to the NW Pacific subarctic, but in the NE Pacific subarctic, summer temperatures range from $10\text{--}15^{\circ}\text{C}$ and winter temperatures are -1.5 to $\sim 5^{\circ}\text{C}$ (based on oceanographic conditions where the species occur). The Arctic and subarctic are warming faster than most of the world's oceans, but the impact this will have on marine photosynthetic organisms is largely unknown. Wassmann *et al.* (2011) cited 51 reports of documented changes in the Arctic marine biota in response to ocean warming, but most focused on marine mammals and fish. Two of these papers focused on benthic marine algae, but not on the corallines, the group that provides the dominant benthic cover of seabed habitats in the photic zone (Adey & Hayek, 2011). Brodie *et al.* (2014) projected a significant decrease of coralline algae in the Arctic because anthropogenic carbon dioxide emissions are causing ocean acidification, which in turn results in waters in the photic zone of the Arctic becoming undersaturated with aragonite. Many coralline algae are susceptible to reductions in the concentration of aragonite as this can make seawater corrosive to their high magnesium calcite skeletons, a response that is mediated by the rate of environmental change (Kamenos *et al.*, 2013, 2016; Martin & Hall-Spencer, 2017; Chan *et al.*, 2020). Climate-change induced permafrost thawing and snow melting at high latitudes also increase freshwater runoff and coastal nutrient inputs (Walvoord & Striegl, 2007; Kendrick *et al.*, 2018), which in turn can alter calcification rates and subsequent coralline growth (McCoy & Kamenos, 2018; Bélanger & Gagnon, 2020) and photo-physiology (Schoenrock *et al.* 2018a). In this regard, Williams *et al.* (2020) observed different responses among species of *Clathromorphum* Foslíe related to their sensitivity to environmental change; thus, the widely distributed *C. compactum* (Kjellman) Foslíe might expand its northern limit whereas the narrow-range *C. nereostratum* Lebednik is expected to decline.

In Arctic and subarctic regions, *Lithothamnion* Heydrich species often dominate coralline algal

assemblages from the low intertidal to the lower limit of the photic zone, contributing significantly to shelf carbonate budgets (Freiwald & Henrich, 1994; Nelson, 2009; Adey & Hayek, 2011; Teed *et al.*, 2020). Several *Lithothamnion* species form maerl, or branched crusts, and these structures significantly increase benthic habitat complexity and biodiversity (Gagnon *et al.*, 2012; Teichert *et al.*, 2014; Jørgensbye & Halfar, 2017; Schoenrock *et al.*, 2018b). Because several *Lithothamnion* species (like most coralline algae) also induce larval settlement and metamorphosis in invertebrates with important functional roles, the genus is considered an ecosystem engineer (Steneck, 1982; Rowley, 1989; Pearce & Schiebling, 1990; Nelson, 2009).

Adey and co-workers have studied Arctic and subarctic subtidal benthic non-geniculate coralline communities for the past 50+ years, publishing on the ecology (Adey, 1964, 1965, 1966a, b, 1970a, 1971; Adey & McKibbin, 1970; Adey & Adey, 1973; Adey *et al.*, 2005), physiology (Adey, 1970a, b, 1973; Adey *et al.*, 2013, 2015a) and biogeography (Adey, 1966a, b; Adey *et al.*, 1976, 2008; Adey & Steneck, 2001) of these algae, and recently have added DNA-based taxonomic and phylogenetic studies. Thus, Arctic and Subarctic species of *Clathromorphum* (Adey *et al.*, 2015a, b), *Neopolyporolithon* W.H.Adey & H.W.Johansen (Gabrielson *et al.*, 2019) and *Phymatolithon* Foslíe (Adey *et al.*, 2018) have largely been resolved, but *Lithothamnion* species still need clarification. This is mainly due to the large number of species and infraspecific taxa named in the late 19th and early 20th century, primarily by the Norwegian corallinologist Mikael Heggelund Foslíe, but also by the Swedish phycologist Frans Reinhold Kjellman. Some of these taxa have been placed in synonymy based on morpho-anatomy, but many are still recognized (Guiry & Guiry, 2020) or are considered *incertae sedis* (Athanasiadis, 2016). Studies of other coralline genera have shown that morpho-anatomy alone cannot distinguish species (Sissini *et al.*, 2014; Peña *et al.*, 2014b, 2015a; Hernández-Kantún *et al.*, 2016; Gabrielson *et al.*, 2018). Here, we assess many of the unresolved species and infraspecific taxa of Arctic and subarctic *Lithothamnion* to provide fundamental taxonomic, ecological and biogeographic knowledge of these species in the face of the anticipated but unknown effects of climate change on the marine flora of these regions.

Materials and methods

Collections studied

Fifty-eight type specimens of *Lithothamnion* species and infraspecific taxa housed in TRH and UPS as well as 11 historical specimens in TRH (herbarium acronyms

follow Thiers, 2021) were considered for DNA analysis (Supplementary table S1, Supplementary note S1). One of us (SCL), as a guest of the Department of Botany, Stockholm University, located Kjellman's type specimens in UPS housed in a room separate from the main algal collection. This may explain why earlier investigators were unable to locate them. These specimens, described by F.R. Kjellman between 1877 and 1889, were later received on loan by PWG; specimens described by M. H. Foslie between 1891 and 1908 were examined by VP or PWG. Most of the specimens had type localities along the Norwegian coast but some were described from Svalbard, Scotland, Greenland, Canada and USA (Kjellman, 1883, 1889; Foslie, 1891, 1895, 1896, 1900; 1905a, b, 1908). In addition, 440 recent collections from Norway, Svalbard, Greenland, and the Atlantic and Pacific coasts of Canada and USA were also sequenced (Supplementary table S2). Most of these specimens were collected subtidally in coralline algal beds (maerl or rhodolith beds) or as crusts, and are preserved in NCU, TRH, SANT, UBC and UNB (see collection details in Supplementary table S2).

DNA sequencing and analyses

Herbarium material was extracted and amplified at five institutions: the Muséum National d'Histoire Naturelle, Paris (MNHN), the University of North Carolina, Chapel Hill (UNC), Hartnell College (HC), the University of British Columbia (UBC) and the University of New Brunswick (UNB). Extractions and amplifications of types and historical collections were accompanied by negative controls at every step, separate from recent collections. At the MNHN, DNA of type specimens and historical collections was extracted using QIAamp[®] DNA Micro Kit (Qiagen SAS, Les Ulis, France) following the manufacturer's protocol for tissues; DNA of recent collections was extracted using a NucleoSpin[®] 96 Tissue kit (Macherey-Nagel, GmbH and Co. KG, Germany). At UNC type material and recent collections were extracted following Gabrielson *et al.* (2011); at HC type material was extracted according to Hernández-Kantún *et al.* (2016) following the precautionary guidelines proposed by Hughey & Gabrielson (2012); at UNB recent collections were extracted following Saunders & McDevit (2012); at UBC recent collections were extracted following Lindstrom & Fredericq (2003). Three genes (*rbcL*, *psbA* and COI) were amplified in this study. For type specimens and historical collections, *rbcL* sequences were obtained with two primer combinations, F1150Cor-R1460 or F1150Cor-RbcS-Start, yielding a fragment trimmed to 263 bp (1172–1434) or 293 bp (1172–1464), respectively; for recent collections, *rbcL* sequences of 1383 bp were obtained with

overlapping primer combinations F57-R1150 and F753-RrbcS, with primer combination F753/RrbcS-Start trimmed to 691 bp (772–1464), or followed Saunders & Moore (2013) for amplifications completed at UNB. For recent collections and for some type specimens and historical collections, *psbA* sequences were obtained by the institutions mentioned above, using the primer pairs *psbA*-F1/*psbA*-R2 and *psbA*-F1/*psbA*-600R (Yoon *et al.*, 2002), following Peña *et al.* (2015b) or Adey *et al.* (2015b). COI-5P sequences were obtained only for recent collections using the primer pairs Gaz-F1/Gaz-R2 and Gaz-F1/GCorR3, following Saunders & Moore (2013) or Peña *et al.* (2015b). PCR products were purified and sequenced at MNHN by Eurofins (Eurofins Scientific, Nantes, France); at UNC according to Hughey *et al.* (2001) and sequenced at the DNA Analysis Core Facility, Center for Marine Sciences, University of North Carolina, Wilmington; and at HC by Functional Biosciences, Inc. (Madison, Wisconsin, USA). Sequences were assembled and aligned with the assistance of CodonCode Aligner[®] (CodonCode Corporation, USA) or with Sequencher (Gene Codes Corp., Ann Arbor, Wisconsin, USA) and adjusted manually using SeaView version 4 (Gouy *et al.*, 2010) or using Sequence Alignment Editor (<http://tree.bio.ed.ac.uk/software/seal/>); sequences were submitted to the Barcode of Life Data Systems (BOLD projects 'NCCAB', 'NGCOR' and dataset 'LITHOTH1', <http://www.boldsystems.org>; Ratnasingham & Hebert, 2007) and/or to GenBank (accession numbers listed in Supplementary tables S1 and S2).

DNA sequencing and analyses. Three data sets were built, one for each gene (*rbcL*, *psbA* and COI-5P), comprising ~526 sequences obtained in this study (Supplementary tables S1 and S2) and supplemented with GenBank sequences publicly available for Arctic and Subarctic collections of *Lithothamnion* as well as for other Hapalidiales genera (*Clathromorphum* and *Phymatolithon*) for which relevant matches were found (Supplementary table S3). As outgroup we used *rbcL* and *psbA* sequences linked to the genotype *Lithophyllum incrustans* Philippi, order Corallinales; for COI-5P we used a sequence generated from the neotype of *Phymatolithon calcareum* (Pallas) Adey & McKibbin, order Hapalidiales (Supplementary table S3). Phylogenetic relationships were inferred with maximum likelihood (RAxML) and Bayesian inference (BI) using Mega 6.06 (Tamura *et al.*, 2013), RAxML 8.1.11 (Stamatakis, 2014; available in CIPRES Science Gateway, Miller *et al.*, 2010) and MrBayes 3.2.1 (Ronquist & Huelsenbeck, 2003). Models of sequence evolution were estimated using the Akaike Information Criterion (AIC) and the Bayesian Information Criterion (BIC) obtained in jModeltest 2.1.3 (Darriba *et al.*, 2012). Maximum likelihood for the *rbcL*, COI-5P and

psbA alignments were performed under a generalized time-reversible with invariant sites heterogeneity model (GTR+I+G). The Bayesian analyses for the *rbcL* and *psbA* alignments were performed under the same model (GTR+I+G) with four Markov chain Monte Carlo method for 10 million generations, and tree sampling every 1000 generations.

Distribution of Arctic/subarctic *Lithothamnion* species

Geographic coordinates were obtained by GPS for each sequenced collection and were estimated for types and historical specimens using Google Earth Pro 7.3.3.7786 (© 2020 Google LLC). Distribution maps were created by projecting latitude and longitude of all specimens delimited for each species using QGIS3.10 (QGIS.org, 2020) with North Pole Lambert Azimuthal Equal Area projection. The following shape file was used for the map background: <https://www.data.gouv.fr/fr/datasets/continents/>.

Results

Of the type specimens (58) and historical collections (11) that were attempted to sequence, we successfully amplified and sequenced 62% for *rbcL* (36 types and five historical specimens) and *psbA* (5 types) (Supplementary table S1).

The *rbcL* alignment comprised 121 sequences of variable length resulting in 81 unique DNA sequences ranging from 205 to 313 bp, with 114 variable sites. Both ML and Bayesian analyses resolved the type specimens and historical collections with moderate to full support in different Hapalidiales lineages encompassing species of *Lithothamnion*, *Phymatolithon* and *Clathromorphum* (Fig. 1). Most of the type specimens and historical collections sequenced were within lineages that included the lectotype of *Lithothamnion glaciale* Kjellman (0–3 bp differences, up to 1.14% divergence (uncorrected p-distance)), the lectotype of *L. soriferum* Kjellman (0–1 bp differences, up to 0.41% divergence) and the neotype of *L. tophiforme* (0–2 bp, up to 0.68% divergence) (Fig. 1). Three type specimens were placed in the genus *Phymatolithon* (Fig. 1, Supplementary table S1): the holotype of *Lithothamnion scabriusculum* Foslie was positioned within a clade encompassing collections of *P. rugulosum* W.H.Adey (1–3 bp differences; 0.3–1% divergence); the lectotype of *L. squarrulosum* f. *palmatifidum* Foslie was resolved within a clade represented by the neotype of *P. calcareum* (2 bp differences, 0.9% divergence); the holotype of *Lithothamnion lenormandii* f. *squamulosum* (Foslie) Cotton was identical in sequence to the isotype of *P. squamulosum* (Foslie) W.H. Adey, Hernández-Kantún & P.W.Gabrielson. Another two lectotypes (*L. coalescens* Foslie and *L. evanescens* Foslie) and one historical collection of *Clathromorphum*

circumscriptum (Strömfelt) Foslie from Norway were identical in sequence to the epitype of *C. circumscriptum* (0 bp, Fig. 1); the infraspecific variation within *C. circumscriptum* ranged up to 13 bp (1.3% uncorrected p-distance) and to 14 bp (1.4%) including two further *rbcL* sequences obtained from recent Alaskan collections (UBC A92115 and UBC A94120, not included in Fig. 1). None of the types and historical collections sequenced were resolved within the lineage of *Lithothamnion lemoineae* W.H.Adey; only three recent collections (UBC A94112, Fig. 1, together with UBC A94113 and UBC A94121, as *Lithothamnion* sp., not included in Fig. 1, Supplementary table S2) appeared to be closely related to *L. lemoineae*, showing at minimum 11 bp differences (1.15% of divergence) between the taxa.

The COI-5P alignment comprised 151 sequences that included 81 unique sequences ranging from 518 to 579 bp, with 153 variable sites. The ML phylogenetic tree resolved seven fully and two moderately supported lineages (Supplementary fig. S1). Four of these lineages are represented by recent collections of *L. glaciale*, *L. tophiforme* (Esper) Unger, *L. lemoineae* and *L. erinaceum* Melbourne & J.Brodie (herein proposed as a synonym of *L. soriferum* Kjellman, see next section below). The remaining three fully supported lineages (as *Lithothamnion* sp. 2 to *L. sp. 4*) and another two moderately supported lineages (*Lithothamnion* sp.1, *L. sp. 5*) corresponded to recent collections pertaining to five *Lithothamnion* species that did not return any relevant match with publicly available GenBank sequences (Supplementary fig. S1, Supplementary tables S2 and S3). The highest intra-lineage variation (uncorrected p-distance) was recorded in *L. glaciale* (up to 2.07%).

The *psbA* alignment comprised 421 sequences that resulted in 124 unique sequences, ranging from 382 to 851 bp with 249 variable sites. The alignment encompassed recent collections, five type collections generated in the present study and publicly available sequences from GenBank such as the holotypes of *L. erinaceum* and *L. lemoineae*, and the isotype of *P. rugulosum* (herein as *P. scabriusculum*, see next section of taxonomic proposals) (Supplementary tables S1–S3). Both RAxML and Bayesian analyses (Supplementary fig. S2) resolved our recent collections in different lineages pertaining to the genera *Clathromorphum* (*C. circumscriptum*), *Phymatolithon* (*P. squamulosum*) and *Lithothamnion* (*L. lemoineae*, *L. tophiforme*, *L. glaciale* and *L. erinaceum* (herein as *L. soriferum*, see next paragraph of taxonomic proposals)). In agreement with results obtained for *rbcL*, both RAxML and Bayesian analyses of *psbA* resolved these type collections in three different genera (Supplementary fig. S2): *Lithothamnion* (neotype of *L. glaciale* f. *subsimpler* Foslie), *Clathromorphum* (lectotypes of *L. coalescens* and *L. evanescens*) and *Phymatolithon* (holotype of *L. lenormandii* f. *squamulosa* and lectotype of

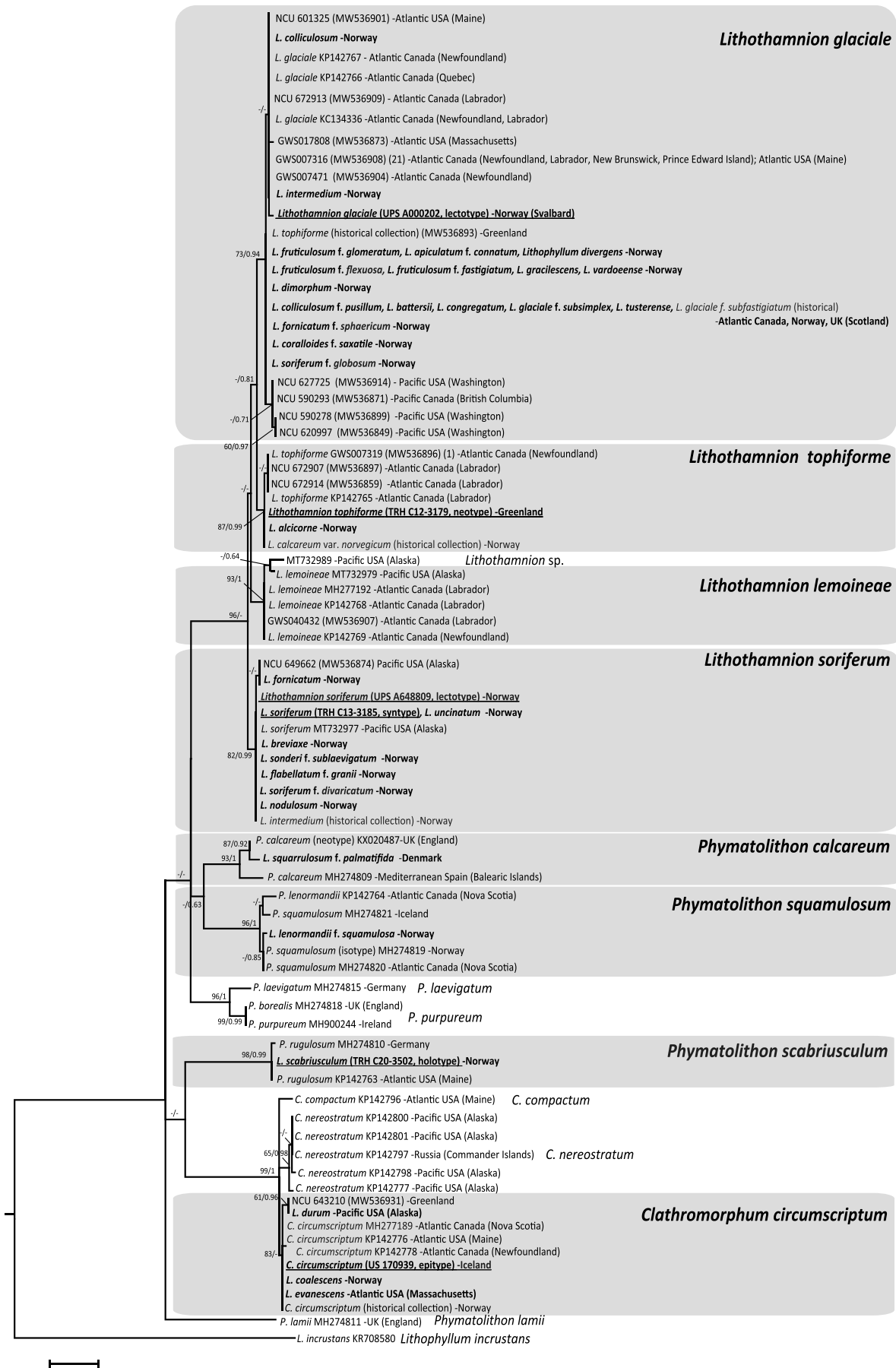


Fig. 1. Phylogenetic tree inferred from maximum likelihood (ML) analyses of *rbcL* sequences included in the present study. Bold formatted font represent sequences generated from type materials. Bootstrap ML values > 60% and posterior probabilities > 0.60 from Bayesian inference shown for each node. Scale bar: 0.05 substitutions per site.

L. squarulosum f. *palmatifida*). However, one recent collection (as *Lithothamnion* sp., Supplementary fig. S2, Supplementary table S2) had a sequence distinct from all other analysed taxa, with no relevant match with publicly available GenBank sequences. In contrast to *rbcL* and COI analyses, the support values obtained were generally lower, particularly for *L. glaciale* with weak support (Supplementary fig. S2).

Given the molecular evidence noted above, and in accordance with Article 11.4 of the International Code of Nomenclature for algae, fungi and plants (ICN, Turland et al., 2018), we present the following taxa with the corresponding heterotypic synonyms from the present study. Note that for each taxon below where it is stated "...the lectotype is narrowed..." we are invoking Article 9.17 of the ICN (Turland et al. 2018).

***Clathromorphum circumscriptum* (Strömfelt) Foslie, 1898a: 5**

BASIONYM: *Lithothamnion circumscriptum* Strömfelt, 1886: 20, pl. 1, figs 4–8.

HOMOTYPIC SYNONYMS:

Phymatolithon compactum f. *circumscriptum* (Strömfelt) Foslie, 1905a: 88.

Clathromorphum compactum f. *circumscriptum* (Strömfelt) Foslie, 1908: 11.

Lithothamnion compactum f. *circumscriptum* (Strömfelt) Lund, 1959: 200.

LECTOTYPE: S; seven microscope slides apparently from the original material designated by Athanasiadis (2016: 251) as the holotype, but as Strömfelt (1886) designated syntype localities, this material is better called a lectotype. This is a correctible error in accordance with Art. 9.10 of the ICN (Turland et al., 2018). *Comment*: Adey et al. (2015b), while designating an epitype for *C. circumscriptum*, inadvertently omitted submitting this epitype sequence to GenBank. This has now been rectified: GenBank MW536846, an *rbcL*-263 (bp 1172–1434) sequence.

HETEROTYPIC SYNONYMS:

***Lithothamnion coalescens* Foslie, 1895: 162 (reprint 134), pl. 19, figs. 15–20.**

***Clathromorphum coalescens* (Foslie) Foslie, 1898b: 8. *Phymatolithon compactum* f. *coalescens* (Foslie) Foslie, 1905a: 8.**

LECTOTYPE: TRH C21-3503; 12.viii.1893, leg. unknown.

TYPE LOCALITY: Inderøen, Strømmen, Trondheimsfjorden, Norway.

Lectotype DNA sequences: *psbA* and *rbcL*-263 (bp 1172–1434), GenBank MW564561 and MW536929.

Comment: Following his description, Foslie (1895) transferred the species without comment to *Clathromorphum* (Foslie, 1898b). Later, Foslie

(1905a) reduced *Clathromorphum* to a subgenus of *Phymatolithon* and reduced *C. coalescens* to a form of *Phymatolithon*, as *P. compactum* f. *coalescens*. This name was not treated by Lebednik (1977) nor by Adey et al. (2015b), but was listed by Athanasiadis (2016) as a synonym of *C. compactum* (Kjellman) Foslie. According to Woelkerling et al. (2005), the lectotype of *L. coalescens* is a blue box with five specimens designated by Woelkerling (1993: 52) as the lectotype, noting that Foslie (1895: 163) had cited two syntype localities. Upon examination, the box contained four specimens illustrated in Foslie (1895: pl. 19, figs 15–20), one of which was sequenced, and herein the lectotype is narrowed to that sequenced specimen (GenBank MW564561 and MW536929). Both the *rbcL* and *psbA* sequences obtained are identical to GenBank sequences of *C. circumscriptum* (voucher US 169083), which were confirmed as identical to the epitype (voucher US 170939, Adey et al., 2015a, b: 195).

Lithothamnion durum Kjellman, 1889: 22, pl. 1, figs 3–5.

Clathromorphum durum (Kjellman) Foslie, 1898b: 8.

HOLOTYPE: UPS A-000297, vii.1877, leg. F. R. Kjellman.

TYPE LOCALITY: Port Clarence, Alaska, USA.

Holotype DNA sequence: The *rbcL*-263 (bp 1172–1434) sequence was obtained from the holotype specimen, and over this sequence length differed by 1 bp from the epitype of *Clathromorphum circumscriptum*. This position is variable in *C. circumscriptum*, with specimens from Iceland, Labrador, Newfoundland and Maine sharing the same single nucleotide polymorphism (SNP) and likewise those from Greenland and Alaska (Port Clarence and Juneau) sharing the same SNP.

Comment: This synonymy was first proposed by Foslie (1900: 10) and accepted by Lebednik (1977: 64), who noted that a fragment, apparently from the holotype, was in TRH. This fragment is now considered an isotype (Art. 8.3, Turland et al. 2018). The holotype illustrated by Kjellman (1889: pl. 1, fig. 3), was found in UPS and the DNA sequence was obtained from the specimen labelled 'b' (Kjellman, 1889: pl. 1, fig. 3). We did not sequence the fragment in TRH.

Lithothamnion evanescens Foslie, 1895: 137.

Clathromorphum evanescens (Foslie) Foslie, 1898b: 8.

Phymatolithon evanescens (Foslie) Foslie, 1905a: 92.

LECTOTYPE: TRH C21-3518, iv.1889, leg. F.S. Collins.

TYPE LOCALITY: Marblehead, Massachusetts, USA.

Lectotype DNA sequences: *psbA* and *rbcL*-263 (bp 1172–1434), GenBank MW564560 and MW536911.

Comment: Foslie (1895: 137, pl. 22, figs 6, 7) cited and illustrated specimens from two syntype localities,

Marblehead, Massachusetts, USA collected by F. S. Collins and from Mastervik, Malangen, Norway collected by himself. Foslie transferred the species twice, first, without comment, to *Clathromorphum* (Foslie 1898b), and later to *Phymatolithon* after admitting that *Clathromorphum* should be considered a subgenus of the latter (Foslie, 1905a: 87). Lebednik (1977) first proposed that this species was a synonym of *C. circumscriptum*, and this was accepted by Athanasiadis (2016). Woelkerling (1993: 87) designated as lectotype a single specimen collected by Collins in Marblehead, Massachusetts and illustrated by both Foslie (1895: pl. 22, fig 6) and Printz (1929: pl. 41, fig. 13). Woelkerling (1993) justified the selection of this specimen as lectotype because 'it was in better condition and had numerous conceptacles'. Both *rbcL* and *psbA* sequences obtained for this lectotype specimen are identical to GenBank sequences of *C. circumscriptum* (voucher US 169083), which was confirmed as identical to the epitype (voucher US 170939, Adey *et al.*, 2015b: 195).

Historical collection:

TRH C20-3495, as *Lithothamnion circumscriptum*. Tamsøya, Finnmark, Norway, 31.vii.1897, no habitat data, leg. M. H. Foslie. DNA sequence: *rbcL*-263 (bp 1172–1434), GenBank MW536916 (Supplementary table S1). The largest fragment of the four in the box was sequenced.

Recent collections:

Norway: Porsangerfjorden (Finnmark) and Krøttøya (Troms). Intertidal to subtidal (6 m depth), encrusting pebbles and pottery, on hard substrata and associated with maerl beds. One specimen collected in Krøttøya had uniporate conceptacles (gametangial or carposporangial). DNA sequences: *psbA* (Supplementary table S2).

Lithothamnion glaciale Kjellman, 1883: 123–127, pls 2, 3.

LECTOTYPE, herein designated: UPS A-000202, xi-xii.1872, leg. F. R. Kjellman.

TYPE LOCALITY: Mosselbay, Spitsbergen.

Lectotype DNA sequence: *rbcL*-263 (bp 1172–1434), GenBank MW536933.

Comment: Adey (1970a) made a provisional lectotypification based on 'a Spitzbergen specimen (No. 241, Institute of Taxonomy, Uppsala) collected by Kjellman in 1872–1873'. Adey (1970a) further stated that this specimen was not one illustrated by Kjellman (1883) that accompanied the original description. The ICN does not accept provisional lectotypes (Art. 7.11, Turland *et al.* 2018). Chamberlain & Irvine (1994) repeated Adey's

(1970a) lectotypification, thus making it acceptable, but stated that they did not see the specimen.

Among Kjellman's type collections was the single individual rhodolith of *L. glaciale* illustrated by Kjellman (1883: pls 2, 3), with some artistic licence (Supplementary fig. S3A), along with a collection label stating the type locality of Mosselbay on the island of Spetsbergen (Spitzbergen) and dated November and December 1872, collected while the expedition aboard the Polhem was iced in until August 1873 (Wynne, 1995). We here designate this specimen from which we obtained a partial *rbcL* sequence as the lectotype of *L. glaciale*. All other sequences of *L. glaciale* differ by 1 bp from the lectotype sequence, including all the type sequences of synonyms listed below.

Lectotype SEM observations: A cross-section through a protuberance showed radial construction and a buried conceptacle (Supplementary fig. S3B). Thallus construction was monomerous with elongate hypothallial cells (Supplementary fig. S3C–D). Abundant fusions linked cells from adjacent perithallial filaments (Supplementary fig. S3E) and secondary pit connections were absent. The epithallus was single layered and epithallial cells were flared; intercalary meristematic cells (subepithallial initials) were shorter or about the same length as subtending perithallial cells (Supplementary fig. S3F).

HETEROTYPIC SYNONYMS:

Lithothamnion apiculatum f. *connatum* Foslie, 1895: 54, pl. 15, figs 9–13 (as 'connata').

LECTOTYPE: TRH B20-2669, 12.vii.1893, no habitat data, leg. H.H. Gran.

TYPE LOCALITY: Drøbak, Norway.

Lectotype DNA sequence: *rbcL*-293 (bp 1172–1464), GenBank MW536892.

Comment: Woelkerling (1993) located four of five specimens as part of the protologue of *L. apiculatum* f. *connatum* and designated these as lectotype. They were illustrated by Foslie (1895: pl. 15, figs 9–12) and by Printz (1929: pl. 21, figs 11–15) under the name *L. colliculosum* f. *pusilla*. One of these four specimens, branched and epilithic on a pebble (among the specimens illustrated as figs 9–11, Foslie 1895: pl. 15) was sequenced, and herein this lectotype is narrowed to that specimen.

Lithothamnion battersii Foslie, 1896: 1, pl. 1, figs 1–5.

HOLOTYPE: TRH C10-3098, viii.1891, leg. E. Batters.

TYPE LOCALITY: Cumbrae, Scotland.

Holotype DNA sequence: *rbcL*-293 (bp 1172–1464), GenBank MW536898.

Comment: The holotype collection comprises five individuals illustrated by Foslie (1896: pl. 1, figs 1–5); the

specimen sequenced is depicted in Foslie's (1896) fig. 2. Based on morpho-anatomy, Chamberlain & Irvine (1994: 182) and Athanasiadis (2016: 217) correctly listed *L. battersii* as a synonym of *L. glaciale*.

Lithothamnion colliculosum Foslie, 1891: 43, pl. 3, fig. 1. LECTOTYPE: TRH B11-2311, 8.ix.1890, leg. M. H. Foslie (designated by Woelkerling, 1993: 53). TYPE LOCALITY: Skorpen, Kvænangen, Norway. *Lectotype DNA sequence*: *rbcL*-293 (bp 1172–1464), GenBank MW536855.

Comment: Foslie (1891: 43–45, pl. 3, fig. 1) described and illustrated eight individual specimens that he ascribed to this species. Adey & Lebednik (1967: 71) could not locate any of these specimens, and therefore Adey (1970c) designated as neotype one specimen from Kragerø collected in 1890. Later, Woelkerling (1993: 54) located in TRH numerous specimens with the original collection data of *L. colliculosum*, including four of the eight individuals comprising the holotype and depicted by Foslie (1891, pl. 3, fig. 1). Because the other four individuals comprising the holotype remain missing, Woelkerling designated the found specimens as the lectotype of *L. colliculosum*, superseding Adey's neotype. The lectotype is narrowed herein to the individual sequenced crust among the original specimens depicted by Foslie (1891: pl. 3, fig. 1, bottom row, second from right). Based on morpho-anatomy, Athanasiadis (2016: 224) listed *L. colliculosum* as *incertae sedis*; DNA sequence data has confirmed the placement of the species in *L. glaciale*.

Lithothamnion colliculosum f. *pusillum* Foslie, 1905a: 35 (as '*pusilla*').

LECTOTYPE: TRH B20-2706, 12.vii.1898, leg. H. H. Gran (designated by Woelkerling 1993: 185).

TYPE LOCALITY: Drøbak, Norway.

Lectotype DNA sequence: *rbcL*-293 (bp 1172–1464), GenBank MW536921.

Comment: We sequenced one of the 14 specimens comprising the lectotype, which is located separately within a blue box with label 'Prep. 76-77'. The lectotype is narrowed herein to the sequenced specimen. Based on morpho-anatomy, Athanasiadis (2016: 224) listed *L. colliculosum* f. *pusillum* as *incertae sedis*; DNA sequence data has confirmed the placement of the species in *L. glaciale*.

Lithothamnion congregatum Foslie, 1895: 142, pl. 20, figs 1–6.

HOMOTYPIC SYNONYM: *Lithothamnion nodulosum* f. *congregatum* (Foslie) Foslie, 1900: 13.

LECTOTYPE: TRH C7-3062, 20.vii.1894, leg. M. H. Foslie (designated by Woelkerling, 1993: 60–61).

TYPE LOCALITY: Skjørn (now Stjørna), Trondheimsfjord, Norway (Woelkerling *et al.*, 2005: 424).

Lectotype DNA sequence: *rbcL*-293 (bp 1172–1464), GenBank MW536865.

Comment: Foslie (1895: 142–144, pl. 20, figs 1–6) described and illustrated this species based on six individuals from a single locality, and compared it with two other species named in the same publication, *L. dehiscens* Foslie and *L. nodulosum* Foslie. Later, Foslie (1900) reduced *L. congregatum* to a form of *L. nodulosum*. The sequenced specimen is illustrated in Foslie (1895: pl. 20, fig. 2), and the lectotype is here narrowed to that sequenced specimen. Based on morpho-anatomy Athanasiadis (2016: 224) listed *L. congregatum* as *incertae sedis*; DNA sequence data has confirmed the placement of the species in *L. glaciale*.

Lithothamnion corallioides f. *saxatile* Foslie, 1895: 90, pl. 16, figs 12–23 (as '*saxatilis*').

LECTOTYPE: TRH C9-3097, 1.viii.1894, leg. M. H. Foslie (designated by Woelkerling, 1993: 195).

TYPE LOCALITY: Røberg (now Raudberget), Norway (Woelkerling *et al.*, 2005: 413).

Lectotype DNA sequence: *rbcL*-293 (bp 1172–1464), GenBank MW536900.

Comment: Woelkerling (1993: 195–196) located and designated as the lectotype four of the original 12 specimens included by Foslie (1895: pl. 16, figs 14–17) in the original protologue of this form. The specimen sequenced had a green label 'Prep. 100-101'; it resembled the specimen illustrated in Foslie (1895: pl. 16, fig. 16). The lectotype is here narrowed herein to this single sequenced specimen.

Lithothamnion dimorphum Foslie, 1895: 68, pl. 10, figs 1–6.

HOMOTYPIC SYNONYM: *Lithothamnion fornicatum* f. *dimorphum* (Foslie) Foslie, 1905a: 38.

LECTOTYPE: TRH B25-2773, 10.vii.1894, 0–5.5 m depth on sandy and stony bottom, leg. M. H. Foslie (designated by Woelkerling, 1993: 75).

TYPE LOCALITY: Frøjen (now Frøya), Rottingsundet, Trondeland, Norway (Woelkerling *et al.*, 2005: 375).

Lectotype DNA sequence: *rbcL*-293 (bp 1172–1464), GenBank MW536934.

Comment: Foslie (1895: pl. 10, figs 1–6) illustrated six specimens belonging to this species, but did not designate a holotype. Woelkerling (1993: 74–75) designated as the lectotype four of the six specimens depicted in figs 1, 3, 5 and 6 (Foslie, 1895: pl. 10). The lectotype is narrowed herein to the Foslie 1895: pl. 10, fig. 3 specimen that we sequenced. Based on morpho-anatomy, Athanasiadis (2016: 225) listed *L. dimorphum* as *incertae sedis*; DNA sequence data have placement of the species in *L. glaciale*.

Lithothamnion divergens Foslie, 1895: 96, pl. 16, figs 43–50.

HOMOTYPIC SYNONYMS: *Lithothamnion ungeri* f. *divergens* (Foslie) Foslie, 1900: 11; *Lithothamnion tophiforme* f. *divergens* (Foslie) Foslie, 1905a: 51.

HOLOTYPE: C11-3167, 8.ix.1890, leg. M. H. Foslie.

TYPE LOCALITY: Kvaenangen, Skørpen (now Skorpa), Norway (Woelkerling *et al.*, 2005: 438).

Holotype DNA sequence: *rbcL*-293 (bp 1172–1464), GenBank MW536922.

Comment: The holotype material comprised two boxes (one round and one square) with seven specimens and fragments (Woelkerling, 1993: 80; Woelkerling *et al.*, 2005: 438). The sequenced specimen is located in the round box with the green tag 'Lith. Mon. pl. 20, f. 8' and illustrated in Foslie (1895: pl. 16, fig. 48) and Printz (1929: pl. 20, fig. 8). Based on morpho-anatomy, Athanasiadis (2016: 226) listed *L. divergens* as *incertae sedis*; DNA sequence data confirm the placement of the species in *L. glaciale*.

Lithothamnion fornicatum f. *sphaericum* Foslie, 1900: 12 (as '*sphaerica*').

HOLOTYPE: TRH B26-2789, 20.vii.1894, no habitat data, leg. M. H. Foslie.

TYPE LOCALITY: Skjørn, Dalsøren (now Stjørna, Daleøra), Trondheimsfjorden, Norway (Woelkerling *et al.*, 2005: 380).

Holotype DNA sequence: *rbcL*-293 (bp 1172–1464), GenBank MW536918.

Comment: Foslie (1900) only provided a reference to a previously published figure (Foslie 1895: pl. 12, fig. 1) for the protologue of this form, but Woelkerling (1993: 205) considered this a validly published name. We sequenced the same individual rhodolith cited by Foslie (1900) and illustrated in Foslie (1895: pl. 12, fig. 1).

Lithothamnion fruticosum f. *fastigiatum* Foslie, 1895: 46, pl. 5.

LECTOTYPE: TRH B25-2777, 6.vii.1894, leg. M. H. Foslie (designated by Woelkerling, 1993: 91).

TYPE LOCALITY: Bejan (now Beian), Beiskjaeret, Norway (Woelkerling *et al.*, 2005: 377).

Lectotype DNA sequence: *rbcL*-293 (bp 1172–1464), GenBank MW536847.

Comment: Foslie (1895: pl. 5, figs 1–7) illustrated seven individual rhodoliths that according to Woelkerling (1993) came from two collections from neighbouring localities on successive days. Woelkerling (1993: 91) designated as the lectotype collection nine specimens comprising two of those illustrated in the protologue (Foslie, 1895: pl. 5, figs 5 and 7) and seven other specimens. The lectotype is narrowed herein to the sequenced specimen that is

marked with label 'nr. 2', which is cited as part of the lectotype in Woelkerling *et al.* (2005: 377).

Lithothamnion fruticosum f. *flexuosa* Foslie, 1895: pl. 7, figs 1–3.

LECTOTYPE: TRH B27-2805, 15.viii.1890, leg. M. H. Foslie (designated by Woelkerling, 1993: 95).

TYPE LOCALITY: Tromsø, Norway.

Lectotype DNA sequence: *rbcL*-293 (bp 1172–1464), GenBank MW536923.

Comment: Foslie (1895) based this form on collections from several localities in Norway, but did not designate a type. Woelkerling (1993) designated the specimen illustrated by Foslie (1895: pl. 7, fig. 3) as the lectotype of this form. According to Woelkerling *et al.* (2005), the lectotype has two green tags, and this was the specimen from which the DNA sequence was obtained.

Lithothamnion fruticosum f. *glomeratum* Foslie, 1895: 46, pl. 4, fig. 3 (as '*glomerata*').

LECTOTYPE: TRH B8-2153, 12.vi.1892, leg. unknown (designated by Printz, 1929: pl. 22, fig. 5 legend).

TYPE LOCALITY: Lyngø (now Lyngøya), near Tromsø, Norway (designated by Woelkerling, 1993: 108, further information in Woelkerling *et al.* 2005: 288).

Lectotype DNA sequence: *rbcL*-293 (bp 1172–1464), GenBank MW536882.

Comment: Foslie (1895) cited specimens from two localities in Norway, Lyngø and Vardø, but did not designate a type. Printz (1929) designated as lectotype the one rhodolith illustrated by Foslie (1895: 46, pl. 4, fig. 3) and this is the specimen sequenced in the current study.

Lithothamnion gracilescens Foslie, 1895: 87, pl. 15, figs 20–27, *nom. illeg.*

HOMOTYPIC SYNONYM: *Lithothamnion nodulosum* f. *gracilescens* Foslie, 1900: 13, *nom. illeg.*

LECTOTYPE: TRH C6-3037, 6.vi.1894, leg. M. H. Foslie (designated by Woelkerling, 1993: 109; further information in Woelkerling *et al.*, 2005: 419).

TYPE LOCALITY: Rotvold (now Rotvoll), Trondheimsfjord, Norway (Woelkerling *et al.*, 2005: 419).

Lectotype DNA sequence: *rbcL*-293 (bp 1172–1464), GenBank MW536881.

Comment: Foslie (1895) proposed *Lithothamnion gracilescens* for the coralline that Unger (1858: 19) had called *Lithothamnion byssoides*, but Kjellman (1883: 120) already had named this entity *Lithothamnion ungeri*. Foslie (1895: 90) listed three syntype localities, Madal, Dröbak and Rotvold, and from the last location illustrated eight individuals (Foslie 1895: pl. 15, figs 20–27). Later, Foslie (1900) without comment reduced *L. gracilescens* to a form of *L. nodulosum* as *L. nodulosum* f. *gracilescens*. The specimen sequenced

corresponds to Foslie (1895: pl. 15, fig. 24), to which the lectotype is narrowed as allowed. Based on morpho-anatomy Athanasiadis (2016: 228) listed *L. gracilescens* as *incertae sedis*; DNA sequence data have confirmed the placement of the species in *L. glaciale*.

Lithothamnion intermedium Kjellman, 1883: 127, pl. 4, figs 1–10.

HOMOTYPIC SYNONYMS: *Lithothamnion fruticulosum* f. *intermedium* (Kjellman) Foslie, 1895: 46; *Lithothamnion ungeri* f. *intermedium* (Kjellman) Foslie, 1898b: 5.

LECTOTYPE herein designated: UPS A648805, vi.1875, leg. F.R.Kjellman.

TYPE LOCALITY: Carlsö (now Karlsøy), Tromsø, Norway.

Lectotype DNA sequence: rbcL-263 (bp 1172–1434), GenBank MW536854.

Comment: Kjellman (1883) did not designate a type specimen for his new species. In UPS there appears to be only one individual rhodolith with a label in Kjellman's hand and with the specific locality of Karlsøy cited in the protologue of *L. intermedium*, although two individuals are illustrated by Kjellman (1883: pl. 4, figs 1, 2). Thus, we designate UPS A648805 as the lectotype.

Lithothamnion soriferum f. *globosum* Foslie, 1891: 41, pl. 3, fig. 3 (as 'globosa').

LECTOTYPE: C11-3142, 20.vi.1882, no habitat data, leg. M. H. Foslie (designated by Woelkerling, 1993: 107).

TYPE LOCALITY: Honningsvaag (now Honningsvåg), Finnmark, Norway (Woelkerling *et al.*, 2005: 434).

Lectotype DNA sequence: rbcL-293 (bp 1172–1464), GenBank MW536925.

Comment: Woelkerling (1993: 107) located two of the four specimens illustrated by Foslie (1891: pl. 3, fig. 3). The specimen sequenced is illustrated in Foslie (1891: pl. 3, fig. 3, second specimen from the left), and it is this specimen to which the lectotype is narrowed herein. Athanasiadis (2016: 234) lists as *incertae sedis*; DNA sequence data have confirmed the placement of the species in *L. glaciale*.

Lithothamnion tusterense Foslie, 1905a: 65.

HOLOTYPE: TRH C9-3089, 10.viii.1898, leg. M. H. Foslie.

TYPE LOCALITY: Tusteren (now Tustna), Kristiansund, Norway (Woelkerling *et al.*, 2005: 428).

Holotype DNA sequence: rbcL-293 (bp 1172–1464), GenBank MW536924.

Comment: Woelkerling (1993: 229) considered the material in the Foslie herbarium illustrated by Printz (1929: pl. 22, figs 6–13) to be the holotype, and we agree. The specimen sequenced is marked

with a green tag 'pl. 27, fig. 9', but the specimen corresponds to the plate 22, fig. 9 in Printz (1929), as was noted by Woelkerling *et al.* (2005: 428). Based on morpho-anatomy, Athanasiadis (2016: 235) listed *L. tusterense* as *incertae sedis*; DNA sequence data have confirmed the placement of the species in *L. glaciale*.

Lithothamnion vardoeense Foslie, 1905b: 3 (as *vardöense*).

LECTOTYPE: TRH C8-3077, 6.ix.1897, leg. M. H. Foslie. Woelkerling (1993: 233) designated as lectotype the specimens illustrated by Printz (1929: pl. 33, figs 12, 13, 15).

TYPE LOCALITY: Svolvær, Lofoten, Norway.

Lectotype DNA sequence: rbcL-293 (bp 1172–1464), GenBank MW536872.

Comment: Foslie (1905b) based this species on two collections, one dead, excavated from Vardø, Norway, the other living from Lofoten, Svolvær, Norway. Adey & Lebednik (1967: 77) examined material in TRH under this name, but did not designate a lectotype; this was done by Woelkerling (1993: 233). The specimen sequenced corresponds to the one depicted in Printz (1929: pl. 32, fig. 12), and the lectotype is narrowed herein to this specimen. Based on morpho-anatomy, Athanasiadis (2016: 223) listed *L. vardoeense* as *incertae sedis*; DNA sequence data have confirmed the placement of the species in *L. glaciale*.

Historical collections

TRH C12-3177, as *Lithothamnion tophiforme*. Sukkertoppen, Greenland, no date, leg. Petersen. DNA sequence: rbcL-263 (bp 1172–1434), GenBank MW536893.

TRH B10-2305, as *Lithothamnion glaciale* f. *subfastigiatum* (as 'subfastigiata'). Bekkarfjord, Alten (now Alta), Norway, 21.viii.1897, leg. M. H. Foslie. DNA sequence: rbcL-293 (bp 1172–1464), GenBank MW536930.

Comment: The largest fragment in the collection was sequenced. The sequence was identical to the lectotype sequence of *Lithothamnion colliculosum* f. *pusillum*, shown herein as a heterotypic synonym of *L. glaciale*. *L. glaciale* f. *subfastigiatum* is considered a superfluous substitute name for *Lithothamnion varians* f. *variens* Foslie (Woelkerling *et al.*, 2005: 306); the lectotype of *L. varians* f. *variens* (TRH C23-3649) was DNA-extracted but failed to amplify (see Supplementary note S1).

Intraspecific taxa of *Lithothamnion glaciale* confirmed as *L. glaciale*.

Lithothamnion glaciale f. *subsimplex* Foslie, 1905a: 27. NEOTYPE: TRH B9-2255, 22.vi.1900, leg. E. Bay. Woelkerling (1993: 215) designated as neotype the specimen illustrated by Printz (1929: pl. 23, fig. 5).

TYPE LOCALITY: The southern coast of Ellesmereland, Havnefjorden; Northwest Territories, Canada (Woelkerling, 1993: 215; Woelkerling *et al.*, 2005: 300).

Neotype DNA sequences: *psbA* and *rbcL*-263 (bp 1172–1434), GenBank MW56455 and MW536844.

Comment: Athanasiadis (2016) listed this taxon as a synonym of *L. glaciale*, but with a query (?); DNA sequence data have confirmed this synonymy. The neotype sequence was identical to the lectotype sequence of *Lithothamnion colliculosum* f. *pusillum*, shown herein as a heterotypic synonym of *L. glaciale*.

***Lithothamnion soriferum* Kjellman, 1883: 117, pl. 1, figs 1–19.**

LECTOTYPE: herein designated, UPS A648809, viii.1876, leg. F. R. Kjellman.

TYPE LOCALITY: Maasö (now Måsøy), Finnmark, Norway.

Lectotype DNA sequence: *rbcL*-263 (bp 1172–1434), GenBank MW536886.

Comment: Kjellman (1883) did not designate a type specimen for his new species. As with *L. glaciale*, one of us (SCL) located in UPS type material of *L. soriferum* that agrees, with some artistic licence, to the three entire specimens illustrated by Kjellman (1883: pl. 1, figs 1–4). In the figure legends, Kjellman refers to the fig. 1 specimen as young (ungt), the fig. 2 specimen as older (äldre) and seen from above (ofvanifrån), the fig. 3 specimen, the same (samma) specimen (as in fig. 2) seen from below (underifrån), and the fig. 4 specimen as full grown (fullvuxet). An *rbcL*-263 sequence was obtained from each of these specimens, and the sequences are identical to each other. Kjellman (1883: 120) listed six syntype localities, Tromsö, Carlsö, Maasö, Magerö, Honningsvaag and Lebesby, the last two localities based on specimens sent to Kjellman by Foslie; the syntype corresponding to the latter locality – Lebesby – was also sequenced (TRH C13-3185, see below). The three specimens in UPS were found in a single envelope (Supplementary fig. S4A) with the locality ‘Norway. Finnmark: Hammerfest, Måsö (Måsöya)’. Following Article 9.3 (Turland *et al.*, 2018) we herein designate these three specimens as the lectotype of *L. soriferum*. The identical *rbcL*-263 sequences of all three UPS specimens are an exact match to GenBank sequences of the recently described *Lithothamnion erinaceum* (Melbourne *et al.*, 2017). Following Article 11.4 of the ICN (Turland *et al.*, 2018), the correct name is the combination of the final epithet of the earliest legitimate name of the taxon at the same rank. Consequently, *L. soriferum* has nomenclatural priority over *L. erinaceum*, and it is the correct name for this taxon. Further information about the heterotypic synonym *L. erinaceum* is in the entry below.

SYNTYPE: TRH C13-3185, 2.viii.1882, leg. M. H. Foslie (identified by Kjellman, Woelkerling *et al.*, 2005: 440).

TYPE LOCALITY: Lebesby, Finmarken (now Finnmark), Norway (Woelkerling *et al.*, 2005: 441).

Syntype DNA sequence: *rbcL*-263 (bp 1172–1434), GenBank MW536919.

Comment: The specimen sequenced is the one that according to Woelkerling *et al.* (2005: 441) is illustrated in Foslie (1891: pl. 3, fig. 3, as *Lithothamnion soriferum* f. *globosa*).

Lectotype SEM observations: A vertical section through a protuberance showed the radial construction (Supplementary fig. S4B–D) and an extensive perithallus. Thallus construction was monomerous with elongate hypothallial cells (Supplementary fig. S4E). Fusions occurred between cells of adjacent perithallial filaments (Supplementary fig. S4F), and secondary pit connections were absent. There was a single layer of epithallial cells, and each epithallial cell had flared walls (Supplementary fig. S4F–H). A single layer of intercalary meristematic cells (subepithallial initials) was composed of cells shorter than or as long as subtending perithallial cells (Supplementary fig. S4F–H).

HETEROTYPIC SYNONYMS:

Lithothamnion brevixae Foslie, 1895: 44, pl. 2, figs 1–2.

LECTOTYPE: TRH B12-2327, 3.viii.1887, leg. M. H. Foslie (designated by Adey & Lebednik 1967: 63).

TYPE LOCALITY: Kjelmø (now Sør-Varanger, Kjelmøya), Sydvaranger, Finnmark, Norway (Woelkerling *et al.* 2005: 310).

Lectotype DNA sequence: *rbcL*-293 (bp 1172–1464), GenBank MW536888.

Comment: Foslie (1895: 44, pl. 2, figs 1–2) described this species based on several specimens collected at one locality (Kjelmø, Norway), but illustrated only two. We obtained an *rbcL* sequence from the designated lectotype (Foslie 1895: pl. 2, fig. 1) and it was identical to the lectotype sequence of *L. soriferum*. Based on morpho-anatomy, Athanasiadis (2016: 223) listed *L. brevixae* as *incertae sedis*; DNA sequence data have confirmed the placement of the species in synonymy with *L. soriferum*.

Lithothamnion erinaceum Melbourne & J.Brodie in Melbourne *et al.*, 2017: 7, figs 3, 7–9, 11.

HOLOTYPE: BM 001150576, 13.x.2014, leg. A. Mogg.

TYPE LOCALITY: Loch Creran, Oban, Scotland (Melbourne *et al.*, 2017).

Holotype DNA sequences: GenBank KX828452 (*psbA*) and KX828509 (COI-5P) (Melbourne *et al.*, 2017); GenBank MH697546 and MH697547 (*rbcL*, Hofmann & Heesch, 2018).

Comment: According to Melbourne *et al.* (2017), collections from Northern Ireland, Iceland, Norway and

British Columbia provided in Pardo *et al.* (2014) as *Lithothamnion* sp. 2 corresponded to *L. erinaceum*. Based on DNA sequences, these collections are also assigned to *L. soriferum*, as well as the remaining specimens from the UK identified as *Lithothamnion* sp. in Melbourne *et al.* (2017, table S1). Additionally, GenBank records from Norway identified as *L. erinaceum* (specimens 'NCCA' in Supplementary table S3) correspond to *L. soriferum* (Anglés d'Auriac *et al.*, 2019).

Lithothamnion fornicatum Foslie, 1891: 38, pl. 2 (bottom specimen).

LECTOTYPE: TRH B21-2712, 20.ix.1890, leg. unknown (designated by Adey & Lebednik, 1967: 71). TYPE LOCALITY: Melangen (now Malangen), Mestervik, Tromsø county, Norway (Woelkerling *et al.*, 2005: 366).

Lectotype DNA sequence: *rbcL*-293 (bp 1172–1464), GenBank MW536912.

Comment: Foslie (1891) described and illustrated three specimens from the same locality. Adey (1970c) noted that the lectotype, designated by Adey & Lebednik (1967: 71), comprised two sets of specimens and that the selected set had a specimen pictured in the original description, but Adey (1970c) did not indicate which of the three originally pictured specimens is the designated lectotype. Woelkerling (1993: 97) and Woelkerling *et al.* (2005: 366) provided information about the lectotype specimen illustrated in Foslie (1891: pl. 2, bottom specimen) and marked with green tag 'Præp. 151'. Based on morpho-anatomy, Athanasiadis (2016: 228) listed *L. fornicatum* as *incertae sedis*; DNA sequence data have confirmed the placement of the species in synonymy with *L. soriferum*.

Lithothamnion granii (Foslie) Foslie, 1900: 11.

BASIONYM: *Lithothamnion flabellatum* f. *granii* Foslie, 1895: 98, pl. 17, figs 1–7, pl. 22, fig. 1.

HOMOTYPIC SYNONYMS: *Lithothamnion glaciale* var. *granii* (Foslie) Rosenvinge, 1917: 222, figs 138–142, pl. 3, fig. 4; pl. 4: figs 1–4; *Lithothamnion glaciale* f. *granii* (Foslie) Foslie 1905a: 10.

LECTOTYPE: TRH C10-3114, 12.vii.1893, no habitat data, leg. H. H. Gran (designated by Adey & Lebednik, 1967: 78).

TYPE LOCALITY: Drøbak, Norway.

Lectotype DNA sequence: *rbcL*-293 (bp 1172–1464), GenBank MW536917.

Comment: The specimen sequenced is located in a large, round blue box; the label indicates illustrations in Foslie (1895: pl. 17, fig. 3 and pl. 22, fig. 1) and Printz (1929: pl. 18, fig. 15). Foslie (1895: 98, pl. 17, figs 1–7) described this new form, listed numerous syntype localities and illustrated seven specimens. Later, Foslie (1900) elevated this form to specific rank. Adey & Lebednik

(1967) lectotypified the specimens collected by Gran, who is honoured by the form name. Subsequent to the original description, Foslie named five additional forms, f. *robustum* (Foslie, 1895), f. *grandifrons*, f. *sphaericum* (Foslie, 1900), and f. *obcrateriforme* and f. *tuberculatum* (Foslie, 1905a). We have not sequenced type material of any of these forms, hence they are not listed as synonyms. Based on morpho-anatomy, Athanasiadis (2016: 228) listed *L. granii* as *incertae sedis*; DNA sequence data have confirmed the placement of the species in synonymy with *L. soriferum*.

Lithothamnion nodulosum Foslie, 1895: 144, pl. 21, figs 1–6.

HOMOTYPIC SYNONYM: *Lithothamnion nodulosum* f. *typicum* Foslie, 1905a: 62, *nom. inval.*

LECTOTYPE: TRH C5-2999, 18.vii.1894, leg. M. H. Foslie (designated by Woelkerling, 1993: 158).

TYPE LOCALITY: Brækstad (now Brekstad), Trondheimsfjorden, Norway (Woelkerling *et al.*, 2005: 414). Lectotype DNA sequence: *rbcL*-293 (bp 1172–1464), GenBank MW536857.

Comment: We sequenced one of the three rhodoliths comprising the lectotype from Brekstad, Norway, and the sequence was identical to *L. soriferum*. The specimen sequenced is preserved in a round, red box; it is illustrated in Printz (1929: pl. 25, fig. 2) and not in pl. 21 as marked on the box (see Woelkerling *et al.*, 2005: 414). The lectotype is narrowed herein to the sequenced specimen. Based on morpho-anatomy, Athanasiadis (2016: 228) listed *L. nodulosum* as *incertae sedis*; DNA sequence data have confirmed the placement of the species in synonymy with *L. soriferum*.

Lithothamnion sonderi f. *sublaevigatum* Foslie, 1905a: 24.

HOLOTYPE: TRH B15-2426, 21.vii.1902, leg. M. H. Foslie.

TYPE LOCALITY: The islet in front of the lighthouse, Røvær, Norway (Woelkerling, *et al.*, 2005: 323).

Holotype DNA sequence: *rbcL*-293 (bp 1172–1464), GenBank MW536887.

Comment: The partial *rbcL* sequence of the holotype is identical over its entire length to the corresponding type sequences of *L. soriferum*. This is the only type specimen of a synonym of *L. soriferum* that is an encrusting, epilithic coralline; all others are rhodoliths. The holotype material comprised six epilithic crusts, with the piece illustrated in Printz (1929: pl. 4, fig. 8) in a separate box (Woelkerling, 1993: 211). We sequenced the specimen located separately within a blue, round box that corresponds to the piece illustrated in plate 4, fig. 8 (Printz, 1929).

Lithothamnion soriferum f. *divaricatum* Foslie, 1891: 41, pl. 3, fig. 2.

LECTOTYPE: TRH C11-3161, 5.viii.1882, leg. M. H. Foslie (designated by Woelkerling, 1993: 79).
TYPE LOCALITY: Tromsø, Norway.
Lectotype DNA sequence: *rbcL*-293 (bp 1172–1464), GenBank MW536891.

Comment: Woelkerling *et al.* (2005: 437) noted that there was one specimen in the lectotype collection with a green tag: 'Lith. Mon. pl. 20, f. 9' (corresponding to Printz, 1929: pl. 20, fig. 9), and another specimen with the annotation, 'Specimen matches Foslie 1891a, pl. 3, fig. 2, lower left'. Previously, Woelkerling, (1993: 79) designated as lectotype element the collection containing this latter specimen because no further type material had been found at that time. The specimen selected for sequencing was the specimen with the green tag 'Lith. Mon. pl. 20, f. 9' (corresponding to Printz, 1929: pl. 20, fig. 9) among the five rhodoliths contained in the lectotype collection. The lectotype is narrowed herein to the sequenced specimen. Based on morpho-anatomy, Athanasiadis (2016: 228) listed *L. soriferum* f. *divaricatum* as *incertae sedis*; DNA sequence data have confirmed the placement of the taxon in *L. soriferum*.

Lithothamnion uncinatum Foslie, 1895: 154, pl. 19, figs 11–14.

HOMOTYPIC SYNONYMS: *Lithothamnion calcareum* f. *uncinatum* (Foslie) Foslie, 1897: 9; *Lithothamnion norvegicum* f. *uncinatum* (Foslie) Foslie, 1900: 13.

HOLOTYPE: TRH C3-2998, 1890, leg. unknown.

TYPE LOCALITY: Kragerø, Norway.

Holotype DNA sequence: *rbcL*-293 (bp 1172–1464), GenBank MW536848.

Comment: According to Woelkerling (1993: 231), the holotype collection comprises several rhodolith specimens illustrated in Foslie (1895: pl. 19, figs 11–14). The specimen depicted in Foslie (1895: pl. 19, fig. 11) was sequenced, and is identical to *L. soriferum*. Athanasiadis (2016: 231) listed this name as a synonym of *Lithothamnion norvegicum*, which he considers *incertae sedis* (see below).

Historical collection

UPS A648806, as *Lithothamnion intermedium*, Mestervik, Tromsø, Norway, 20.ix.1890, leg. Foslie. DNA sequence: *rbcL*-263 (bp 1172–1434), GenBank MW536906 (Supplementary table S1).

***Lithothamnion tophiforme* (Esper) Unger, 1858: 21, pl. 5, fig. 14.**

BASIONYM: *Millepora polymorpha* f. *tophiformis* Esper, 1789: pl. XV (Millepora).

NEOTYPE: TRH C12-3179, no date, no habitat data, leg. C. Ryberg (designated by Adey, 1970c).

TYPE LOCALITY: Julianehaab, Greenland.

Neotype DNA sequence: *rbcL*-263 (bp 1172–1464), GenBank MW536858.

Comment: We sequenced the neotype designated by Adey *et al.* (2005), and the GenBank sequences used in Adey *et al.* (2015b) are in agreement with the neotype sequence.

HETEROTYPIC SYNONYMS:

Lithothamnion alcornae Kjellman, 1883: 121, pl. 5, figs 1–8.

HOMOTYPIC SYNONYMS:

Lithothamnion soriferum f. *alcornae* Foslie, 1891: 41, pl. 3, fig. 4; *Lithothamnion tophiforme* f. *alcornae* Foslie, 1895: 147 (as '*alcornis*').

LECTOTYPE: TRH C13-3203 (designated herein), 5. viii.1882, leg. M. H. Foslie.

TYPE LOCALITY: Tromsø, Norway.

Lectotype DNA sequence: *rbcL*-293 (bp 1172–1464), GenBank MW536851.

Comment: The *rbcL* sequence obtained is identical to the neotype sequence of *L. tophiforme*. Kjellman (1883: 122) stated that this species was from Tromsø and that Foslie was the collector. Woelkerling *et al.* (2005: 443) called TRH C13-3203 syntype material. The specimen selected for sequencing and designated herein as lectotype was illustrated by Printz (1929: pl. 19, fig. 11). Athanasiadis (2016: 221) cited this species as *incertae sedis*; DNA sequence data have confirmed the synonymy of the species with *L. tophiforme*.

Historical collection

TRH C3-2948, Viprandsund, Haugesund, Norway, 17.v.1897, leg. M. H. Foslie.

DNA sequence: *rbcL*-293 sequence (bp 1172–1464), GenBank MW536878; identical to the neotype sequence of *L. tophiforme*.

Comment: This collection is topotype material of *Lithothamnion norvegicum* (Areschoug) Kjellman (1883: 122, basionym: *Lithothamnion calcareum* var. *norvegicum* Areschoug, 1875: 4). The box contains a large collection of rhodoliths but the specimen sequenced is located separately within a small box marked 'Prep. 522'.

Areschoug (1875: 4) cited Wittrock as the collector of *L. calcareum* var. *norvegicum*, but he did not illustrate material, nor indicate a type. We have been unable to locate any material in either L or UPS where other Areschoug material is located. Eleven of Foslie's collections in TRH are listed under *L. norvegicum* (Woelkerling *et al.*, 2005: 407–408), but only the sequenced specimen is topotype material. A collection by Wittrock is in TRH (C3-2985) and illustrated in Printz (1929: pl. 16, figs 37–38) but the date of collection and habitat data are lacking, making it difficult to know if this is type material.

Woelkerling & Verheij (1995: 67) noted syntype material is present in L. The material in TRH and in L needs to be sequenced to understand the correct application of *L. norvegicum*.

'Lithothamnion' species and infraspecific taxa that belong in Phymatolithon

***Phymatolithon calcareum* (Pallas) W.H.Adey & McKibbin**

Lithothamnion squarrulosum f. *palmatifida* Foslíe, 1895: 6.

LECTOTYPE: TRH C1-2892, 12.v.1893, leg. L. K. Rosenvinge; designated by Woelkerling *et al.* (2005: 398). TYPE LOCALITY: Fladen, østl. (= Eastern) Kattegat, Denmark (Woelkerling *et al.*, 2005: 398).

DNA sequences: *psbA* and *rbcL*-293 (bp 1172–1464), GenBank MW564559 and MW536910, respectively.

Comment: Collection consisted of several rhodoliths. The specimen tagged with a blank green label was selected for DNA sequencing. The *rbcL* sequence differed by 2 bp from the neotype sequence of *P. calcareum*, while the *psbA* sequences were identical (neotype specimen BM000712373, Supplementary table S3).

***Phymatolithon scabriusculum* (Foslíe) V.Peña, P.W. Gabrielson & Hughey, comb. nov.**

BASIONYM: *Lithothamnion scabriusculum* Foslíe, 1895: 170.

HOLOTYPE: TRH C20-3502, 5–10 fathoms, 2.viii.1887, leg. M. H. Foslíe.

Type locality: Kjelmø (now Kjelmøya), Finnmark, Norway (Woelkerling *et al.*, 2005: 493).

DNA sequence: *rbcL*-293 (bp 1172–1464), GenBank MW536920.

Comment: The largest fragment preserved in a small box marked '520' (further information in Woelkerling *et al.*, 2005: 493) was selected for DNA sequencing. Identical *rbcL* sequences were obtained independently by VP and by PWG/JRH, which differed by 1–3 bp from the GenBank sequences of *P. rugulosum* (vouchers US 170942 and BM000659095) collected in Gulf of Maine and Helgoland, Germany, respectively (Adey *et al.*, 2015b). By the rule of priority (Art. 11.4 of the ICN, Turland *et al.*, 2018), this name must be adopted for *P. rugulosum*.

HETEROTYPIC SYNONYM:

Phymatolithon rugulosum W.H.Adey, 1964: 381, figs 15–20, 27–29, 35–36, 39–44, 51–64.

HOLOTYPE: Adey 61-41A-3 in MICH, 2.xi.1961, 3–5 m depth, leg. W. H. Adey.

TYPE LOCALITY: Merchant Island, East Penobscot Bay, Maine.

***Phymatolithon squamulosum* (Foslíe) W.H.Adey, Hernandez-Kantun & P.W.Gabrielson**

BASIONYM: *Lithothamnion squamulosum* Foslíe, 1895: 183.

HOLOTYPE: TRH B5-1962, vii. 1894, leg. P. Boye.

TYPE LOCALITY: Sogn, Sulen (now Sula), indre (= inner), Stensund (now Steinsund), Norway (Woelkerling *et al.*, 2005: 265).

Holotype DNA sequences: *psbA* and *rbcL*-293 (bp 1172–1464), GenBank MW564558 and MW536870, respectively.

Comment: The collection comprises a larger box with two smaller boxes, one square and one round (Woelkerling *et al.*, 2005: 265). The specimen in the round box with the annotation 'Prep. 65' was sequenced. Recently this taxon was transferred to *Phymatolithon* according to the molecular data obtained from an isotype preserved in BM (BM000044670, Box 434, Adey *et al.*, 2018). The DNA sequencing of the holotype confirms this result; the *rbcL* sequences of both type collections were identical.

Recent collections

Norway: Krøttøya (Troms) and Averøya. Intertidal to subtidal (9 m depth), encrusting on cobble, pebbles and shells, and on hard substrata. Specimens with uniporate (gametangial or carposporangial) and multiporate conceptacles. DNA sequences: *psbA* (Supplementary table S2).

N.B. We have not dealt with *Lithothamnion sonderi* Hauck in this paper as we have not sequenced the type material, even though the species is thought to be widespread in crustose forms at low light levels in the NE Atlantic, from Nordland (Norway) to northern Spain (Chamberlain & Irvine, 1994).

Discussion

Since the first DNA sequences from type specimens of geniculate (Gabrielson *et al.*, 2011) and non-geniculate (Sissini *et al.*, 2014) corallines were published, it has become increasingly clear that the primary method to unequivocally apply a historical name is to obtain DNA sequences from the type material to compare with sequences from other historical or more recently collected specimens (Martone *et al.*, 2012; Hind *et al.*, 2014a, b, 2015; Hernández-Kantún *et al.*, 2015a, 2016; Richards *et al.*, 2017, 2018; Gabrielson *et al.*, 2018, 2019; Peña *et al.*, 2018; Jeong *et al.*, 2020; Maneveldt *et al.*, 2020; Puckree-Padua *et al.*, 2020). Herein, we have applied that methodology to the numerous species and infraspecific names of Arctic and subarctic non-geniculate corallines published by Kjellman (1883, 1889) and

later by Foslie (1891, 1895, 1896, 1899, 1900, 1905a, b, 1908) and others.

With the exception of *Lithothamnion tophiforme* (Unger, 1858), first published as *Millepora polymorpha* var. *tophiformis* Esper (1789), the oldest names applicable to Arctic and Subarctic non-geniculate corallines are those of Kjellman (1877, 1883, 1889). By sequencing type material, Adey *et al.* (2015b) confirmed the application of two of Kjellman's names, *L. compactum* Kjellman (1883) to *Clathromorphum*, and *L. loculosum* Kjellman (1889) to *Neopolyporolithon*, and showed that a third, *Lithothamnion foecundum* Kjellman (1883), currently placed in *Leptophytum* W.H.Adey, does not belong in that genus, but its generic position remains unresolved. Lectotype material of the oldest name, *Lithophyllum arcticum* Kjellman (1877), collected at Uddebay, Novaya Zemlya, Russia, provided an earlier available name for *Neopolyporolithon loculosum* (Kjellman) W.H.Adey, P. W.Gabrielson, G.P.Johnson & Hernández-Kantún, namely *N. arcticum* (Kjellman) P.W.Gabrielson, S.C. Lindstrom & Hughey (Gabrielson *et al.*, 2019). *Lithothamnion flavescens* Kjellman (1883) was transferred to *Leptophytum* by Athanasiadis (2016), based on morpho-anatomy, which has been shown to be problematic in correct generic placement of non-geniculate species (Hind *et al.*, 2016, 2018; Gabrielson *et al.*, 2019). Of the remaining six Kjellman names, five are treated herein, *L. allicorne*, *L. durum*, *L. glaciale*, *L. intermedium* and *L. soriferum*. Attempts to amplify *L. ungeri* Kjellman (1883) were unsuccessful. We sequenced 35 type specimens of *Lithothamnion* species and infraspecific taxa described by Foslie. Below we discuss the systematics of the Arctic and Subarctic *Lithothamnion* species that we recognize, including *L. lemoineae*, and one of the species of *Clathromorphum*, *C. circumscriptum*, for which we found an additional synonym. Distributions, habits and habitat data for each species are updated, including range maps for the *Lithothamnion* species.

***Clathromorphum circumscriptum*.** DNA sequencing confirmed two earlier proposed heterotypic synonyms for this species, *L. durum* and *L. evanescens*, the first proposed by Foslie (1900) and the second by Lebednik (1977). Added to these is *L. coalescens*, which had been considered a synonym of *C. compactum* by Foslie (1905a) and recently by Athanasiadis (2016).

The habit and habitat of *C. circumscriptum* are provided by Adey *et al.* (2015b), and the sequenced specimens confirm this information. The species is reported to be circum-Arctic ranging south to the Subarctic in both the Atlantic and Pacific Oceans based on morpho-anatomy and its distinct habit (Adey, 1965; Adey *et al.*, 2013, 2015a, b). In the NW Atlantic Subarctic, *C. circumscriptum* is generally more abundant at depths ≤ 10 m on moderately exposed rocky shores (Steneck, 1978; Adey & Hayek, 2011). DNA sequences confirm its presence in Greenland, but material from the Russian Arctic

and NW Pacific Ocean has not been sequenced. DNA sequences from the western Gulf of Alaska are from specimens collected in mid- (GenBank MT732997) and high intertidal pools (MT733001). Other mid-pool (MT732990) and low intertidal collections (MT732992, MT732993, MT732996) from this area represent an undescribed species of *Clathromorphum*. Records based on morpho-anatomy from SE Alaska may also represent an undescribed species.

***Lithothamnion glaciale*.** There is no doubt that the lectotype specimen designated herein is the one illustrated by Kjellman (1883: pls 2, 3), despite multiple listed syntype localities. The partial *rbcL* sequence from the lectotype differs by 1 bp from all other sequences, including one from Spitzbergen. DNA sequencing also shows that 18 specific and infraspecific *Lithothamnion* taxa later named by Foslie are heterotypic synonyms of *L. glaciale*. *Lithothamnion intermedium*, described in the same publication as *L. glaciale* (Kjellman, 1883), was listed most recently by Athanasiadis (2016) as *incertae sedis*. Kjellman provided three syntype localities for *L. intermedium*, but he himself only collected the specimen at Karlsøy (Carlsö); specimens from the other two localities (Tromsø and Vadsø) were collected by Foslie. In UPS only two specimens could be located, one from Karlsøy, collected by Kjellman and with a label in his handwriting, and the other collected by Foslie from Mestervik, Tromsø. The Kjellman specimen from Karlsøy is designated as the lectotype; its sequence differs by 1 bp from the *L. glaciale* lectotype. From its DNA sequence the specimen collected by Foslie is *L. soriferum*. *Lithothamnion glaciale* and *L. intermedium* were published at the same time and are the same species so either name can be used for this species. We selected *L. glaciale* because of its long-standing use by the coralline research community and because the lectotype material is homotypic, whereas *L. intermedium* mostly has been ignored.

The habit and habitat of *L. glaciale* were described by Adey (1966a) and Adey *et al.* (2005) based primarily on NW Atlantic material identified by morpho-anatomy. Specimens ranged from epilithic crusts to free living rhodoliths. More recently, encrusting epilithic forms of *L. glaciale* have been reported to be very common from the low intertidal to the photic limit (Adey & Hayek, 2011). Most collections, however, are from the low intertidal to a depth of ~ 15 m, more a reflection of collecting limits than the species' true vertical distribution. Numerous studies over the past two decades have documented the presence of rhodoliths throughout the North Atlantic and Arctic at depths of ~ 3 to 50 m, and while most studies have assumed *L. glaciale* is the main species, little to no corroborative DNA sequencing work has been carried out (Halfar *et al.*, 2000; Blake & Maggs, 2003; Kamenos & Law, 2010; Gagnon *et al.*, 2012; Teichert *et al.*, 2012, 2014; Adey *et al.*, 2015a; Millar &

Gagnon, 2018; Schoenrock *et al.*, 2018b; Bélanger & Gagnon, 2020; Teed *et al.*, 2020). Although this assumption is legitimate given the ubiquity of *L. glaciale* in both oceans, morphological deviations from the norm in a few *L. glaciale* rhodoliths from Newfoundland and Labrador suggests that rhodoliths may also include other species of corallines such as *L. tophiforme* and *C. compactum* (D. Bélanger & P. Gagnon, unpublished data). In Norway, Anglés d'Auriac *et al.* (2019) reported multi-species maerl beds mainly composed of *L. glaciale* and species of *Phymatolithon* and *Lithophyllum*.

We confirm by DNA sequencing the presence of *L. glaciale* throughout the North Atlantic (Fig. 2). We have not confirmed many of the Arctic Ocean reports. The observation of uniporate conceptacles (mostly carposporangial) and multiporate tetra/bisporangial conceptacles in our collections from Norway confirmed the common occurrence of gametophytes and tetra/bisporophytes for this species, as suggested in the literature (e.g. Chamberlain & Irvine, 1994).

In the North Pacific *L. glaciale* was first reported by Saunders (1901: 442) from Prince William Sound, Kukak Bay and the Shumagin Islands, identified by Kjellman. Although we have not confirmed the identity of these specimens, Bringloe & Saunders (2019) reported this species from Nome, Alaska, USA (Bering Strait), and we have sequenced specimens from Malcolm Island, central British Columbia, Canada, southwards to Monterey County, California, USA (Fig. 2). In the NE Pacific, only encrusting epilithic specimens were found, although they may completely cover pebbles so that they appear to be rhodoliths. We cannot confirm reports based on morpho-anatomy from Japan and Arctic Russia, but *L. glaciale* is probably present in those areas as well. Reports of this species from any tropical and warm temperate regions (see AlgaeBase; Guiry & Guiry, 2020) are highly improbable. Reports from the Subantarctic (Heydrich, 1900; Lemoine, 1913) need to be confirmed.

***Lithothamnion lemoineae*.** Melbourne *et al.* (2017) provided a *psbA* sequence from the holotype of *L. lemoineae* from the NW Atlantic (Maine, USA)

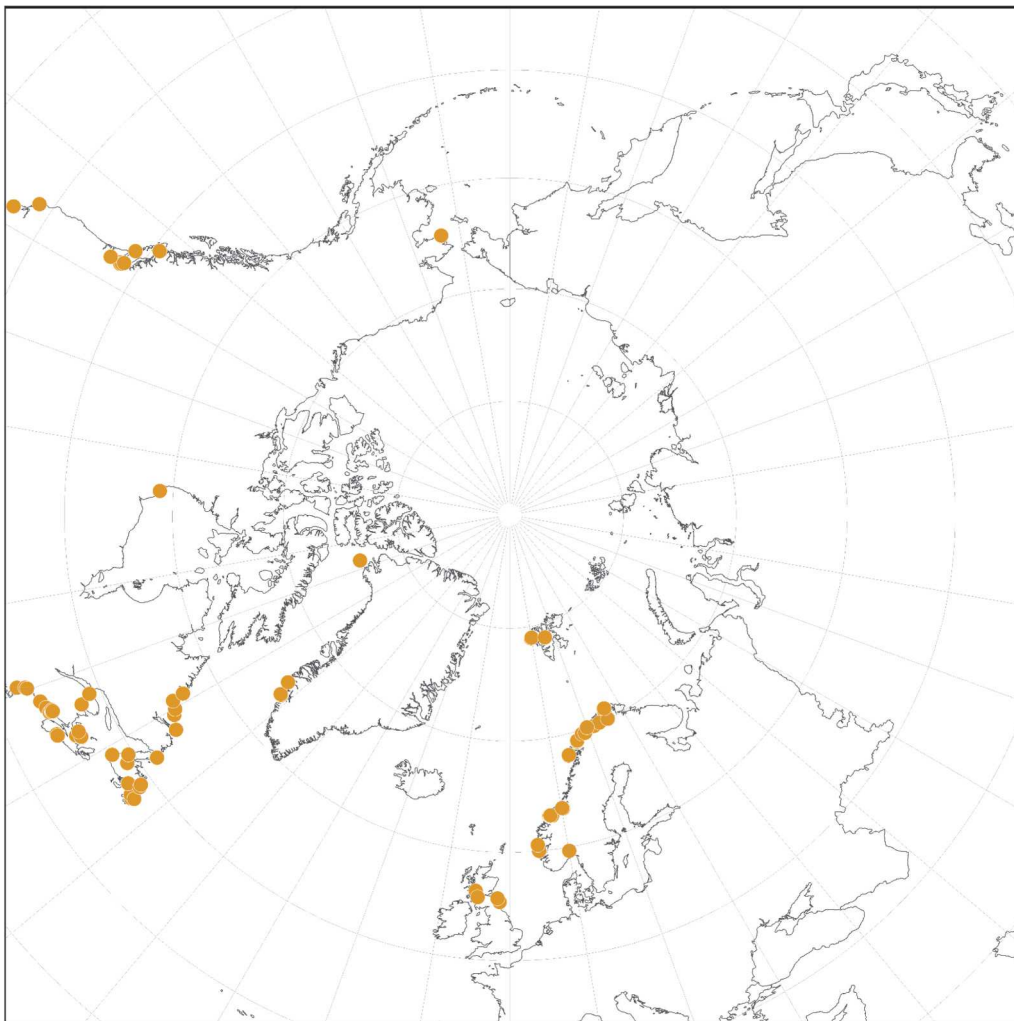


Fig. 2: Distribution of *Lithothamnion glaciale* obtained for collections analysed in the molecular studies, type collections and historical specimens.

to unequivocally link DNA sequences from field-collected material to the name. Based on DNA sequenced specimens, we expand the habit of *L. lemoineae* from encrusting epilithic to epiphytic, to epizoic on shells, and as rhodoliths. The species can also occur in the intertidal, as well as in the shallow subtidal to 12 m depth. In the NW Atlantic Subarctic, *L. lemoineae* often dominates rock on exposed shores (Adey & Hayek, 2011), particularly at 10–15 m depth (R. Steneck, *pers. obs.*).

Melbourne *et al.* (2017) found that specimens from England, thought to be *L. lemoineae* based on morpho-anatomy (Chamberlain & Irvine, 1994), were not that species based on DNA sequencing. However, based on DNA sequenced material, we corroborated a recent record of *L. lemoineae* from the same region in the NE Atlantic (Svalbard, Norway; Hofmann & Heesch, 2018), and likewise Bringloe & Saunders (2019) have the first confirmed record from the NE Pacific at Nome, Alaska, USA. Here, we confirm its occurrence on Kodiak Island, Gulf of Alaska (GenBank MT733005), on low intertidal bedrock. Its

report from the NW Pacific by Lee (2008) needs to be verified by DNA sequencing. We also confirm its distribution in the NW Atlantic from Labrador, Canada to Maine, USA (Fig. 3).

***Lithothamnion soriferum*.** We located in UPS three specimens of *L. soriferum* in an envelope with a label in Kjellman's handwriting including from one of the cited localities, Carlsö (now Karlsøy). These appear to have been illustrated and published by Kjellman (1883: pl. 1, figs 1–4) with some artistic licence. This is similar to what we found for *L. durum* (Kjellman, 1889) and *L. glaciale* (Kjellman, 1883); the specimens are convincing matches to the illustrations. DNA sequences from type specimens of seven species and infraspecific taxa later named by Foslie are all exact matches to the lectotype specimens of *L. soriferum*. The recently described *L. erinaceum* (Melbourne *et al.*, 2017) also is a heterotypic synonym of *L. soriferum*, which has had a chequered history, sometimes recognized as a distinct species (Foslie, 1905a; Zinova, 1955) but mostly being considered a synonym of *L. tophiforme*

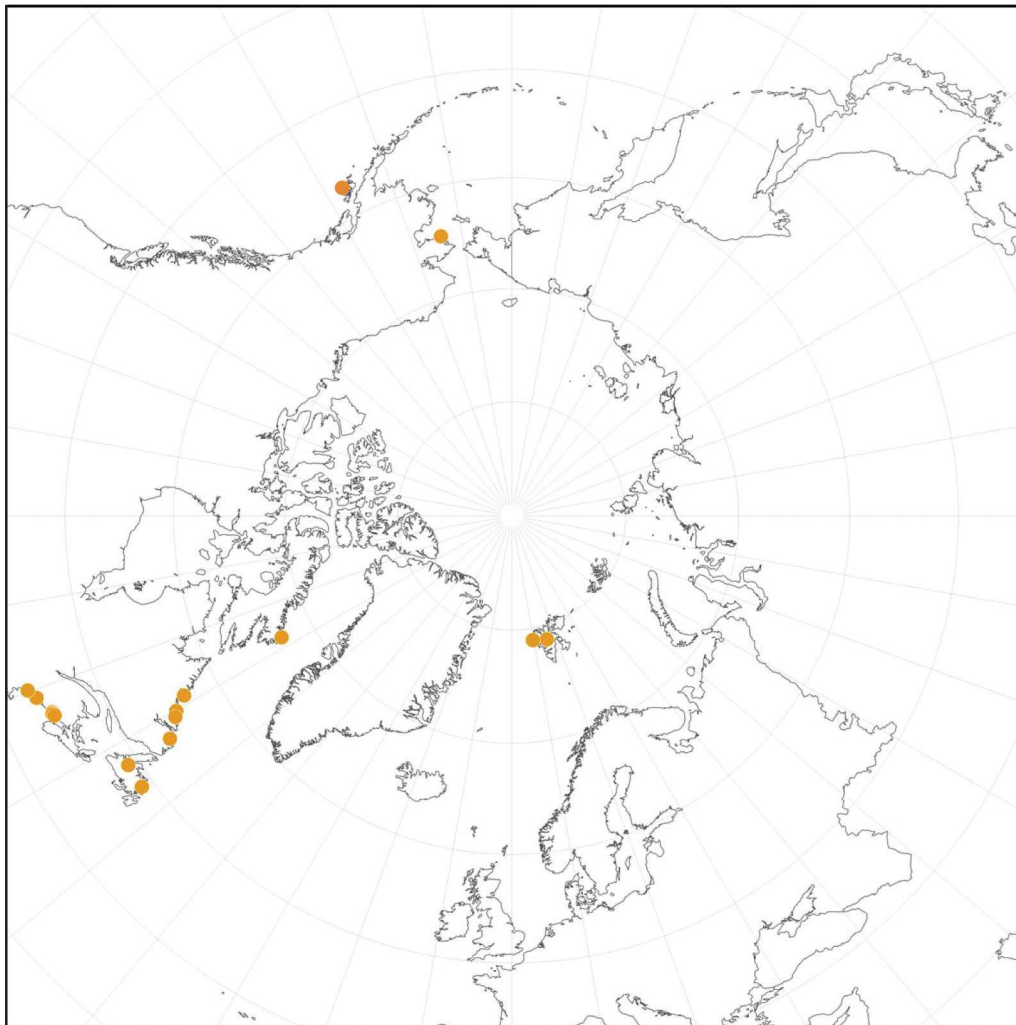


Fig. 3: Distribution of *Lithothamnion lemoineae* obtained for collections analysed in the molecular studies, type collections and historical specimens.

(Foslie, 1895; Lund, 1959; Jaasund, 1965; Lee, 1969; Adey, 1970a; Vinogradova, 2010). Interestingly, Adey *et al.* (2005), in a detailed examination of *L. tophiiforme*, did not mention *L. soriferum*, and, most recently, Athanasiadis (2016) treated the species as *incertae sedis*.

Based on DNA sequences, *L. soriferum* is a distinct species and occurs as an epilithic, epiphytic or epizoic (specimen on a worm tube) crust or as a free-living rhodolith. Specimens are primarily subtidal to 27 m depth, but can be intertidal. In contrast to *L. glaciale*, gametangial plants have not been observed in any of the collections. Only multiporate tetra/bisporangial conceptacles were observed, as indicated in the type collections of two heterotypic synonyms (*L. brevix* and *L. granii*, Woelkerling *et al.*, 2005) and in the literature (Melbourne *et al.*, 2017).

The species is widespread in the central and eastern North Atlantic (Greenland, Iceland, UK, Norway), but there is no evidence of its occurrence in the NW Atlantic; in the NE Pacific there are

sporadic records from the Aleutian Islands (Robinson *et al.*, 2017) and Prince William Sound (Konar *et al.*, 2006), Alaska, USA south to Gwaii Haanas, British Columbia, Canada (Fig. 4). For such a widespread distribution, this species appears uncommon compared with *L. glaciale*. In the first report of *L. soriferum* from the NE Pacific (Konar *et al.*, 2006), this species was misidentified as *Phymatolithon calcareum* based on morphoanatomy. This appears to be because the cell types in the cross-sectional image (Konar *et al.*, 2006: fig. 3B) were misidentified. The figure clearly shows flared epithallial cells characteristic not of any *Phymatolithon* species, but of *Lithothamnion* species. All reports of *P. calcareum* outside boreal NE Atlantic and the Mediterranean Sea waters based on morphoanatomy are doubtful and need to be confirmed by DNA sequences.

***Lithothamnion tophiiforme*.** The sequence of the neotype specimen, TRH C12-3179, designated by Adey *et al.* (2005), confirms the identity of the specimen used by Adey *et al.* (2015b) to represent this species.

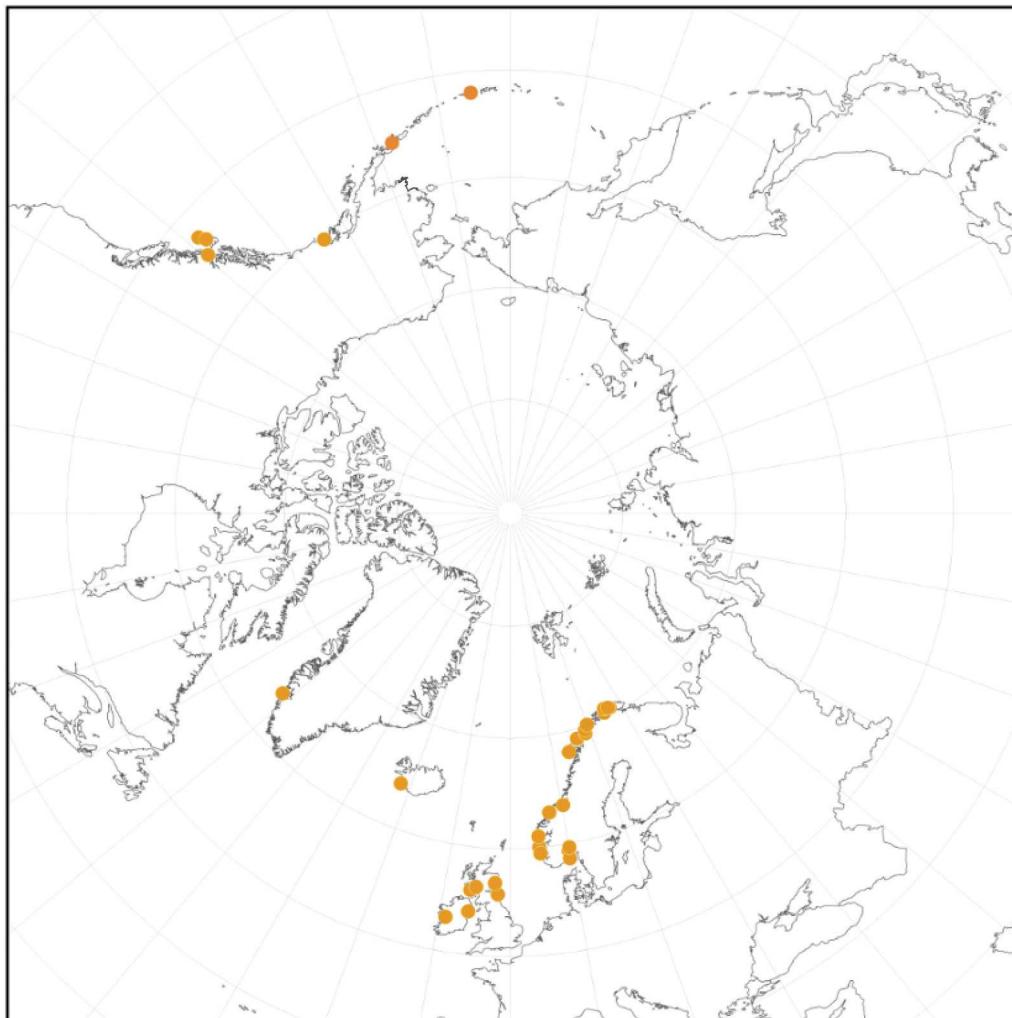


Fig. 4: Distribution of *Lithothamnion soriferum* obtained for collections analysed in the molecular studies, type collections and historical specimens.

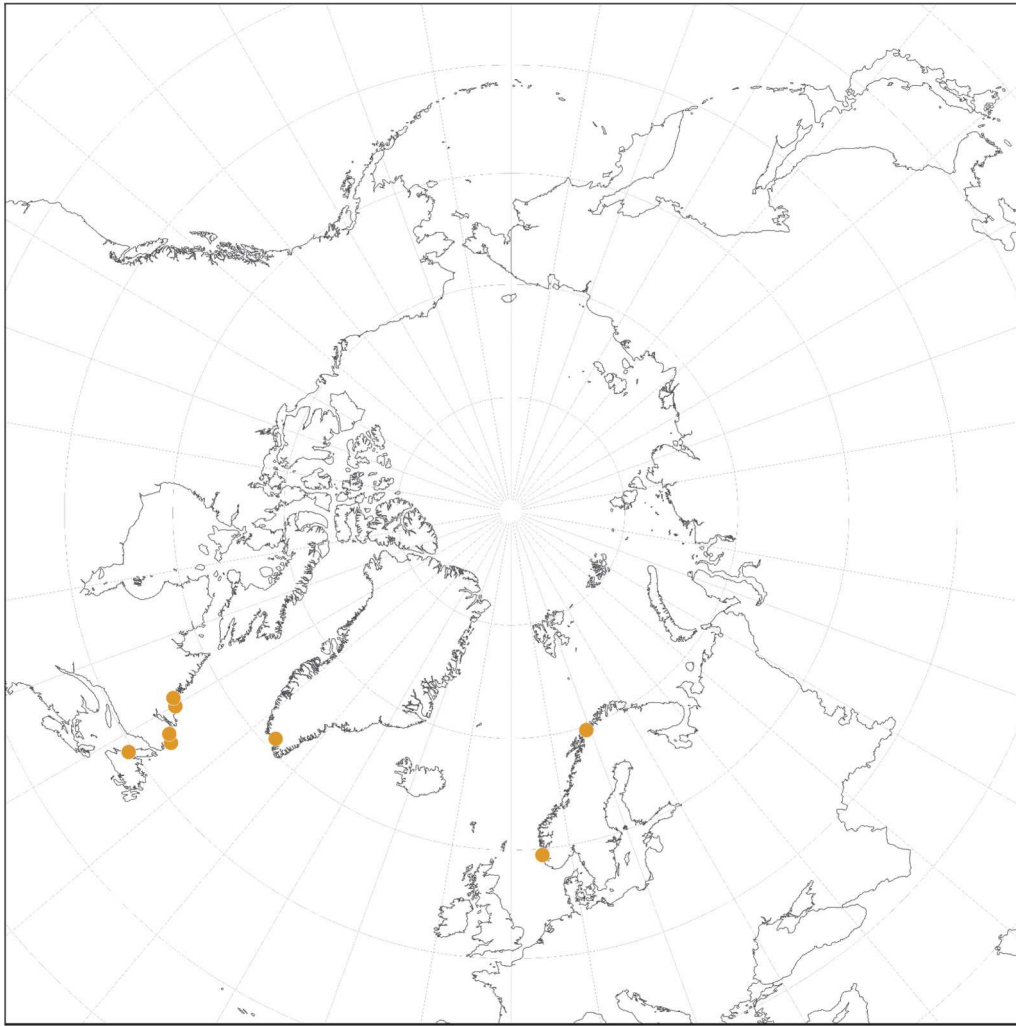


Fig. 5: Distribution of *Lithothamnion tophiforme* obtained for collections analysed in the molecular studies, type collections and historical specimens.

Adey (1970a) reported this species to be encrusting, especially on shells or shell fragments, and also growing as free-living rhodoliths. All of the sequenced specimens to date have been rhodoliths. Adey *et al.* (2005) considered *L. tophiforme* an Arctic species, but also stated that its abundance in the high Arctic is unknown, a situation that remains unchanged. They also noted that it is found only in colder waters below 10 m depth and at temperatures below 10°C, and the sequenced specimens confirm this pattern as all were collected below 15 m depth. All recently collected sequenced specimens are from the NW Atlantic, from Newfoundland, Canada northward (Fig. 5). The neotype specimen is the only confirmed specimen from Greenland, and only two historical specimens from the 19th century are from Norway, where the species was not found recently in an extensive collection effort presented herein.

In the NW Atlantic Subarctic, *L. tophiforme* rhodoliths commonly co-occur with *L. glaciale* rhodoliths, dominating at depths >25 m (Adey *et al.*, 2015a). In rhodolith beds of both species, thalli of

L. tophiforme and *L. glaciale* sometimes merge, forming multi-species rhodoliths with a characteristic colour mosaic with *L. tophiforme* generally more brownish-orangy in colour than *L. glaciale* (D. Bélanger & P. Gagnon, unpublished data). Our sequenced specimens of *L. tophiforme* show a variety of shapes and sizes, from a few cm-long twig-like thalli, to large (>10 cm across) branching spheroidal rhodoliths. A few specimens presented a distinct growth form with fanned branches. The phenotypic plasticity of *L. tophiforme* highlights the importance of DNA sequencing for identification.

Identifying non-geniculate coralline algae to species

These Arctic and Subarctic *Lithothamnion* species exemplify the difficulties of identifying non-geniculate coralline species using morpho-anatomy. DNA sequencing has revealed that by the first decade of the 20th century, 26 specific and infraspecific names had been given to three species: *L. glaciale*,

L. soriferum and *L. tophiforme*. Recently, based on morpho-anatomy, the vast majority of these were listed as *incertae sedis* by Athanasiadis (2016) including, for example *L. alcornae*, *L. breviae* and *L. soriferum*. In the >100 years since these had been named and examined by coralline morpho-anatomists, their identity could not be determined with any certainty. There remain another 21 species or infraspecific taxa of *Lithothamnion* named by Foslie, 20 from Norway and one from Scotland, from which we were unable to amplify DNA using PCR. It is highly unlikely, however, that any of these names would apply, due to the extensive sequencing of Norwegian specimens reported herein and the rule of priority. With the exception of *L. lemoineae*, which has never been recorded from Norway, the applied *Lithothamnion* names “predate” any of those published by Foslie.

Further complicating the naming of specimens without DNA sequencing is that all of these species can occur either as encrusting corallines attached to a substrate or as unattached rhodoliths – encrusting a core or not – sometimes occurring singly, but also in beds. *Lithothamnion lemoineae* previously had only been reported to occur as an epilithic crust, whereas *L. soriferum* (also as *L. erinaceum*) had not been known as an epilithic crust. In some regions, species can have restricted morphologies, for example in Norway *L. glaciale* is found as an epilithic crust, or as free-living maerl, whereas in the NE Pacific it has so far only been reported as an epilithic crust. And three of the four species, *L. glaciale*, *L. lemoineae* and *L. soriferum*, can occur from the intertidal to, at minimum, 12 m depth.

The finding by DNA sequencing that four Arctic and Subarctic *Lithothamnion* species had been named as multiple specific and infraspecific taxa using morpho-anatomy is clearly opposed to the cryptic diversity commonly recorded in temperate corallines (e.g. Pardo *et al.*, 2014, 2017; Hernández-Kantún *et al.*, 2015a, b; Peña *et al.*, 2015a, b; Richards *et al.*, 2018; Pezzolesi *et al.*, 2019). However, this plethora of specific and infraspecific names in the Arctic and Subarctic regions was primarily the work of Foslie, who, as illustrated in the taxonomic results, changed his mind numerous times about which taxa should be recognized and at what rank. In tropical regions, DNA sequencing of non-geniculate corallines has shown that some species are widely distributed, whereas most have local distributions (Sissini *et al.*, 2014; Peña *et al.*, 2014b; Hernández-Kantún *et al.* 2016; Gabrielson *et al.*, 2018; Maneveldt *et al.*, 2019).

In the Arctic and Subarctic additional species of *Lithothamnion* and *Clathromorphum* need to be recognized based on the DNA sequencing reported

herein (Supplementary table S2). It is also likely that the Arctic and Subarctic *Lithothamnion* species will need to be transferred to a new genus, as the genotype of *Lithothamnion*, *L. muelleri* Lenormand ex Rosanoff, belongs in a different clade (Jeong *et al.*, 2020).

It is critical in this time of rapid ocean warming and acidification, particularly in polar regions, that we have a firm understanding of the taxa currently present in order to document future changes in their habitats and distributions. Importantly, the biogeography of coralline algae appears especially sensitive to ocean thermogeography (Adey & Steneck, 2001; Adey & Hayek, 2011). The relevance of non-geniculate coralline algae in these regions as ecosystem engineers cannot be overstated, whether occurring as encrusting species attached primarily to rock substratum (Freiwald & Henrich, 1994; Adey *et al.*, 2005, 2015a) or as free-living maerl (Pardo *et al.*, 2014; Teichert, 2014; Teed *et al.*, 2020). As polar seas warm and become increasingly acidified, these coralline algal species will either be forced to live at lower depths, where they will be limited by the availability of photosynthetically active radiation through the water column, or they will become extinct. DNA barcoding of organisms in these habitats, coupled with DNA sequencing of type and historical specimens, provides the foundation to document these imperiled species.

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Supplementary information

The following supplementary material is accessible via the Supplementary Content tab on the article's online page at <http://dx.doi.org/10.1080/09670262.2021.1880643>

Supplementary note 1. Type collections and historical specimens DNA-extracted but unsuccessfully sequenced for *psbA* and *rbcL*.

Supplementary table S1. Type collections and historical specimens sequenced in the study.

Supplementary table S2. Collection and vouchers details for the recent specimens sequenced in the study. For each species, specimens are sorted by collection areas: NE Atlantic, NW Atlantic and NE Pacific.

Supplementary table S3. List of GenBank accession numbers used in this study with details of locality information and references.

Supplementary fig. S1. Maximum likelihood (ML) tree of COI-5P included in the present study. Bootstrap ML values >50% shown for each node. Scale bar: 0.05 substitutions per site.

Supplementary fig. S2. Phylogenetic tree inferred from RAXML analyses of *psbA* sequences included in the present study. Bootstrap ML values >50% and posterior probabilities >0.50 from Bayesian inference shown for each node. Scale bar: 0.02 substitutions per site.

Supplementary fig. S3. Morpho-anatomy of *Lithothamnion glaciale*, UPS A-000202. Fig. A. Thallus habit and herbarium labels including label handwritten by Kjellman. Fig. B. Vertical fracture of protuberance showing radial construction and location of overgrown and buried conceptacle (black arrow). Fig. C. Vertical fracture of protuberance with conceptacle (black arrow) overgrown by a secondary hypothallus (arrowheads). Fig. D. Magnified view of secondary hypothallus (bracket) over conceptacle roof. Fig. E. Perithallus with cell fusions (white arrows). Fig. F. Perithallus (lower bracket), intercalary meristem (middle bracket, *), and a single-layered epithallus (upper bracket) of flared cells (e), one with cell roof intact (white arrow). Scale bars: Figs B–C = 100 µm; Figs D–F = 10 µm.

Supplementary fig. S4. Morpho-anatomy of *Lithothamnion soriferum*, UPS A-648809. Fig. A. Thallus habit of specimens and herbarium label handwritten by Kjellman. Figs B–D. Vertical fractures of protuberance showing radial construction. Fig. E. Magnified view of secondary hypothallus (arrowhead, bracket) over the thallus surface of the older growth layer. Fig. F. Perithallus (lower bracket) with cell fusions (white arrows), intercalary meristem (middle bracket, *), and epithallus (upper bracket). Figs G–H. Magnified view of meristematic cells (*) and a single-layered epithallus of flared

cells (e), one with cell roof intact (white arrow, Fig. H). Scale bars: Fig. A = 2 cm. Figs B–D = 100 µm. Figs E–H = 10 µm.

Author contributions

V. Peña: original concept, type sequencing, writing, contemporary collections; D. Bélanger: writing, contemporary collections; P. Gagnon: writing, contemporary collections; J.L. Richards: morpho-anatomy of type specimens, writing; L. Le Gall: type sequencing, distribution maps, writing, contemporary collections; J. R. Hughey: type sequencing, writing; G.W. Saunders: sequencing of contemporary collections, contemporary collections; S.C. Lindstrom: sequencing of contemporary collections, writing, contemporary collections; E. Rinde: led the field sampling in the CoralAlg project that funded the analysis of TRH specimens, writing, contemporary collections; V. Husa: sampling of type collections at the TRH, led the field sampling in the AKVAKYST III project, contemporary collections; H. Christie: contemporary collections; S. Fredriksen: writing, contemporary collections; J.M. Hall-Spencer: writing, contemporary collections; R.S. Steneck: writing, contemporary collections; K. M. Schoenrock: contemporary collections; J. Gitmark: contemporary collections; E.S. Grefsrud: contemporary collections; M.B. Anglès d'Auriac: writing, contemporary collections; E. Legrand: contemporary collections; J. Grall: contemporary collections; T. F. Mumford: contemporary collections; N.A. Kamenos: writing, contemporary collections; P.W. Gabrielson: original concept, type sequencing, writing, contemporary collections.

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