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

Peña, Viviana; Bélanger, David; Gagnon, Patrick; Richards, Joseph L.; Le, Gall L; Hughey, Jeffery R.; Saunders, Gary W.; Lindstrom, Sandra C.; Rinde, Eli; Husa, Vivian; Christie, Hartvig; Fredriksen, Stein; Hall-Spencer, Jason M.; Steneck, Robert S.; Schoenrock, Kathryn M.; Gitmark, Janne; Grefsrud, Ellen Sofie; Anglès, d'Auriac MB; Legrand, Erwann; Grall, Jacques; Mumford, Thomas F.; Kamenos, Nicholas A.; Gabrielson, Paul W.

Published in:

European Journal of Phycology

DOI:

[10.1080/09670262.2021.1880643](https://doi.org/10.1080/09670262.2021.1880643)

Publication date:

2021

Link:

[Link to publication in PEARL](#)

Citation for published version (APA):

Peña, V., Bélanger, D., Gagnon, P., Richards, J. L., Le, G. L., Hughey, J. R., Saunders, G. W., Lindstrom, S. C., Rinde, E., Husa, V., Christie, H., Fredriksen, S., Hall-Spencer, J. M., Steneck, R. S., Schoenrock, K. M., Gitmark, J., Grefsrud, E. S., Anglès, DA. MB., Legrand, E., ... Gabrielson, P. W. (2021). Lithothamnion (Hapalidiales, Rhodophyta) in the changing Arctic and Subarctic: DNA sequencing of type and recent specimens provides a systematics foundation*. *European Journal of Phycology*, 0(0), 1-26.
<https://doi.org/10.1080/09670262.2021.1880643>

1 This is the author's accepted manuscript. The final published version of this work (the
2 version of record) was published by Taylor & Francis in the *European Journal of*
3 *Phycology* online on 16 June 2021 at
4 <https://www.tandfonline.com/doi/abs/10.1080/09670262.2021.1880643>
5
6

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10 ***Lithothamnion* species (Hapalidiales, Rhodophyta) in the Arctic and Subarctic:**
11 **providing a systematics foundation in a time of rapid climate change based on DNA**
12 **sequencing of type and recent specimens***
13

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52 *We dedicate this paper to Walter H. Adey and William J. Woelkerling for their cataloging
53 and scholarship on the Foslie collection and for their mentorship of the next generation of
54 corallinologists.

55

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58

59 **Running Head:** Arctic and Subarctic *Lithothamnion* species

60

61 **Abstract**

62
63 Coralline red algae in the non-geniculate genera *Clathromorphum*, *Phymatolithon* and
64 *Lithothamnion* are important benthic ecosystem engineers in the photic zone of the Arctic
65 and Subarctic. In these regions, the systematics and biogeography of *Clathromorphum* and
66 *Phymatolithon* species have mostly been resolved whereas *Lithothamnion* species have not,
67 until now. Seventy-three specific and infraspecific names have been given to Arctic and
68 Subarctic *Lithothamnion* specimens in the late 19th and early 20th century by Frans R.
69 Kjellman and particularly by Mikael H. Foslie. DNA sequences from 36 type specimens,
70 five historical specimens, and an extensive sampling of recent collections, resulted in the
71 recognition of four Arctic and Subarctic *Lithothamnion* species, *L. glaciale*, *L. lemoineae*,
72 *L. soriferum* and *L. tophiforme*. Three genes were sequenced, two plastid encoded, *rbcL*
73 and *psbA*, and the mitochondrial encoded COI-5P; *rbcL* and COI-5P segregated *L. glaciale*
74 from *L. tophiforme* but *psbA* did not. Partial *rbcL* sequences obtained from type collections
75 enabled us to correctly apply the earliest available names and to correctly place the
76 remainder in synonymy. We were unable to sequence another 22 type specimens, but all of
77 these are more recent names than those that are now applied. It is difficult to identify these
78 species solely on morpho-anatomy as they can all occur as encrusting corallines or as maerl
79 (rhodoliths). We demonstrate the importance of sequencing historical type specimens by
80 showing that the recently proposed northeast Atlantic *L. erinaceum* is a synonym of one of
81 the earliest published Arctic species of *Lithothamnion*, *L. soriferum*, itself incorrectly
82 placed in synonymy under *L. tophiforme* based on morpho-anatomy. Based on sequenced
83 specimens, we update the distributions and ecology of these species.

84 **Key words:** coralline red algae; *cox1*; DNA barcoding; distribution; morpho-anatomy;

85 *psbA*; *rbcL*; systematics; taxonomy; type collections.

86

87 **Introduction**

88 Coralline algae are important ecosystems engineers worldwide through the formation of
89 extensive and biodiverse cover on hard substrata and as unattached maerl (rhodoliths,
90 Freiwald & Henrich, 1994; Foster, 2001; Amado-Filho *et al.*, 2010; Riosmena *et al.*, 2017).
91 Approximately one-third of the total continental carbonate production takes place in
92 temperate and polar coastal waters with a significant amount coming from coralline algae
93 (Nelson, 2009). In cold-water habitats, coralline algae can live for hundreds of years
94 (Freiwald & Henrich, 1994; Halfar *et al.*, 2013; Adey *et al.*, 2015a), providing habitats for
95 other seaweeds (Peña *et al.*, 2014a) and for many epibenthic and cryptic macrofauna
96 (Gagnon *et al.*, 2012; Teichert, 2014). Over the past two decades, surveys have shown that
97 rhodolith beds are widespread in the NE Pacific (Robinson *et al.*, 2017), NW Atlantic
98 (Gagnon *et al.*, 2012; Copeland *et al.*, 2013; Adey *et al.*, 2015a), Labrador Sea and Western
99 Greenland (Jørgensbye & Halfar, 2017; Schoenrock *et al.*, 2018a,b) and the Arctic (Teichert
100 *et al.*, 2012; 2014); this habitat is clearly much more abundant in Arctic environments than
101 was previously assumed.

102 Adey & Steneck (2001) identified as Arctic those marine habitats ranging in temperature
103 from ≤ 5 °C in summer to ~ -1.5 °C in winter, and as Subarctic, those experiencing 5-15 °C
104 in summer and -1.5 to +1 °C in winter. This characterization also applies to the NW Pacific
105 Subarctic, but in the NE Pacific Subarctic, summer temperatures range from 10-15 °C and
106 winter temperatures -1.5 to ~ 5 °C (based on oceanographic conditions where the species
107 occur). The Arctic and Subarctic are warming faster than most of the world's oceans, but
108 the impact this will have on marine photosynthetic organisms is largely unknown.

109 Wassmann *et al.* (2011) cited 51 reports of documented changes in the Arctic marine biota

110 in response to ocean warming, but most focused on marine mammals and fish. Two of
111 these papers focused on benthic marine algae, but neither on the corallines, the group that
112 provides the dominant benthic cover of seabed habitats in the photic zone (Adey & Hayek,
113 2011). Based on research carried out elsewhere, Brodie *et al.* (2014), however, projected a
114 significant decrease of coralline algae in the Arctic because anthropogenic carbon dioxide
115 emissions are causing ocean acidification, which in turn is causing waters in the photic
116 zone of the Arctic to become undersaturated with aragonite. Many coralline algae are
117 susceptible to reductions in the concentration of aragonite as this can make seawater
118 corrosive to their high magnesium calcite skeletons, a response that is mediated by the rate
119 of environmental change (Kamenos *et al.*, 2013; 2016; Martin & Hall-Spencer, 2017; Chan
120 *et al.*, 2020). Climate-change induced permafrost thawing and snow melting at high
121 latitudes also increase freshwater runoff and coastal nutrient inputs (Walvoord & Striegl,
122 2007; Kendrick *et al.*, 2018), which in turn can alter calcification rates and subsequent
123 coralline growth (McCoy & Kamenos, 2018; Bélanger & Gagnon, 2020) and
124 photophysiology (Schoenrock *et al.* 2018a). In this regard, Williams *et al.* (2020) observed
125 different responses among species of *Clathromorphum* Foslíe related to their sensitivity to
126 environmental change; thus, the widely distributed *C. compactum* (Kjellman) Foslíe might
127 expand its northern limit whereas the narrow-range *C. nereostratum* Lebednik is expected
128 to decline.

129 In Arctic and Subarctic regions, *Lithothamnion* Heydrich species often dominate
130 coralline algal assemblages from the low intertidal to the lower limit of the photic zone,
131 contributing significantly to shelf carbonate budgets (Freiwald & Henrich, 1994; Nelson,
132 2009; Adey & Hayek, 2011; Teed *et al.*, 2020). Several *Lithothamnion* species form maerl,

133 or branched crusts, and these structures significantly increase benthic habitat complexity
134 and biodiversity (Gagnon *et al.*, 2012; Teichert *et al.*, 2014; Jørgensbye & Halfar, 2017;
135 Schoenrock *et al.*, 2018b). Because several *Lithothamnion* species (like most coralline
136 algae) also induce larval settlement and metamorphosis in invertebrates with important
137 functional roles, the genus is considered an ecosystem engineer (Steneck, 1982; Rowley,
138 1989; Pearce & Schiebling, 1990; Nelson, 2009).

139 Adey and co-workers have been studying Arctic and Subarctic subtidal benthic non-
140 geniculate coralline communities for the past 50+ years, publishing numerous papers on the
141 ecology (Adey, 1964; 1965; 1966a, b; 1970a; 1971; Adey & McKibbin, 1970; Adey &
142 Adey, 1973; Adey *et al.*, 2005), physiology (Adey, 1970b; 1973; Adey *et al.*, 2013; 2015a)
143 and biogeography (Adey, 1966b; Adey *et al.*, 1976; 2008; Adey & Steneck, 2001) of these
144 algae, and recently have added DNA-based taxonomic and phylogenetic studies. Thus,
145 Arctic and Subarctic species of *Clathromorphum* (Adey *et al.*, 2015b), *Neopolyporolithon*
146 W.H.Adey & H.W.Johansen (Gabrielson *et al.*, 2019) and *Phymatolithon* Foslie (Adey *et*
147 *al.*, 2018) have largely been resolved, but *Lithothamnion* species still need clarification.
148 This is primarily due to the large number of species and infraspecific taxa that were named
149 in the late 19th and early 20th century primarily by the Norwegian corallinologist Mikael
150 Heggelund Foslie, but also by the Swedish phycologist Frans Reinhold Kjellman. Some of
151 these taxa have been placed in synonymy based on morpho-anatomy, but many are still
152 recognized (Guiry & Guiry, 2020) or are considered *Incertae Sedis* (Athanasiadis, 2016).
153 Studies of other coralline genera have shown increasingly that morpho-anatomy alone
154 cannot distinguish species (Sissini *et al.*, 2014; Peña *et al.*, 2014b; 2015a; Hernández-
155 Kantún *et al.*, 2016; Gabrielson *et al.*, 2018). Here, we assess many of the unresolved

156 species and infraspecific taxa of Arctic and Subarctic *Lithothamnion* to provide
157 fundamental taxonomic, ecological and biogeographic knowledge of these species in the
158 face of the anticipated but unknown effects of climate change on the marine flora of these
159 regions.

160

161 **Materials and Methods**

162 *Collections studied.* Fifty-eight type specimens of *Lithothamnion* species and infraspecific
163 taxa housed in TRH and UPS as well as eleven historical specimens in TRH (herbarium
164 acronyms follow Thiers, 2020) were considered for DNA analysis (Supplementary table
165 S1, Supplementary note S1). One of us (SCL), as a guest of the Department of Botany,
166 Stockholm University, located Kjellman's type specimens in UPS that are housed in a room
167 separate from the main algal collection. This may explain why earlier investigators were
168 unable to locate them. These specimens, described by F. R. Kjellman between 1877 and
169 1889 were later received on loan by PWG; specimens described by M. H. Foslie between
170 1891 and 1908 were examined by VP or PWG. Most of the specimens had their type
171 localities along the Norwegian coast but some of them were described from Svalbard,
172 Scotland, Greenland, Canada and USA (Kjellman, 1883; 1889; Foslie, 1891; 1895; 1896;
173 1900; 1905a, b; 1908). In addition, 440 recent collections from Norway, Svalbard,
174 Greenland, and the Atlantic and Pacific coasts of Canada and USA have also been
175 sequenced (Supplementary table S2). Most of these specimens were collected subtidally in
176 coralline algal beds (known as maerl or rhodolith beds) or as crusts, and they are preserved
177 in NCU, TRH, SANT, UBC and UNB (see collection details in Supplementary table S2).

178 *DNA sequencing and analyses.* Herbarium material was extracted and amplified at five
179 different institutions: the Muséum National d'Histoire Naturelle, Paris (MNHN), the
180 University of North Carolina, Chapel Hill (UNC), Hartnell University (HC), the University
181 of British Columbia (UBC), and the University of New Brunswick (UNB). Extractions and
182 amplifications of types and historical collections were accompanied by negative controls at
183 every step, and they were performed separately from recent collections. At the MNHN,
184 DNA of type specimens and historical collections were extracted using QIAamp[®]DNA
185 Micro Kit (Qiagen S.A.S., Les Ulis, France) following the manufacturer's protocol for
186 tissues; recent collections were DNA-extracted using a NucleoSpin[®] 96 Tissue kit
187 (Macherey-Nagel, GmbH and Co. KG, Germany). At UNC type material and recent
188 collections were extracted following Gabrielson *et al.* (2011); at HC type material was
189 extracted according to Hernández-Kantún *et al.* (2016) following the precautionary
190 guidelines proposed by Hughey & Gabrielson (2012); at UNB recent collections were
191 extracted following Saunders & McDevit (2012); at UBC recent collections were extracted
192 following Lindstrom & Fredericq (2003). Three genes (*rbcL*, *psbA* and COI) were
193 amplified in this study. For type specimens and historical collections, *rbcL* sequences were
194 obtained with two primer combinations, F1150Cor-R1460 or F1150Cor - RbcS-Start,
195 yielding a fragment trimmed to 263 bp (1172-1434) or 293 bp (1172-1464), respectively;
196 for recent collections, *rbcL* sequences of 1383 bp were obtained with two overlapping
197 primer combinations F57-R1150 and F753-RrbcS or with primer combination F753/RrbcS-
198 Start trimmed to 691 bp (772-1464), or followed Saunders & Moore (2013) for
199 amplifications completed at UNB. For recent collections and for some type specimens and
200 historical collections, *psbA* sequences were obtained by the institutions mentioned above,

201 using the primer pairs psbA-F1/psbA-R2 and psbA-F1/psbA-600R (Yoon *et al.*, 2002),
202 following Peña *et al.* (2015b) or Adey *et al.* (2015b). COI-5P sequences were obtained only
203 for recent collections using the primer pairs Gaz-F1/Gaz-R2 and Gaz-F1/GCorR3,
204 following Saunders & Moore (2013) or Peña *et al.* (2015b). PCR products were purified
205 and sequenced at MNHN by Eurofins (Eurofins Scientific, Nantes, France); at UNC
206 according to Hughey *et al.* (2001) and sequenced at the DNA Analysis Core Facility,
207 Center for Marine Sciences, University of North Carolina, Wilmington; and at HC by
208 Functional Biosciences, Inc. (Madison, WI, USA). Sequences were assembled and aligned
209 with the assistance of CodonCode Aligner® (CodonCode Corporation, USA) or with
210 Sequencher (Gene Codes Corp., Ann Arbor, MI, USA) and adjusted manually using
211 SeaView version 4 (Gouy *et al.*, 2010) or using Sequence Alignment Editor
212 (<http://tree.bio.ed.ac.uk/software/seal/>); sequences were submitted to the Barcode of Life
213 Data Systems (BOLD projects ‘NCCAB’, ‘NGCOR’ and dataset ‘LITHOTH1’,
214 <http://www.boldsystems.org>; Ratnasingham & Hebert, 2007) and/or to GenBank (accession
215 numbers listed in Supplementary tables S1 and S2).

216 *DNA sequencing and analyses.* Three data sets were built, one for each gene (*rbcL*, *psbA*
217 and COI-5P), comprising *ca.* 526 sequences obtained in this study (Supplementary tables
218 S1 and S2) and supplemented with GenBank sequences publicly available for Arctic and
219 Subarctic collections of *Lithothamnion* as well as for other Hapalidiales genera
220 (*Clathromorphum* and *Phymatolithon*) for which relevant matches were found
221 (Supplementary table S3). As out-group we used *rbcL* and *psbA* sequences linked to the
222 generitype *Lithophyllum incrustans* Philippi, order Corallinales; for COI-5P we used a
223 sequence generated from the neotype of *Phymatolithon calcareum* (Pallas) Adey &

224 McKibbin, order Hapalidiales (Supplementary table S3). Phylogenetic relationships were
225 inferred with maximum likelihood (RAxML) and Bayesian inference (BI) using Mega 6.06
226 (Tamura *et al.*, 2013), RAxML 8.1.11 (Stamatakis, 2014; available in CIPRES Science
227 Gateway, Miller *et al.*, 2010) and MrBayes 3.2.1 (Ronquist & Huelsenbeck, 2003). Models
228 of sequence evolution were estimated using the Akaike Information Criterion (AIC) and the
229 Bayesian Information Criterion (BIC) obtained in jModeltest 2.1.3 (Darriba *et al.*, 2012).
230 Maximum likelihood for the *rbcL*, COI-5P and *psbA* alignments were performed under a
231 generalized time-reversible with invariant sites heterogeneity model (GTR+I+G). The
232 Bayesian analyses for the *rbcL* and *psbA* alignments were performed under the same model
233 (GTR+I+G) with four Markov Chain Monte Carlo method for 10 million generations, and
234 tree sampling every 1,000 generations.

235 *Distribution of Arctic/Subarctic Lithothamnion species studied.* Geographic coordinates
236 were obtained by GPS for each sequenced collection and were estimated for types and
237 historical specimens using Google Earth Pro 7.3.3.7786 (© 2020 Google LLC).

238 Distribution maps were created by projecting latitude and longitude of all specimens
239 delimited for each species using QGIS3.10 (QGIS.org, 2020) with North Pole Lambert
240 Azimuthal Equal Area projection. The following shape file was used for the map
241 background: <https://www.data.gouv.fr/fr/datasets/continents/>

242

243 **Results**

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

247 The *rbcL* alignment comprised 121 sequences of variable length resulting in 81
248 unique DNA sequences ranging from 205 to 313 bp, with 114 variable sites. Both ML and
249 Bayesian analyses resolved the type specimens and historical collections with moderate to
250 full support in different Hapalidiales lineages encompassing species of *Lithothamnion*,
251 *Phymatolithon* and *Clathromorphum*, Fig. 1). Most of the type specimens and historical
252 collections sequenced were situated within lineages represented by the lectotype of
253 *Lithothamnion glaciale* Kjellman (0-3 bp differences, up to 1.14 % divergence -uncorrected
254 p-distance-), followed by the lectotype of *L. soriferum* Kjellman (0-1 bp differences, up to
255 0.41% divergence) and then the neotype of *L. tophiforme* (0-2 bp, up to 0.68% divergence)
256 (Fig. 1). Three type specimens were placed in the genus *Phymatolithon* (Fig. 1,
257 Supplementary table S1): the holotype of *Lithothamnion scabriusculum* Foslie was
258 positioned within a clade encompassing collections of *P. rugulosum* W.H.Adey (1-3 bp
259 differences; 0.3-1% divergence); the lectotype of *L. squarulosum* f. *palmatifidum* Foslie
260 was resolved within a clade represented by the neotype of *P. calcareum* (2 bp differences,
261 0.9% divergence); the holotype of *Lithothamnion lenormandii* f. *squamulosum* (Foslie)
262 Cotton was identical in sequence to the isotype of *P. squamulosum* (Foslie) W.H.Adey,
263 Hernández-Kantún & P.W.Gabrielson. Another two lectotypes (*L. coalescens* Foslie and *L.*
264 *evanescens* Foslie) and one historical collection of *Clathromorphum circumscriptum*
265 (Strömfelt) Foslie from Norway were identical in sequence to the epitype of *C.*
266 *circumscriptum* (0 bp differences, Fig. 1); the infraspecific variation within *C.*
267 *circumscriptum* ranged up to 13 bp differences (1.3% uncorrected p-distance) and it
268 increased up to 14 bp differences (1.4%) after comparison with two further *rbcL* sequences
269 obtained from recent collections from Alaska (UBC A92115 and UBC A94120, not

270 included in Fig. 1). None of the types and historical collections sequenced were resolved
271 within the lineage of *Lithothamnion lemoineae* W.H.Adey; only three recent collections
272 (UBC A94112, Fig. 1, together with UBC A94113 and UBC A94121, as *Lithothamnion*
273 sp., not included in Fig 1, Supplementary table S2) appeared to be closely related to *L.*
274 *lemoineae*, showing at minimum 11 bp differences (1.15 % of divergence) between the
275 taxa.

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

288 The *psbA* alignment comprised 421 sequences that resulted in 124 unique
289 sequences, ranging from 382 to 851 bp with 249 variable sites. The alignment encompassed
290 recent collections, five type collections generated in the present study and publicly
291 available sequences from GenBank such as the holotypes of *L. erinaceum* and *L.*
292 *lemoineae*, and the isotype of *P. rugulosum* (herein as *P. scabriusculum*, see next section of

293 taxonomic proposals) (Supplementary tables S1-S3). Both RAxML and Bayesian analyses
294 (Supplementary fig. S2) resolved our recent collections in different lineages pertaining to
295 the genera *Clathromorphum* (*C. circumscriptum*), *Phymatolithon* (*P. squamulosum*), and
296 *Lithothamnion* (*L. lemoineae*, *L. tophiforme*, *L. glaciale* and *L. erinaceum* [herein as *L.*
297 *soriferum*, see next paragraph of taxonomic proposals]). In agreement with results obtained
298 for *rbcL*, both RAxML and Bayesian analyses of *psbA* resolved these type collections in
299 three different genera (Supplementary fig. S2): *Lithothamnion* (neotype of *L. glaciale* f.
300 *subsimplex* Foslie), *Clathromorphum* (lectotypes of *L. coalescens* and *L. evanescens*) and
301 *Phymatolithon* (holotype of *L. lenormandii* f. *squamulosa* and lectotype of *L. squarrulosum*
302 f. *palmatifida*). However, one recent collection (as *Lithothamnion* sp., Supplementary fig.
303 S2, Supplementary table S2) was distinct in sequence from all other analyzed taxa, and it
304 did not return any relevant match with publicly available GenBank sequences. In contrast to
305 *rbcL* and COI analyses, the support values obtained were generally lower, particularly for
306 *L. glaciale* with weak support (Supplementary fig. S2).

307 Given the molecular evidence noted above, and in accordance with Article 11.4 of
308 the International Code of Nomenclature for algae, fungi, and plants (ICN, Turland *et al.*,
309 2018), we present the following taxa with the corresponding heterotypic synonyms from
310 the present study.

311

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

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

314 HOMOTYPIC SYNONYMS:

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

316 *Clathromorphum compactum* f. *circumscriptum* (Strömfelt) Foslie, 1908: 11.
317 *Lithothamnion compactum* f. *circumscriptum* (Strömfelt) Lund, 1959: 200.
318 LECTOTYPE: S; seven microscope slides apparently from the original material designated
319 by Athanasiadis (2016: 251) as the holotype, but as Strömfelt (1886) designated syntype
320 localities, this material is better called a lectotype. This is a correctible error in accordance
321 with Art. 9.10 of the ICN (Turland *et al.*, 2018).
322 *Comment*: Adey *et al.* (2015b), while designating an epitype for *C. circumscriptum*
323 inadvertently omitted submitting this epitype sequence to GenBank. This has now been
324 rectified: GenBank XXXXXXXXX, an *rbcL*-263 (bp 1172-1434) sequence.
325
326 HETEROTYPIC SYNONYMS:
327 *Lithothamnion coalescens* Foslie, 1895: 162 (reprint 134), pl. 19, figs. 15-20.
328 *Clathromorphum coalescens* (Foslie) Foslie, 1898b: 8.
329 *Phymatolithon compactum* f. *coalescens* (Foslie) Foslie, 1905a: 8.
330 LECTOTYPE: TRH C21-3503; 12.viii.1893, leg. unknown.
331 TYPE LOCALITY: Inderøen, Strømmen, Trondheimsfjord, Norway.
332 *Lectotype DNA sequences*: *psbA* and *rbcL*-263 (bp 1172-1434), GenBank XXXXXXXXX
333 and XXXXXXXXX.
334 *Comment*: Following his description, Foslie (1895) transferred the species without
335 comment to *Clathromorphum* (Foslie, 1898b). Later, Foslie (1905a) reduced
336 *Clathromorphum* to a subgenus of *Phymatolithon* and reduced *C. coalescens* to a form of
337 *Phymatolithon*, as *P. compactum* f. *coalescens*. This name was not treated by Lebednik
338 (1977) nor by Adey *et al.* (2015b), but was listed by Athanasiadis (2016) as a synonym of

339 *C. compactum* (Kjellman) Foslie. According to Woelkerling *et al.* (2005), the lectotype of
340 *L. coalescens* is a blue box with five specimens that was earlier designated by Woelkerling
341 (1993: 52) as the lectotype, noting that Foslie (1895: 163) had cited two syntype localities.
342 Upon examination, the box contained four specimens illustrated in Foslie (1895, pl. 19,
343 among figs. 15-20), one of which was sequenced, and herein the lectotype is narrowed to
344 that sequenced specimen (GenBank XXXXXXXXX and XXXXXXXX) as allowed by Art.
345 9.17 of the ICN (Turland *et al.*, 2018). Both the *rbcL* and *psbA* sequences obtained are
346 identical to GenBank sequences of *C. circumscriptum* (voucher US 169083), which were
347 confirmed as identical to the epitype (voucher US 170939, Adey *et al.*, 2015b: 195).

348

349 *Lithothamnion durum* Kjellman, 1889: 22, pl 1. figs. 3-5.

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

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

352 TYPE LOCALITY: Port Clarence, Alaska, USA.

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

359 *Comment*: This synonymy was first proposed by Foslie (1900: 10) and was accepted by
360 Lebednik (1977: 64); the latter noted that a fragment, apparently from the holotype, was in
361 TRH. This fragment is now considered an isotype (Art. 8.3, Turland *et al.* 2018). The

362 holotype illustrated by Kjellman (1889, pl. 1, fig. 3), was found in UPS, and the DNA
363 sequence was obtained from the specimen labeled "b" (Kjellman, 1889, pl. 1, fig. 3). We
364 did not sequence the fragment in TRH.
365
366 *Lithothamnion evanescens* Foslie, 1895: 137.
367 *Clathromorphum evanescens* (Foslie) Foslie, 1898b: 8.
368 *Phymatolithon evanescens* (Foslie) Foslie, 1905a: 92.
369 LECTOTYPE: TRH C21-3518, iv.1889, leg. F.S. Collins.
370 TYPE LOCALITY: Marblehead, Massachusetts, USA.
371 *Lectotype DNA sequences: psbA and rbcL-263* (bp 1172-1434), GenBank XXXXXXXXX
372 and XXXXXXXXX.
373 *Comment:* Foslie (1895: 137, Pl. 22 figs. 6, 7) cited and illustrated specimens from two
374 syntype localities, Marblehead, Massachusetts, USA collected by F. S. Collins and from
375 Mastervik, Malangen, Norway collected by himself. Foslie transferred the species twice,
376 first, without comment, to *Clathromorphum* (Foslie 1898b), and later to *Phymatolithon*
377 after admitting that *Clathromorphum* should be considered a subgenus of the latter (Foslie,
378 1905a: 87). Lebednik (1977) first proposed that this species was a synonym of *C.*
379 *circumscriptum*, and this was accepted by Athanasiadis (2016). Woelkerling (1993: 87)
380 designated as lectotype a single specimen collected by Collins in Marblehead,
381 Massachusetts and illustrated by both Foslie (1895, Pl. 22, fig 6) and Printz (1929, pl. 41,
382 fig. 13). Woelkerling (1993) justified the selection of this specimen as lectotype because
383 "...it was in better condition and had numerous conceptacles". Both *rbcL* and *psbA*
384 sequences obtained for this lectotype specimen are identical to GenBank sequences of *C.*

385 *circumscriptum* (voucher US 169083), which was confirmed as identical to the epitype
386 (voucher US 170939, Adey *et al.*, 2015b: 195).

387

388 *Historical collection:*

389 TRH C20-3495, as *Lithothamnion circumscriptum*. Tamsøya, Finnmark, Norway, vii.1897,

390 no habitat data, no collector. *DNA sequence: rbcL-263* (bp 1172-1434), GenBank

391 XXXXXXXXX (Supplementary table S1). The largest fragment of the four in the box was

392 sequenced.

393

394 *Recent collections:*

395 Norway: Porsangerfjorden (Finnmark) and Krøttøya (Troms). Intertidal to subtidal (6 m

396 depth), encrusting pebbles and pottery, on hard substrata and associated with maerl beds.

397 One specimen collected in Krøttøya had uniporate conceptacles (gametangial or

398 carposporangial). *DNA sequences: psbA* (Supplementary table S2).

399

400 ***Lithothamnion glaciale* Kjellman, 1883: 123-127, pls. 2, 3.**

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

402 TYPE LOCALITY: Mosselbay, Spitsbergen.

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

404 *Comment:* Adey (1970a) made a provisional lectotypification based on "... a Spitzbergen

405 specimen (No. 241, Institute of Taxonomy, Uppsala) collected by Kjellman in 1872-1873."

406 Adey (1970a) further stated that this specimen was not one illustrated by Kjellman (1883)

407 that accompanied the original description. The ICN does not accept provisional lectotypes

408 (Art. 7.11, Turland *et al.* 2018). Chamberlain & Irvine (1994), repeated Adey's (1970a)
409 lectotypification, thus making it acceptable, but stated that they did not see the specimen.

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

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

425

426 HETEROTYPIC SYNONYMS:

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

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

429 TYPE LOCALITY: Drøbak, Norway.

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

431 *Comment:* Woelkerling (1993) located four of five specimens as part of the protologue of *L.*
432 *apiculatum* f. *connatum* and designated these lectotype. They have been illustrated by
433 Foslie (1895, pl. 15, figs. 9-12) and by Printz (1929, pl. 21, figs. 11-15) under the name *L.*
434 *colliculosum* f. *pusilla*. One of these four specimens, branched and epilithic on a pebble
435 (among the specimens illustrated as figs. 9-11, Foslie 1895, pl. 15) was sequenced, and
436 herein this lectotype is narrowed to that specimen as allowed by Art. 9.17 of the ICN
437 (Turland *et al.*, 2018).

438

439 *Lithothamnion battersii* Foslie, 1896: 1, pl. 1, figs. 1-5.

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

441 TYPE LOCALITY: Cumbrae, Scotland.

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

443 *Comment:* The holotype collection comprises five individuals illustrated by Foslie (1896,
444 pl. 1, figs. 1-5); the specimen sequenced is depicted in Foslie's (1896) figure 2. Based on
445 morpho-anatomy, Chamberlain & Irvine (1994: 182) and Athanasiadis (2016: 217)
446 correctly listed *L. battersii* as a synonym of *L. glaciale*.

447

448 *Lithothamnion colliculosum* Foslie, 1891: 43, pl. 3, fig. 1.

449 LECTOTYPE: TRH B11-2311, 8.ix.1890, leg. M. H. Foslie (designated by Woelkerling,
450 1993: 53).

451 TYPE LOCALITY: Skorpen, Kvænanen, Norway.

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

453 *Comment:* Foslie (1891: 43-45, pl. 3, fig. 1) described and illustrated eight individual
454 specimens that he ascribed to this species. Adey & Lebednik (1967: 71) could not locate
455 any of these specimens, and therefore Adey (1970c) designated as neotype one specimen
456 from Kragerø collected in 1890. Later, Woelkerling (1993: 54) located in TRH numerous
457 specimens with the original collection data of *L. colliculosum*, including four of the eight
458 individuals comprising the holotype and depicted by Foslie (1891, pl. 3, fig. 1). Because the
459 other four individuals comprising the holotype remain missing, Woelkerling designated the
460 found specimens as the lectotype of *L. colliculosum*, superseding Adey's neotype. As
461 allowed by Article 9.17 of the ICN (Turland *et al.*, 2018), we herein narrow the lectotype to
462 the individual sequenced crust among the original specimens depicted by Foslie (1891, pl.
463 3, fig. 1, bottom row, second from right). Based on morpho-anatomy Athanasiadis (2016:
464 224) listed *L. colliculosum* as *Incertae Sedis*; DNA sequence data has confirmed the
465 placement of the species in *L. glaciale*.

466

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

468 LECTOTYPE: TRH B20-2706, 12.vii.1898, leg. H. H. Gran (designated by Woelkerling
469 1993: 185).

470 TYPE LOCALITY: Drøbak, Norway.

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

472 *Comment:* We sequenced one of the 14 specimens comprising the lectotype, which is
473 located separately within a blue box with label “Prep. 76-77”. As allowed by Art. 9.17 of
474 the ICN (Turland *et al.*, 2018) we narrow the lectotype to the sequenced specimen. Based

475 on morpho-anatomy Athanasiadis (2016: 224) listed *L. colliculosum* f. *pusillum* as *Incertae*
476 *Sedis*; DNA sequence data has confirmed the placement of the species in *L. glaciale*.

477

478 *Lithothamnion congregatum* Foslie, 1895: 142, pl. 20, figs. 1-6.

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

480 1900: 13.

481 LECTOTYPE: TRH C7-3062, 20.vii.1894, leg. M. H. Foslie (designated by Woelkerling,

482 1993: 60-61).

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

484 2005: 424).

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

486 *Comment:* Foslie (1895: 142-144, pl. 20, figs. 1-6) described and illustrated this species
487 based on six individuals from a single locality, and he compared the species to two other
488 species that he named in the same publication, *L. dehiscens* Foslie and *L. nodulosum* Foslie.

489 Later, Foslie (1900) reduced *L. congregatum* to a form of *L. nodulosum*. The sequenced
490 specimen is illustrated in Foslie (1895, pl. 20, fig. 2), and the lectotype is here narrowed to

491 that sequenced specimen as allowed by Art. 9.17 of the ICN (Turland *et al.*, 2018). Based

492 on morpho-anatomy Athanasiadis (2016: 224) listed *L. congregatum* as *Incertae Sedis*;

493 DNA sequence data has confirmed the placement of the species in *L. glaciale*.

494

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

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

497 1993: 195).

498 TYPE LOCALITY: Røberg (now Raudberget), Norway (Woelkerling *et al.*, 2005: 413).
499 *Lectotype DNA sequence: rbcL-293* (bp 1172-1464), GenBank XXXXXXXXX.
500 *Comment:* Woelkerling (1993: 195-196) located and designated as the lectotype four of the
501 original 12 specimens included by Foslie (1895, pl. 16, figs. 14-17) in the original
502 protologue of this form. The specimen sequenced had a green label “Prep. 100-101”; it
503 resembled the specimen illustrated in Foslie (1895, pl. 16, fig. 16). The lectotype is here
504 narrowed to this single sequenced specimen as allowed by Art. 9.17 of the ICN (Turland *et*
505 *al.*, 2018).
506
507 *Lithothamnion dimorphum* Foslie, 1895: 68, pl. 10, figs. 1-6.
508 HOMOTYPIC SYNONYM: *Lithothamnion fornicatum* f. *dimorphum* (Foslie) Foslie,
509 1905a: 38.
510 LECTOTYPE: TRH B25-2773, 10.vii.1894, 0-5.5 m depth on sandy and stony bottom, leg.
511 M. H. Foslie (designated by Woelkerling, 1993: 75).
512 TYPE LOCALITY: Frøjen (now Frøya), Rottingsundet, Trondeland, Norway (Woelkerling
513 *et al.*, 2005: 375).
514 *Lectotype DNA sequence: rbcL-293* (bp 1172-1464), GenBank XXXXXXXXX.
515 *Comment:* Foslie (1895, pl. 10, figs. 1-6) illustrated six specimens belonging to this species,
516 but did not designate a holotype. Woelkerling (1993: 74-75) designated as the lectotype
517 four of the six specimens depicted in figs. 1, 3, 5 and 6 (Foslie, 1895, pl. 10). Herein, as
518 allowed by Article 9.17 of the ICN (Turland *et al.*, 2018), we narrow the lectotype to the
519 Foslie 1895, pl. 10, fig. 3 specimen that we sequenced. Based on morpho-anatomy,

520 Athanasiadis (2016: 225) listed *L. dimorphum* as *Incertae Sedis*; DNA sequence data have
521 confirmed the placement of the species in *L. glaciale*.
522

523 *Lithothamnion divergens* Foslie, 1895: 96, pl. 16, figs. 43-50.
524 HOMOTYPIC SYNONYMS: *Lithothamnion ungeri* f. *divergens* (Foslie) Foslie, 1900: 11;
525 *Lithothamnion tophiforme* f. *divergens* (Foslie) Foslie, 1905a: 51.
526 HOLOTYPE: C11-3167, 8.ix.1890, leg. M. H. Foslie.
527 TYPE LOCALITY: Kvaenangen, Skørpen (now Skorpa), Norway (Woelkerling *et al.*,
528 2005: 438).
529 *Holotype DNA sequence*: rbcL-293 (bp 1172-1464), GenBank XXXXXXXXX.

530 *Comment*: The holotype material comprised two boxes (one round and one quadratic) with
531 seven specimens and fragments (Woelkerling, 1993: 80; Woelkerling *et al.*, 2005: 438).
532 The sequenced specimen is located in the round box with the green tag “Lith. Mon. pl. 20,
533 f. 8” and illustrated in Foslie (1895, pl. 16, fig. 48) and Printz (1929, pl. 20, fig. 8). As
534 allowed by Art. 9.17 of the ICN (Turland *et al.*, 2018), the holotype is here narrowed to the
535 one sequenced specimen. Based on morpho-anatomy, Athanasiadis (2016: 226) listed *L.*
536 *divergens* as *Incertae Sedis*; DNA sequence data confirm the placement of the species in *L.*
537 *glaciale*.
538

539 *Lithothamnion fornicatum* f. *sphaericum* Foslie, 1900: 12 (as '*sphaerica*').
540 HOLOTYPE: TRH B26-2789, 20.vii.1894, no habitat data, leg. M. H. Foslie.
541 TYPE LOCALITY: Skjørn, Dalsøren (now Stjørna, Daleøra), Trondheimsfjorden, Norway
542 (Woelkerling *et al.*, 2005: 380).

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

544 *Comment:* Foslie (1900) only provided a reference to a previously published figure (Foslie
545 1895, pl. 12, fig. 1) for the protologue of this form, but Woelkerling (1993: 205) considered
546 this a validly published name. We sequenced the same individual rhodolith cited by Foslie
547 (1900) and illustrated in Foslie (1895, pl. 12, fig. 1).

548

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

550 LECTOTYPE: TRH B25-2777, 6.vii.1894, leg. M. H. Foslie (designated by Woelkerling,
551 1993: 91).

552 TYPE LOCALITY: Bejan (now Beian), Beiskjaeret, Norway (Woelkerling *et al.*, 2005:
553 377).

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

555 *Comment:* Foslie (1895, pl. 5, figs. 1-7) illustrated seven individual rhodoliths that
556 according to Woelkerling (1993) came from two collections from neighboring localities on
557 successive days. Woelkerling (1993: 91) designated as the lectotype collection nine
558 specimens comprising two of those illustrated in the protologue (Foslie, 1895, pl. 5, figs. 5
559 and 7) and seven other specimens. As allowed by Art. 9.17 of the ICN (Turland *et al.*,
560 2018), the lectotype is here narrowed to the sequenced specimen that is marked with label
561 “nr. 2”, which is cited as part of the lectotype in Woelkerling *et al.* (2005: 377).

562

563 *Lithothamnion fruticulosum f. flexuosa* Foslie, 1895, pl. 7, figs. 1-3.

564 LECTOTYPE: TRH B27-2805, 15.viii.1890, leg. M. H. Foslie (designated by Woelkerling,
565 1993: 95).

566 TYPE LOCALITY: Tromsø, Norway.

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

568 *Comment:* Foslie (1895) based this form on collections from several localities in Norway,
569 but did not designate a type. Woelkerling (1993) designated the specimen illustrated by
570 Foslie (1895, pl. 7, fig. 3) as the lectotype of this form. According to Woelkerling *et al.*
571 (2005), the lectotype has two green tags, and this was the specimen from which the DNA
572 sequence was obtained.

573

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

575 LECTOTYPE: TRH B8-2153, 12.vi.1892, leg. unknown (designated by Printz, 1929, pl.
576 22, fig. 5 legend).

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

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

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

584

585 *Lithothamnion glaciale f. subsimplex* Foslie, 1905a: 27.

586 NEOTYPE: TRH B9-2255, 22.vi.1900, leg. E. Bay. Woelkerling (1993: 215) designated as
587 neotype the specimen illustrated by Printz (1929, pl. 23, fig. 5).

588 TYPE LOCALITY: the southern coast of Ellesmereland, Havnefjorden; Northwest
589 Territories, Canada (Woelkerling 1993: 215; Woelkerling *et al.*, 2005: 300).
590 *Neotype DNA sequence: rbcL-293* (bp 1172-1464), GenBank XXXXXXXXX.
591 *Comment:* Athanasiadis (2016) listed this taxon as a synonym of *L. glaciale*, but with a
592 query (?); DNA sequence data have confirmed this synonymy.
593
594 *Lithothamnion gracilescens* Foslie, 1895: 87, pl. 15, figs. 20-27, *nom. illeg.*
595 HOMOTYPIC SYNONYM: *Lithothamnion nodulosum* f. *gracilescens* Foslie, 1900: 13,
596 *nom. illeg.*
597 LECTOTYPE: TRH C6-3037, 6.vi.1894, leg. M. H. Foslie (designated by Woelkerling,
598 1993: 109; further information in Woelkerling *et al.*, 2005: 419).
599 TYPE LOCALITY: Rotvold [now Rotvoll], Trondsheimsfjord, Norway (Woelkerling *et*
600 *al.*, 2005: 419).
601 *Lectotype DNA sequence: rbcL-293* (bp 1172-1464), GenBank XXXXXXXXX.
602 *Comment:* Foslie (1895) proposed *Lithothamnion gracilescens* for the coralline that Unger
603 (1858: 19) had called *Lithothamnion byssoides*, but Kjellman (1883: 120) already had
604 named this entity *Lithothamnion ungeri*. Foslie (1895: 90) listed three syntype localities,
605 Madal, Dröbak and Rotvold, and from the last location illustrated eight individuals (Foslie
606 1895, pl. 15, figs. 20-27). Later, Foslie (1900) without comment reduced *L. gracilescens* to
607 a form of *L. nodulosum* as *L. nodulosum* f. *gracilescens*. The specimen sequenced
608 corresponds to Foslie (1895, pl. 15, fig. 24), to which the lectotype is narrowed as allowed
609 by Art. 9.17 of the ICN (Turland *et al.*, 2018). Based on morpho-anatomy Athanasiadis

610 (2016: 228) listed *L. gracilescens* as *Incertae Sedis*; DNA sequence data have confirmed the
611 placement of the species in *L. glaciale*.

612

613 *Lithothamnion intermedium* Kjellman, 1883: 127, pl. 4, figs. 1-10.

614 HOMOTYPIC SYNONYMS: *Lithothamnion fruticosum* f. *intermedium* (Kjellman)

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

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

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

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

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

624

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

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

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

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

631 *Comment*: Woelkerling (1993: 107) located two of the four specimens illustrated by Foslie
632 (1891, pl. 3, fig. 3). The specimen sequenced is illustrated in Foslie (1891, pl. 3, fig. 3,

633 second specimen from the left), and it is this specimen to which the lectotype is here
634 narrowed as allowed by Art. 9.17 of the ICN (Turland *et al.*, 2018). Athanasiadis (2016:
635 234) lists as *Incertae Sedis*; DNA sequence data have confirmed the placement of the
636 species in *L. glaciale*.

637

638 *Lithothamnion tusterense* Foslie, 1905a: 65.

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

640 TYPE LOCALITY: Tusteren (now Tustna), Kristiansund, Norway (Woelkerling *et al.*,
641 2005: 428).

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

643 *Comment:* Woelkerling (1993: 229) considered the material in the Foslie herbarium
644 illustrated by Printz (1929, pl. 22, figs. 6-13) to be the holotype, and we agree. The
645 specimen sequenced is marked with a green tag “pl. 27, fig. 9”, but the specimen
646 corresponds to the plate 22, figure 9 in Printz (1929), as was noted by Woelkerling *et al.*
647 (2005: 428). Based on morpho-anatomy, Athanasiadis (2016: 235) listed *L. tusterense* as
648 *Incertae Sedis*; DNA sequence data have confirmed the placement of the species in *L.*
649 *glaciale*.

650

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

652 LECTOTYPE: TRH C8-3077, 6.ix.1897, leg. M. H. Foslie. Woelkerling (1993: 233)
653 designated as lectotype the specimens illustrated by Printz (1929, pl. 33, figs. 12, 13 and
654 15).

655 TYPE LOCALITY: Svolvær, Lofoten, Norway.

656 *Lectotype DNA sequence: rbcL-293* (bp 1172-1464), GenBank XXXXXXXXX.
657 *Comment:* Foslie (1905b) based this species on two collections, one dead, excavated from
658 Vardø, Norway, the other living from Lofoten, Svolvær, Norway. Adey & Lebednik (1967:
659 77) examined material in TRH under this name, but did not designate a lectotype; this was
660 done by Woelkerling (1993: 233). The specimen sequenced corresponds to the one depicted
661 in Printz (1929, pl. 32, fig. 12), and as allowed by Art. 9.17 of the ICN (Turland *et al.*,
662 2018), the lectotype is here narrowed to this specimen. Based on morpho-anatomy,
663 Athanasiadis (2016: 223) listed *L. vardoense* as *Incertae Sedis*; DNA sequence data have
664 confirmed the placement of the species in *L. glaciale*.

665

666 *Historical collections:*

667 TRH C12-3177, as *Lithothamnion tophiforme*. Sukkertoppen, Greenland, no date, leg.
668 Petersen. *DNA sequence: rbcL-263* (bp 1172-1434), GenBank XXXXXXXXX.
669 TRH B10-2305, as *Lithothamnion glaciale f. subfastigiatum* (as '*subfastigiata*').
670 Bekkarfjord, Alten [now Alta], Norway, 21.viii.1897, leg. M. H. Foslie. *DNA sequence:*
671 *rbcL-293* (bp 1172-1464), GenBank XXXXXXXXX. *Comment:* The largest fragment in the
672 collection was sequenced. The sequence was identical to the lectotype sequence of
673 *Lithothamnion colliculosum f. pusillum*, shown herein as a heterotypic synonym of *L.*
674 *glaciale*. *L. glaciale f. subfastigiatum* is considered a superfluous substitute name for
675 *Lithothamnion varians f. varians* Foslie (Woelkerling *et al.*, 2005: 306); the lectotype of *L.*
676 *variens f. variens* (TRH C23-3649) was DNA-extracted but failed to amplify (see
677 Supplementary note S1).

678

679 **Infraspecific taxa of *Lithothamnion glaciale* confirmed as *L. glaciale*.**

680 *Lithothamnion glaciale* f. *subsimplex* Foslie, 1905a: 27.

681 NEOTYPE: TRH B9-2255, 22.vi.1900, leg. E. Bay, designated by Woelkerling *et al.*

682 (2005: 300).

683 *Type locality*: the southern coast of Ellesmereland, Havnefjorden; Northwest Territories,

684 Canada (Woelkerling *et al.*, 2005: 300).

685 *Neotype DNA sequence*: *rbcL*-293 (bp 1172-1464), GenBank XXXXXXXXX.

686 *Comment*: The neotype sequence was identical to the lectotype sequence of *Lithothamnion*

687 *colliculosum* f. *pusillum*, shown herein as a heterotypic synonym of *L. glaciale*.

688

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

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

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

692 *Lectotype DNA sequences*: *rbcL*-263 (bp 1172-1434), GenBank XXXXXXXXX,

693 XXXXXXXXX and XXXXXXXXX.

694 *Comment*: Kjellman (1883) did not designate a type specimen for his new species. As with

695 *L. glaciale*, one of us (SCL) located in UPS type material of *L. soriferum* that agrees, with

696 some artistic license, to the three entire specimens illustrated by Kjellman (1883, pl. 1, figs.

697 1-4). In the figure legends, Kjellman refers to the figure 1 specimen as young (ungt), the

698 figure 2 specimen as older (äldre) and seen from above (ofvanifrån), the figure 3 specimen,

699 the same (samma) specimen (as in figure 2) seen from below (underifrån), and the figure 4

700 specimen as full grown (fullvuxet). An *rbcL*-263 sequence was obtained from each of these

701 specimens, and the sequences are identical to each other. Kjellman (1883: 120) listed six

702 syntype localities Tromsö, Carlsö, Maasö, Magerö, Honningsvaag and Lebesby, the last
703 two localities based on specimens sent to Kjellman by Foslie; the syntype corresponding to
704 the latter locality –Lebesby– was also sequenced (TRH C13-3185, see below). The three
705 specimens in UPS were found in a single envelope (Supplementary fig. S4A) with the
706 locality "Norway. Finnmark: Hammerfest, Måsö [Måsöya]". Following Article 9.3
707 (Turland et al. 2018) we herein designate these three specimens as the lectotype of *L.*
708 *soriferum*.

709 The identical *rbcL*-263 sequences of all three UPS specimens are an exact match to
710 GenBank sequences of the recently described *Lithothamnion erinaceum* (Melbourne *et al.*,
711 2017). Following Article 11.4 of the ICN (Turland *et al.*, 2018), the correct name is the
712 combination of the final epithet of the earliest legitimate name of the taxon at the same
713 rank. Consequently, *L. soriferum* has nomenclatural priority over *L. erinaceum*, and it is the
714 correct name for this taxon. Further information about the heterotypic synonym *L.*
715 *erinaceum* is in the entry below.

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

718 TYPE LOCALITY: Lebesby, Finmarken (now Finnmark), Norway (Woelkerling *et al.*,
719 2005: 441).

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

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

723 *Lectotype SEM observations:* A vertical section through a protuberance showed the radial
724 construction (Supplementary fig. S4B-D) and an extensive perithallus. Thallus construction

725 was monomerous with elongate hypothallial cells (Supplementary Fig. S4E). Fusions
726 occurred between cells of adjacent perithallial filaments (Supplementary fig. S4F), and
727 secondary pit connections were absent. There was a single layer of epithallial cells, and
728 each epithallial cell had flared walls (Supplementary Fig. S4F-H). A single layer of
729 intercalary meristematic cells (subepithallial initials) was composed of cells shorter than or
730 as long as subtending perithallial cells (Supplementary fig. S4F-H).

731

732 HETEROTYPIC SYNONYMS:

733 *Lithothamnion breviaxe* Foslie, 1895: 44, pl. 2, figs. 1-2.

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

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

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

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

745

746 *Lithothamnion erinaceum* Melbourne & J.Brodie, 2017: 7, figs. 3, 7-9, 11.

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

748 TYPE LOCALITY: Loch Creran, Oban, Scotland (Melbourne *et al.*, 2017).
749 *Holotype DNA sequences*: GenBank KX828452 (*psbA*) and KX828509 (COI-5P)
750 (Melbourne *et al.*, 2017); GenBank MH697546 and MH697547 (*rbcL*, Hofman & Heesch
751 2018).
752 *Comment*: According to Melbourne *et al.* (2017), collections from Northern Ireland,
753 Iceland, Norway and British Columbia provided in Pardo *et al.* (2014) as *Lithothamnion* sp.
754 2 corresponded to *L. erinaceum*. Based on DNA sequences, these collections are also
755 assigned to *L. soriferum*, as well as the remaining specimens from the UK identified as
756 *Lithothamnion* sp. in Melbourne *et al.* (2017, Table S1). Additionally, GenBank records
757 from Norway identified as *L. erinaceum* (specimens “NCCA” in Supplementary Table S3)
758 correspond to *L. soriferum* (Anglés d’Auriac *et al.*, 2019).
759
760 *Lithothamnion fornicatum* Foslie, 1891: 38, pl. 2 (bottom specimen).
761 LECTOTYPE: TRH B21-2712, 20.ix.1890, leg. unknown (designated by Adey & Lebednik
762 1967: 71).
763 TYPE LOCALITY: Melangen [now Malangen], Mestervik, Tromsø county, Norway
764 (Woelkerling *et al.*, 2005: 366).
765 *Lectotype DNA sequence*: *rbcL*-293 (bp 1172-1464), GenBank XXXXXXXXX.
766 *Comment*: Foslie (1891) described and illustrated three specimens from the same locality.
767 Adey (1970c) noted that the lectotype, designated by Adey & Lebednik (1967: 71),
768 comprised two sets of specimens and that the selected set had a specimen pictured in the
769 original description, but Adey (1970c) did not indicate which of the three originally
770 pictured specimens is the designated lectotype. Woelkerling (1993: 97) and Woelkerling *et*

771 *al.* (2005: 366) provided information about the lectotype specimen illustrated in Foslie
772 (1891, pl. 2, bottom specimen) and marked with green tag “Præp. 151”. Based on morpho-
773 anatomy, Athanasiadis (2016: 228) listed *L. fornicatum* as *Incertae Sedis*; DNA sequence
774 data have confirmed the placement of the species in synonymy with *L. soriferum*.
775
776 *Lithothamnion granii* (Foslie) Foslie, 1900: 11.
777 BASIONYM: *Lithothamnion flabellatum* f. *granii* Foslie, 1895: 98, pl. 17, figs. 1-7, pl. 22,
778 fig. 1.
779 HOMOTYPIC SYNONYMS: *Lithothamnion glaciale* var. *granii* (Foslie) Rosenvinge,
780 1917: 222, figs. 138-142, pl. 3, fig. 4; pl. 4: figs. 1-4; *Lithothamnion glaciale* f. *granii*
781 (Foslie) Foslie 1905a: 10.
782 LECTOTYPE: TRH C10-3114, 12.vii.1893, no habitat data, leg. H. H. Gran (designated by
783 Adey & Lebednik, 1967: 78).
784 TYPE LOCALITY: Drøbak, Norway.
785 *Lectotype DNA sequence: rbcL-293* (bp 1172-1464), GenBank XXXXXXXXX.
786 *Comment:* The specimen sequenced is located in a large, round blue box; the label indicates
787 illustrations in Foslie (1895, pl. 17, fig. 3 and pl. 22, fig. 1) and Printz (1929, pl. 18, fig.
788 15). Foslie (1895: 98, pl. 17, figs. 1-7) described this new form, listed numerous syntype
789 localities and illustrated seven specimens. Later, Foslie (1900) elevated this form to specific
790 rank. Adey & Lebednik (1967) lectotypified the specimens collected by Gran, who is
791 honored by the form name. Subsequent to the original description, Foslie named five
792 additional forms, f. *robustum* (Foslie, 1895), f. *grandifrons*, f. *sphaericum* (Foslie, 1900),
793 and f. *obcrateriforme* and f. *tuberculatum* (Foslie, 1905a). We have not sequenced type

794 material of any of these forms, hence they are not listed as synonyms. Based on morpho-
795 anatomy, Athanasiadis (2016: 228) listed *L. granii* as *Incertae Sedis*; DNA sequence data
796 have confirmed the placement of the species in synonymy with *L. soriferum*.

797

798 *Lithothamnion nodulosum* Foslie, 1895: 144, pl. 21, figs. 1-6.

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

801 LECTOTYPE: TRH C5-2999, 18.vii.1894, leg. M. H. Foslie (designated by Woelkerling,
802 1993: 158).

803 TYPE LOCALITY: Brækstad (now Brekstad), Trondheimsfjorden, Norway (Woelkerling
804 *et al.*, 2005: 414).

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

806 *Comment:* We sequenced one of the three rhodoliths comprising the lectotype from
807 Brekstad, Norway, and the sequence was identical to *L. soriferum*. The specimen sequenced
808 is preserved in a round, red box; it is illustrated in Printz (1929, pl. 25, fig. 2) and not in pl.
809 21 as marked on the box (see Woelkerling *et al.*, 2005: 414). As allowed by Art. 9.17 of the
810 ICN (Turland *et al.*, 2018), the lectotype is here narrowed to the sequenced specimen.

811 Based on morpho-anatomy, Athanasiadis (2016: 228) listed *L. nodulosum* as *Incertae*
812 *Sedis*; DNA sequence data have confirmed the placement of the species in synonymy with
813 *L. soriferum*.

814

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

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

817 TYPE LOCALITY: The islet in front of the lighthouse, Røvær, Norway (Woelkerling *et al.*
818 2005: 323).

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

820 *Comment:* The partial *rbcL* sequence of the holotype is identical over its entire length to the
821 corresponding type sequences of *L. soriferum*. This is the only type specimen of a synonym
822 of *L. soriferum* that is an encrusting, epilithic coralline; all others are rhodoliths. The
823 holotype material comprised six epilithic crusts, with the piece illustrated in Printz (1929,
824 pl. 4, fig. 8) in a separate box (Woelkerling, 1993: 211). We sequenced the specimen
825 located separately within a blue, round box that corresponds to the piece illustrated in plate
826 4, figure 8 (Printz (1929)).

827

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

829 LECTOTYPE: TRH C11-3161, 5.viii.1882, leg. M. H. Foslie (designated by Woelkerling,
830 1993: 79).

831 TYPE LOCALITY: Tromsø, Norway.

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

833 *Comment:* Woelkerling *et al.* (2005: 437) noted that there was one specimen in the
834 lectotype collection with a green tag: “Lith. Mon. pl. 20, f. 9” (corresponding to Printz
835 1929, pl. 20, fig. 9), and another specimen with the annotation, “Specimen matches Foslie
836 1891a, pl. 3, fig. 2, lower left”. Previously, Woelkerling (1993: 79) designated as lectotype
837 element the collection containing this latter specimen because no further type material had
838 been found at that time. The specimen selected for sequencing was the specimen with the
839 green tag “Lith. Mon. pl. 20, f. 9” (corresponding to Printz, 1929, pl. 20, fig. 9) among the

840 five rhodoliths contained in the lectotype collection. As allowed by Art. 9.17 of the ICN
841 (Turland *et al.*, 2018), the lectotype is here narrowed to the sequenced specimen. Based on
842 morpho-anatomy, Athanasiadis (2016: 228) listed *L.soriferum* f. *divaricatum* as *Incertae*
843 *Sedis*; DNA sequence data have confirmed the placement of the taxon in *L. soriferum*.

844

845 *Lithothamnion uncinatum* Foslie, 1895: 154, pl. 19, figs. 11-14.

846 HOMOTYPIC SYNONYMS: *Lithothamnion calcareum* f. *uncinatum* (Foslie) Foslie,

847 1897: 9; *Lithothamnion norvegicum* f. *uncinatum* (Foslie) Foslie, 1900: 13.

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

849 TYPE LOCALITY: Kragerø, Norway.

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

851 *Comment*: According to Woelkerling (1993: 231), the holotype collection comprises

852 several rhodolith specimens illustrated in Foslie (1895, pl. 19, figs. 11-14). The specimen

853 depicted in Foslie (1895, pl. 19, fig. 11) was sequenced, and is identical to *L. soriferum*.

854 Athanasiadis (2016: 231) listed this name as a synonym of *Lithothamnion norvegicum*,

855 which he considers *Incertae Sedis* (see below).

856

857 *Historical collection*:

858 UPS A648806, Mestervik, Tromsø, Norway, 20.ix.1890, leg. Foslie. *DNA sequence*: *rbcL*-

859 263 (bp 1172-1434), GenBank XXXXXXXXX (Supplementary table S1).

860

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

862 BASIONYM: *Millepora polymorpha* f. *trophiformis* Esper, 1789: pl. XV [*Millepora*]

863 NEOTYPE: TRH C12-3179, no date, no habitat data, leg. C. Ryberg (designated by Adey,
864 1970c).

865 TYPE LOCALITY: Julianehaab, Greenland.

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

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

869

870 HETEROTYPIC SYNONYMS:

871 *Lithothamnion alpicorne* Kjellman, 1883: 121, pl. 5, figs. 1-8.

872 HOMOTYPIC SYNONYMS:

873 *Lithothamnion soriferum* f. *alpicorne* Foslie, 1891: 41, pl. 3, fig. 4.

874 *Lithothamnion tophiforme* f. *alpicorne* Foslie, 1895: 147 (as '*alpicornis*').

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

876 TYPE LOCALITY: Tromsø, Norway.

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

878 *Comment:* The *rbcL* sequence obtained is identical to the neotype sequence of *L.*

879 *tophiforme*. Kjellman (1883: 122) stated that this species was from Tromsø and that Foslie
880 was the collector. Woelkerling *et al.* (2005: 443) called TRH C13-3203 syntype material.

881 The specimen selected for sequencing and designated herein as lectotype was illustrated by

882 Printz (1929, pl. 19, fig. 11). Athanasiadis (2016: 221) cited this species as *Incertae Sedis*;

883 DNA sequence data have confirmed the placement of the species in synonymy with *L.*

884 *tophiforme*.

885

886 *Historical collection:*

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

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

890 *Comment:* This collection is topotype material of *Lithothamnion norvegicum* (Areschoug)
891 Kjellman (1883: 122, basionym: *Lithothamnion calcareum* var. *norvegicum* Areschoug,
892 1875: 4). The box contains a large collection of rhodoliths but the specimen sequenced is
893 located separately within a small box marked “Prep. 522”.

894 Areschoug (1875:4) cited Wittrock as the collector *L. calcareum* var. *norvegicum*,
895 but he did not illustrate material, nor indicate a type. We have been unable to locate any
896 material in either L or UPS where other Areschoug material is located. Eleven collections
897 of Foslie's in TRH are listed under *L. norvegicum* (Woelkerling et al. 2005: 407-408), but
898 only the sequenced specimen is topotype material. A collection by Wittrock is in TRH (C3-
899 2985) and illustrated in Printz (1929, pl. 16, figs. 37-38) but the date of collection and
900 habitat data are lacking, making it difficult to know if this is type material. Woelkerling &
901 Verheij (1995: 67) noted syntype material is present in L. Both the material in TRH and in
902 L needs to be sequenced to understand the correct application of *L. norvegicum*.

903

904 ***“Lithothamnion” species and infraspecific taxa that belong in Phymatolithon***

905

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

907 *Lithothamnion squarulosum* f. *palmatifida* Foslie, 1899: 6.

908 LECTOTYPE: TRH C1-2892, 12.v.1893, leg. L. K. Rosenvinge; designated by
909 Woelkerling *et al.* (2005: 398).
910 TYPE LOCALITY: Fladen, østl. (= Eastern) Kattegat, Denmark (Woelkerling *et al.* 2005:
911 398).

912 *DNA sequences: psbA* and *rbcL-293* (bp 1172-1464), GenBank XXXXXXXXX and
913 XXXXXXXXX, respectively.

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

918

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

920 BASIONYM: *Lithothamnion scabriusculum* Foslie, 1895: 170.

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

922 *Type locality:* Kjelmo (now Kjelmoya), Finnmark, Norway (Woelkerling *et al.*, 2005: 493).

923 *DNA sequence: rbcL-293* (bp 1172-1464), GenBank XXXXXXXXX.

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

931

932 HETEROTYPIC SYNONYM:

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

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

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

936

937 ***Phymatolithon squamulosum* (Foslie) W.H.Adey, Hernandez-Kantun &**

938 **P.W.Gabrielson**

939 BASIONYM: *Lithothamnion squamulosum* Foslie, 1895:183.

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

941 TYPE LOCALITY: Sogn, Sulen (now Sula), indre (= inner), Stensund (now Steinsund),

942 Norway (Woelkerling *et al.* 2005: 265).

943 *Holotype DNA sequences: psbA and rbcL-293* (bp 1172-1464), GenBank XXXXXXXXX

944 and XXXXXXXXX, respectively.

945 *Comment:* The collection comprises a larger box with two smaller boxes, one square and

946 one round (Woelkerling *et al.*, 2005: 265). The specimen in the rounded box with the

947 annotation “Prep. 65” was sequenced. Recently this taxon was transferred to *Phymatolithon*

948 according to the molecular data obtained from an isotype preserved in BM (BM000044670,

949 Box 434, Adey *et al.*, 2018). The DNA sequencing of the holotype confirms this result; the

950 *rbcL* sequences of both type collections were identical.

951

952 *Recent collections:*

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

957

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

962

963 **Discussion**

964 Since DNA sequences from the first type specimens of geniculate (Gabrielson *et al.*, 2011)
965 and non-geniculate (Sissini *et al.*, 2014) corallines were published, it has become
966 increasingly clear that the primary method to unequivocally apply a historical name is to
967 obtain DNA sequences from the type material to compare them to sequences from other
968 historical or more recently collected specimens (Martone *et al.*, 2012; Hind *et al.*, 2014a;
969 2014b; 2015; Hernández-Kantún *et al.*, 2015a; 2016; Richards *et al.*, 2017; 2018;
970 Gabrielson *et al.*, 2018; 2019; Peña *et al.*, 2018; Jeong *et al.*, 2020; Maneveldt *et al.*, 2020;
971 Puckree-Padua *et al.*, 2020). Herein, we have applied that methodology to the numerous
972 species and infraspecific names of Arctic and Subarctic non-geniculate corallines published
973 by Kjellman (1883; 1889) and later by Foslie (1891; 1895; 1896; 1899; 1900; 1905a, b;
974 1908) and others.

975 With the exception of the *Lithothamnion tophiforme* (Unger, 1858), first published
976 as *Millepora polymorpha* var. *tophiformis* Esper (1789), the oldest names applicable to
977 Arctic and Subarctic non-geniculate corallines are those of Kjellman (1877; 1883; 1889).
978 By sequencing type material, Adey *et al.* (2015b) confirmed the application of two of
979 Kjellman's names, *L. compactum* Kjellman (1883) to *Clathromorphum*, and *L. loculosum*
980 Kjellman (1889) to *Neopolyporolithon*, and showed that a third, *Lithothamnion foecundum*
981 Kjellman (1883), currently placed in *Leptophytum* W.H.Adey, does not belong in that
982 genus, but its generic position remains unresolved. Lectotype material of the oldest name,
983 *Lithophyllum arcticum* Kjellman (1877), collected at Uddebay, Novaya Zemlya, Russia,
984 was shown to be an earlier available name for *Neopolyporolithon loculosum* (Kjellman)
985 W.H.Adey, P.W.Gabrielson, G.P.Johnson & Hernández-Kantún, namely *N. arcticum*
986 (Kjellman) P.W.Gabrielson, S.C.Lindstrom & Hughey (Gabrielson *et al.*, 2019).
987 *Lithothamnion flavescens* Kjellman (1883) was transferred to *Leptophytum* by
988 Athanasiadis (2016), but this was based on morpho-anatomy, which has been shown to
989 be problematic in correctly placing non-geniculate species in a genus (Hind *et al.*, 2016;
990 2018; Gabrielson *et al.*, 2019). Of the remaining six Kjellman names, five are treated
991 herein, *L. alcicorne*, *L. durum*, *L. glaciale*, *L. intermedium* and *L. soriferum*. Attempts to
992 amplify *L. ungeri* Kjellman (1883) were unsuccessful. Thirty-five type specimens of
993 *Lithothamnion* species and infraspecific taxa described by Foslie were sequenced. Below
994 we discuss the systematics of the Arctic and Subarctic *Lithothamnion* species that we
995 recognize, including *L. lemoineae*, and one of the species of *Clathromorphum*, *C.*
996 *circumscriptum*, for which we found an additional synonym. Distributions, habits and

997 habitat data for each species are updated, including range maps for the *Lithothamnion*
998 species.

999 *Clathromorphum circumscriptum*. DNA sequencing confirmed two earlier proposed
1000 heterotypic synonyms for this species, *L. durum* and *L. evanescens*, the first proposed by
1001 Foslie (1900) and the second by Lebednik (1977). Added to these is *L. coalescens*, which
1002 had been considered a synonym of *C. compactum* by Foslie (1905a) and recently by
1003 Athanasiadis (2016).

1004 The habit and habitat of *C. circumscriptum* are provided by Adey *et al.* (2015b), and
1005 the sequenced specimens confirm this information. The species is reported to be circum
1006 Arctic ranging south to the Subarctic in both the Atlantic and Pacific Oceans based on
1007 morpho-anatomy and its distinct habit (Adey, 1965; Adey *et al.*, 2013; 2015a, b). In the
1008 NW Atlantic Subarctic, *C. circumscriptum* is generally more abundant at depths of less
1009 than 10 m on moderately exposed rocky shores (Steneck, 1978; Adey & Hayek, 2011).
1010 DNA sequences confirm its presence in Greenland, but material from the Russian Arctic
1011 and NW Pacific Ocean has not been sequenced. DNA sequences from the western Gulf of
1012 Alaska are from specimens collected in mid (GenBank MT732997) and high intertidal
1013 pools (MT733001). Other mid pool (MT732990) and low intertidal collections
1014 (MT732992, MT732993, MT732996) from this area represent an undescribed species of
1015 *Clathromorphum*. Records based on morpho-anatomy from SE Alaska may also represent
1016 an undescribed species.

1017 *Lithothamnion glaciale*. There is no doubt that the lectotype specimen designated
1018 herein is the one illustrated by Kjellman (1883, pls. 2, 3), despite having listed multiple
1019 syntype localities. The partial *rbcL* sequence from the lectotype differs by 1 bp from all

1020 other specimens that thus far have been sequenced, including one from Spitzbergen. DNA
1021 sequencing also shows that eighteen specific and infraspecific *Lithothamnion* taxa later
1022 named by Foslie are heterotypic synonyms of *L. glaciale*. *Lithothamnion intermedium*,
1023 described in the same publication as *L. glaciale* (Kjellman, 1883), was listed most recently
1024 by Athanasiadis (2016) as *Incertae Sedis*. Kjellman provided three syntype localities for *L.*
1025 *intermedium*, but he himself only collected the specimen at Karlsøy (Carlsö); specimens
1026 from the other two localities (Tromsø and Vadsø) were collected by Foslie. In UPS only
1027 two specimens could be located, one from Karlsøy, collected by Kjellman and with a label
1028 in his handwriting, and the other collected by Foslie from Mestervik, Tromsø. The
1029 Kjellman specimen from Karlsøy we have designated as the lectotype; its sequence differs
1030 by 1 bp from the sequence of the *L. glaciale* lectotype. By DNA sequence the specimen
1031 collected by Foslie is *L. soriferum*. *Lithothamnion glaciale* and *L. intermedium* were
1032 published at the same time and are the same species so either name can be used for this
1033 species. We selected *L. glaciale* because of its long-standing use by the coralline research
1034 community and because the lectotype material is homotypic, whereas *L. intermedium*
1035 mostly has been ignored.

1036 The habit and habitat of *L. glaciale* were described by Adey (1966a) and Adey *et al.*
1037 (2005) based primarily on NW Atlantic material identified by morpho-anatomy.
1038 Specimens ranged from epilithic crusts to free living rhodoliths. More recently, encrusting
1039 epilithic forms of *L. glaciale* have been reported to be very common from the low intertidal
1040 to the photic limit (Adey & Hayek, 2011). Most collections, however, are from the low
1041 intertidal to a depth of ~15 m, which is more a reflection of collection limits than the

1042 species' true vertical distribution. Numerous studies in the past two decades have
1043 documented the presence of rhodoliths throughout the North Atlantic and Arctic at depths
1044 of ~3 to 50 m, and while most studies have assumed *L. glaciale* as the forming species,
1045 little to no corroborative DNA sequencing work has been carried out as part of these studies
1046 (Halfar *et al.*, 2000; Blake and Maggs, 2003; Kamenos & Law, 2010; Gagnon *et al.*, 2012;
1047 Teichert *et al.*, 2012; 2014; Adey *et al.*, 2015a; Millar & Gagnon, 2018; Schoenrock *et al.*,
1048 2018b; Bélanger & Gagnon, 2020; Teed *et al.*, 2020). Although this assumption is
1049 legitimate given the ubiquity of *L. glaciale* in both oceans, morphological deviations from
1050 the norm in a few *L. glaciale* rhodoliths from Newfoundland and Labrador suggests that
1051 rhodoliths may also include other species of corallines such as *L. tophiforme* and *C.*
1052 *compactum* (D. Bélanger & P. Gagnon, unpublished data). In Norway, Anglés d'Auriac *et*
1053 *al.* (2019) reported plurispecific maerl mainly composed of *L. glaciale* and associated
1054 species of *Phymatolithon* and *Lithophyllum*.

1055 We confirm by DNA sequencing the presence of *L. glaciale* throughout the North
1056 Atlantic (Fig. 2). We have not confirmed many of the Arctic Ocean reports. The
1057 observation of uniporate conceptacles (mostly carposporangial) and multiporate
1058 tetra/bisporangial conceptacles in our collections from Norway, confirmed the common
1059 occurrence of gametophytes and tetra/bisporophytes for this species, as is suggested in the
1060 literature (e.g., Chamberlain & Irvine, 1994).

1061 In the North Pacific this species was first reported by Saunders (1901: 442) based
1062 on specimens collected in Prince William Sound and further west at Kukak Bay and the
1063 Shumagin Islands and identified by Kjellman. We have not confirmed by DNA sequencing
1064 the identity of these specimens. Recently, however, Bringloe & Saunders (2019) reported

1065 this species from Nome, Alaska, USA (Bering Strait), and we have sequenced specimens
1066 from Malcolm Island, central British Columbia, Canada south to Monterey County,
1067 California, USA (Fig. 2). In the NE Pacific, only encrusting epilithic specimens were
1068 found, although they may completely cover pebbles so that they appear to be rhodoliths.
1069 We cannot confirm reports based on morpho-anatomy from Japan and Arctic Russia, but
1070 likely *L. glaciale* is present in those areas as well. Reports of this species from any tropical
1071 and warm temperate regions as found on AlgaeBase (Guiry & Guiry, 2020) are highly
1072 improbable. Reports from the Subantarctic (Heydrich, 1900; Lemoine, 1913) need to be
1073 confirmed.

1074 *Lithothamnion lemoineae*. Melbourne *et al.* (2017) provided a *psbA* sequence from
1075 the holotype of *L. lemoineae* from the NW Atlantic (Maine, USA) to unequivocally link
1076 DNA sequences from field-collected material to the name. Based on DNA sequenced
1077 specimens, we expand the habit of *L. lemoineae* from encrusting epilithic to epiphytic, to
1078 epizoic on shells, and as rhodoliths. The species can also occur in the intertidal, as well as
1079 in the shallow subtidal to 12 m depth. In the NW Atlantic Subarctic, *L. lemoineae* often
1080 dominates rock on exposed shores (Adey & Hayek, 2011), particularly at 10-15 m depth
1081 (R. Steneck, *pers. obs.*).

1082 Melbourne *et al.* (2017) found that specimens from England, thought to be *L.*
1083 *lemoineae* based on morpho-anatomy (Chamberlain & Irvine, 1994), were not that species
1084 based on DNA sequencing. However, based on DNA sequenced material, we corroborated
1085 a recent record of *L. lemoineae* from the same region in the NE Atlantic (Svalbard,
1086 Norway; Hofmann & Heesch, 2018), and likewise Bringloe & Saunders (2019) have the
1087 first confirmed record from the NE Pacific at Nome, Alaska, USA. Here, we confirm its

1088 occurrence on Kodiak Island, Gulf of Alaska (GenBank MT733005), where it occurred on
1089 low intertidal bedrock. The report of this species from the NW Pacific by Lee (2008) needs
1090 to be verified by DNA sequencing. We also confirm the species distribution in the NW
1091 Atlantic from Labrador, Canada to Maine, USA (Fig. 3).

1092 *Lithothamnion soriferum*. We located in UPS three specimens of *L. soriferum* in an
1093 envelope with a label in Kjellman's handwriting and from one of the cited localities, Carlsö
1094 (now Karlsøy). These appear to have been illustrated and published by Kjellman (1883, pl.
1095 1, figs. 1-4) with some artistic license. This is similar to what we found for *L. durum*
1096 (Kjellman, 1889) and *L. glaciale* (Kjellman, 1883), and in all of these examples the
1097 specimens are convincing matches to the illustrations. DNA sequences from type
1098 specimens of five species and infraspecific taxa later named by Foslie are all exact matches
1099 to the lectotype specimens of *L. soriferum*. The recently described *L. erinaceum*
1100 (Melbourne *et al.*, 2017) also is a heterotypic synonym of *L. soriferum*. Since being
1101 published, *L. soriferum* has had a checkered history, sometimes being recognized as a
1102 distinct species (Foslie, 1905; Zinova, 1955) but mostly it has been considered a synonym
1103 of *L. tophiforme* (Foslie, 1895; Lund, 1959; Jaasund, 1965; Lee, 1969; Adey, 1970a;
1104 Vinogradova, 2010). Interestingly, Adey *et al.* (2005), in a detailed examination of *L.*
1105 *tophiforme*, did not mention *L. soriferum*, and, most recently, Athanasiadis (2016) treated
1106 the species as *Incertae Sedis*.

1107 Based on DNA sequences, *L. soriferum* is a distinct species and occurs as an
1108 epilithic, epiphytic or epizoic (specimen on a worm tube) crust or as a free-living rhodolith.
1109 Specimens are primarily subtidal to 27 m depth, but we have one occurrence in the low
1110 intertidal as an epilithic crust. In contrast to *L. glaciale*, gametangial plants have not been

1111 observed in any of the collections. Only multiporate tetra/bisporangial conceptacles were
1112 observed, as it is indicated in the type collections of two heterotypic synonym (*L. breviaxe*
1113 and *L. granii*, Woelkerling *et al.*, 2005) and in the literature (Melbourne *et al.*, 2017).

1114 The species is widespread in the central and eastern North Atlantic (Greenland,
1115 Iceland, UK, Norway), but there is no evidence of its occurrence in the NW Atlantic; in the
1116 NE Pacific there are sporadic records from the Aleutian Islands (Robinson *et al.*, 2017) and
1117 Prince William Sound (Konar *et al.*, 2006), Alaska, USA south to Gwaii Haanas, British
1118 Columbia, Canada (Fig. 4). For having such a widespread distribution, this species appears
1119 uncommon compared to *L. glaciale*. In the first report of *L. soriferum* from the NE Pacific
1120 (Konar *et al.*, 2006), this species was misidentified as *Phymatolithon calcareum* based on
1121 morpho-anatomy. This appears to be so because the cell types in the cross-section image
1122 (Konar *et al.*, 2006, fig. 3B) were misidentified. The figure clearly shows flared epithallial
1123 cells that are not characteristic of any *Phymatolithon* species, but that are found in
1124 *Lithothamnion* species. All reports of *P. calcareum* outside boreal NE Atlantic and the
1125 Mediterranean Sea waters based on morpho-anatomy are doubtful and need to be confirmed
1126 by DNA sequences.

1127 *Lithothamnion tophiforme*. The sequence of the neotype specimen, TRH C13-3203,
1128 designated by Adey *et al.* (2005), confirms the identity of the specimen used by Adey *et al.*
1129 (2015b) to represent this species. Adey (1970a) reported this species to be both encrusting,
1130 especially on shells or shell fragments, and also as free-living rhodoliths. All of the
1131 sequenced specimens to date have been rhodoliths. Adey *et al.* (2005) considered *L.*
1132 *tophiforme* an Arctic species, but also stated that its abundance in the high Arctic is
1133 unknown, a situation that remains unchanged. They also noted that it is found only in

1134 colder waters below 10 m depth and at temperatures below 10° C, and the sequenced
1135 specimens confirm this pattern as all were collected below 15 m depth. All of the recently
1136 collected sequenced specimens are from the NW Atlantic, from Newfoundland, Canada
1137 northward (Fig. 5). The neotype specimen is the only confirmed specimen from Greenland,
1138 and only two historical specimens from the 19th century are from Norway, where the
1139 species was not found recently in an extensive collection effort presented herein.

1140 In the NW Atlantic Subarctic, *L. tophiforme* rhodoliths commonly co-occur with *L.*
1141 *glaciale* rhodoliths, while dominating at depths >25 m (Adey et al., 2015a). In rhodolith
1142 beds where both species occur, thalli of *L. tophiforme* and *L. glaciale* sometimes merge,
1143 forming plurispecific rhodoliths with a characteristic color mosaic where *L. tophiforme*
1144 generally presents a more brownish-orangy color than *L. glaciale* (D. Bélanger & P.
1145 Gagnon, unpublished data). Our sequenced specimens of *L. tophiforme* presented a variety
1146 of shapes and sizes, from a few centimetre-long twig-like thalli, to large (>10 cm across)
1147 branching spheroidal rhodoliths. A few specimens presented a distinct growth form with
1148 fanned-shaped branches. The phenotypic plasticity of *L. tophiforme* highlights the
1149 importance of DNA sequencing for identification.

1150

1151 *Identifying non-geniculate coralline algae to species.* These Arctic and Subarctic
1152 *Lithothamnion* species exemplify the difficulties of identifying non-geniculate coralline
1153 species using morpho-anatomy. DNA sequencing has revealed that by the first decade of
1154 the 20th Century, 30 specific and infraspecific names had been given to three species: *L.*
1155 *glaciale*, *L. soriferum* and *L. tophiforme*. Recently, based on morpho-anatomy, the vast
1156 majority of these were listed as *Incertae Sedis* by Athanasiadis (2016) including, for

1157 example *L. alcicorne*, *L. breviaxe*, and *L. soriferum*. In the over 100 years since these had
1158 been named and examined by numerous coralline morpho-anatomists, their identity could
1159 not be determined with any certainty. And there remain another 21 species or infraspecific
1160 taxa of *Lithothamnion* named by Foslie, 20 from Norway and one from Scotland from
1161 which we were unable to amplify DNA using PCR. It is highly unlikely, however, that any
1162 of these names would apply, due to the extensive sequencing of Norwegian specimens
1163 reported herein and the rule of priority. With the exception of *L. lemoineae*, which has
1164 never been recorded from Norway, the applied *Lithothamnion* names predate any of those
1165 published by Foslie.

1166 Further complicating the naming of specimens without DNA sequencing is that all
1167 of these species can occur either as encrusting corallines attached to a substrate or as
1168 unattached rhodoliths -encrusting a core or not - sometimes occurring singly, but also in
1169 beds. *Lithothamnion lemoineae* previously had only been reported to occur as an epilithic
1170 crust, whereas *L. soriferum* (also as *L. erinaceum*) had not been known as an epilithic crust.
1171 In some regions, species can have restricted morphologies, for example in Norway *L.*
1172 *glaciale* is found as an epilithic crust, or as free-living maerl, whereas in the NE Pacific it
1173 has so far only been reported as an epilithic crust. And three of the four species, *L. glaciale*,
1174 *L. lemoineae* and *L. soriferum*, can occur from the intertidal to, at minimum, 12 m depth.

1175 The finding by DNA sequencing of four Arctic and Subarctic *Lithothamnion*
1176 species that had been named as multiple specific and infraspecific taxa using morpho-
1177 anatomy is clearly opposite the cryptic diversity commonly recorded in temperate
1178 corallines (e.g., Pardo *et al.*, 2014; 2017; Hernández-Kantún *et al.*, 2015a, b; Peña *et al.*,
1179 2015a, b; Richards *et al.*, 2018; Pezolesi *et al.*, 2019). However, this plethora of specific

1180 and infraspecific names in the Arctic and Subarctic regions was primarily the work of
1181 Foslíe, who, as illustrated in the taxonomic results, changed his mind numerous times about
1182 which taxa should be recognized and at what rank. In tropical regions, DNA sequencing of
1183 non-geniculate corallines has shown that some species are widely distributed, whereas most
1184 have local distributions (Sissini *et al.*, 2014; Peña *et al.*, 2014b; Hernández-Kantún *et al.*
1185 2016; Gabrielson *et al.*, 2018; Maneveldt *et al.*, 2019).

1186 In the Arctic and Subarctic additional species of *Lithothamnion* and
1187 *Clathromorphum* need to be recognized based on the DNA sequencing reported herein
1188 (Supplementary table S2). It is also likely that the Arctic and Subarctic *Lithothamnion*
1189 species will need to be transferred to a new genus, as the generitype of *Lithothamnion*, *L.*
1190 *muelleri* Lenormand ex Rosanoff, belongs in a different clade (Yeong *et al.*, 2020).

1191 It is critical that in this time of rapid ocean warming and acidification,
1192 particularly in polar regions, that we have a firm understanding of the taxa currently present
1193 in order to document future changes in their habitats and distributions. Importantly, the
1194 biogeography of coralline algae appears especially sensitive to ocean thermogeography
1195 (Adey & Steneck, 2001; Adey & Hayek, 2011). The relevance of non-geniculate coralline
1196 algae in these regions as ecosystem engineers cannot be overstated, whether occurring as
1197 encrusting species attached primarily to rock substratum (Freiwald & Henrich, 1994; Adey
1198 *et al.*, 2005; Adey *et al.*, 2015a) or as free-living maerl (Pardo *et al.*, 2014; Teichert, 2014;
1199 Teed *et al.*, 2020). As polar seas warm and become increasingly acidified, these coralline
1200 algal species will either be forced to live at lower depths, where they will be limited by the
1201 availability of photosynthetically active radiation through the water column, or they will
1202 become extinct. DNA barcoding of organisms in these habitats, coupled with DNA

1203 sequencing of type and historical specimens, provides the foundation to document these
1204 imperiled species.

1205

1206 **Acknowledgements**

1207 VP and PWG are very grateful to the following curators and institutions for the loan of type
1208 specimens critical to this study: Tommy Presto and Kristian Hassel (TRH) for Foslie
1209 specimens; Stefan Ekman (UPS) for Kjellman specimens. VP thanks L. Hoffman and J.
1210 Büdenbender for providing specimens from Svalbard; PWG thanks B. Konar for providing
1211 specimens from Prince William Sound, Alaska. Acquisition of part of the molecular data
1212 was carried out at the Service de Systématique Moléculaire of the Muséum National
1213 d'Histoire Naturelle (CNRS - UMS 2700). JLR acknowledges NSF grant DEB-1754504
1214 for rhodolith research to Suzanne Fredericq that funded a portion of this research. PWG
1215 thanks Wilson Freshwater, DNA Analysis Core Facility, University of North Carolina,
1216 Wilmington for sequencing support and Todd Vision, University of North Carolina, Chapel
1217 Hill for research space and equipment. A portion of this research was completed while
1218 PWG was a visiting professor at the Friday Harbor Labs, University of Washington. We are
1219 grateful to the anonymous reviewers for their helpful comments on the manuscript.

1220 **Supplementary information**

1221 **Supplementary Note 1.** Type collections & historical specimens DNA-extracted but
1222 unsuccessfully sequenced for *psbA* and *rbcL*.

1223 **Supplementary Table S1.** Type collections and historical specimens sequenced in the
1224 study.

1225 **Supplementary Table S2.** Collection and vouchering details for the recent specimens
1226 sequenced in the study. For each species, specimens are sorted by collection areas: NE
1227 Atlantic, NW Atlantic and NE Pacific.

1228 **Supplementary Table S3.** List of GenBank accession numbers used in this study with
1229 details of locality information and references.

1230 **Supplementary Figure S1.** Maximum Likelihood (ML) tree of COI-5P included in the
1231 present study. Bootstrap ML values >50% shown for each node. Scale bar: 0.05
1232 substitutions per site.

1233 **Supplementary Figure S2.** Phylogenetic tree inferred from RAxML and Bayesian
1234 inference of *psbA* sequences included in the present study. Bootstrap ML values >50% and
1235 posterior probabilities >0.50 from Bayesian inference shown for each node. Scale bar: 0.02
1236 substitutions per site.

1237 **Supplementary Figure S3.** Morpho-anatomy of *Lithothamnion glaciale*, UPS A-000202.
1238 Fig. A. Thallus habit and herbarium labels including label handwritten by Kjellman. Fig. B.
1239 Vertical fracture of protuberance showing radial construction and location of overgrown
1240 and buried conceptacle (black arrow). Fig. C. Vertical fracture of protuberance with
1241 conceptacle (black arrow) overgrown by a secondary hypothallus (arrowheads). Fig. D.
1242 Magnified view of secondary hypothallus (bracket) over conceptacle roof. Fig. E.
1243 Perithallus with cell fusions (white arrows). Fig. F. Perithallus (lower bracket), intercalary
1244 meristem (middle bracket, *), and a single-layered epithallus (upper bracket) of flared cells
1245 (e), one with cell roof intact (white arrow). Scale bars: Figs. B-C = 100 μm ; Figs. D-F = 10
1246 μm .

1247 **Supplementary Figure S4.** Morpho-anatomy of *Lithothamnion soriferum*, UPS A-648809.
1248 Fig. A. Thallus habit of specimens and herbarium label handwritten by Kjellman. Figs. B-
1249 D. Vertical fractures of protuberance showing radial construction. Fig. E. Magnified view
1250 of secondary hypothallus (arrowhead, bracket) over the thallus surface of the older growth
1251 layer. Fig. F. Perithallus (lower bracket) with cell fusions (white arrows), intercalary
1252 meristem (middle bracket, *), and epithallus (upper bracket). Figs. G-H. Magnified view of
1253 meristematic cells (*) and a single-layered epithallus of flared cells (e), one with cell roof
1254 intact (white arrow, Fig. H). Scale bars: Fig. A = 2 cm. Figs. B-D = 100 μm . Figs. E-H = 10
1255 μm .

1256

1257 **Disclosure statement**

1258 No potential conflict of interest was reported by the authors.

1259

1260 **Author Contributions**

1261 V. Peña & P.W. Gabrielson: original concept; V. Peña, P.W. Gabrielson, L. Le Gall & J.R.
1262 Hughey: DNA sequencing types; J.L. Richards: morpho-anatomy of type specimens; V.
1263 Peña, P. W. Gabrielson, L. Le Gall, S. C. Lindstrom & G. W. Saunders: DNA sequencing
1264 of contemporary collections. L. Le Gall: distribution maps; E. Rinde: led the field sampling
1265 in the CoralAlg project that funded the analysis of TRH specimens; V. Husa: sampling of
1266 type collections at the TRH, led the field sampling in the AKVAKYST III project; V. Peña,
1267 D. Belanger, P. Gagnon, J. L. Richards, L. Le Gall, J. R. Hughey, S. C. Lindstrom, E.

1268 Rinde, S. Fredriksen, J. M. Hall-Spencer, R. S. Steneck, M. B. Anglès d’Auriac, N. A.
1269 Kamenos & P. W. Gabrielson: writing; V. Peña, D. Bélanger, P. Gagnon, L. Le Gall, G.W.
1270 Saunders, S. C. Lindstrom, E. Rinde, V. Husa, H. Christie, S. Fredriksen, J. M. Hall-
1271 Spencer, R. S. Steneck, K. M. Schoenrock, J. Gitmark, E. S. Grefsrud, M. B. Anglès
1272 d’Auriac, E. Legrand, J. Grall, T. F. Mumford, N. A. Kamenos & P. W. Gabrielson:
1273 contemporary collections.

1274

1275 **Funding**

1276 Sequencing of TRH type collections, collection and sequencing of contemporary
1277 Norwegian samples was supported by the research project “Norway’s hidden marine
1278 biodiversity: The hunt for cryptic species within the coralline algae” (Norwegian
1279 Biodiversity Information Center, Project no. 70184235, PI: E. Rinde). Collection and
1280 sequencing of additional contemporary Norwegian collections have been supported by
1281 “AKVAKYST III” (Ministry of Trade, Industry and Fisheries of Norway, PI: V. Husa).
1282 Sequencing of type material at Hartnell College and of contemporary collections and type
1283 material at UNC was supported by a family trust to P.W.G.

1284

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1680 **Figure legends**

1681 **Figure 1.** Phylogenetic tree inferred from maximum likelihood (ML) and Bayesian
1682 inference of *rbcL* sequences included in the present study. Bootstrap ML values >60% and
1683 posterior probabilities >0.60 from Bayesian inference shown for each node. Scale bar: 0.05
1684 substitutions per site.

1685 **Figure 2:** Distribution map of *Lithothamnion glaciale* obtained for collections analyzed in
1686 the molecular studies, type collections and historical specimens.

1687 **Figure 3:** Distribution map of *Lithothamnion lemoineae* obtained for collections analyzed
1688 in the molecular studies, type collections and historical specimens.

1689 **Figure 4:** Distribution map of *Lithothamnion soriferum* obtained for collections analyzed in
1690 the molecular studies, type collections and historical specimens.

1691 **Figure 5:** Distribution map of *Lithothamnion tophiforme* obtained for collections analyzed
1692 in the molecular studies, type collections and historical specimens.