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

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42

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

46

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49

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

51

52 **Abstract**

53

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

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

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

77

78 **Introduction**

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

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

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

101 in response to ocean warming, but most focused on marine mammals and fish. Two of
102 these papers focused on benthic marine algae, but neither on the corallines, the group that
103 provides the dominant benthic cover of seabed habitats in the photic zone (Adey & Hayek,
104 2011). Based on research carried out elsewhere, Brodie *et al.* (2014), however, projected a
105 significant decrease of coralline algae in the Arctic because anthropogenic carbon dioxide
106 emissions are causing ocean acidification, which in turn is causing waters in the photic
107 zone of the Arctic to become undersaturated with aragonite. Many coralline algae are
108 susceptible to reductions in the concentration of aragonite as this can make seawater
109 corrosive to their high magnesium calcite skeletons, a response that is mediated by the rate
110 of environmental change (Kamenos *et al.*, 2013; 2016; Martin & Hall-Spencer, 2017; Chan
111 *et al.*, 2020). Climate-change induced permafrost thawing and snow melting at high
112 latitudes also increase freshwater runoff and coastal nutrient inputs (Walvoord & Striegl,
113 2007; Kendrick *et al.*, 2018), which in turn can alter calcification rates and subsequent
114 coralline growth (McCoy & Kamenos, 2018; Bélanger & Gagnon, 2020) and
115 photophysiology (Schoenrock *et al.* 2018a). In this regard, Williams *et al.* (2020) observed
116 different responses among species of *Clathromorphum* Foslíe related to their sensitivity to
117 environmental change; thus, the widely distributed *C. compactum* (Kjellman) Foslíe might
118 expand its northern limit whereas the narrow-range *C. nereostratum* Lebednik is expected
119 to decline.

120 In Arctic and Subarctic regions, *Lithothamnion* Heydrich species often dominate
121 coralline algal assemblages from the low intertidal to the lower limit of the photic zone,
122 contributing significantly to shelf carbonate budgets (Freiwald & Henrich, 1994; Nelson,
123 2009; Adey & Hayek, 2011; Teed *et al.*, 2020). Several *Lithothamnion* species form maerl,

124 or branched crusts, and these structures significantly increase benthic habitat complexity
125 and biodiversity (Gagnon *et al.*, 2012; Teichert *et al.*, 2014; Jørgensbye & Halfar, 2017;
126 Schoenrock *et al.*, 2018b). Because several *Lithothamnion* species (like most coralline
127 algae) also induce larval settlement and metamorphosis in invertebrates with important
128 functional roles, the genus is considered an ecosystem engineer (Steneck, 1982; Rowley,
129 1989; Pearce & Schiebling, 1990; Nelson, 2009).

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

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

151

152 **Materials and Methods**

153 *Collections studied.* Fifty-eight type specimens of *Lithothamnion* species and infraspecific
154 taxa housed in TRH and UPS as well as eleven historical specimens in TRH (herbarium
155 acronyms follow Thiers, 2020) were considered for DNA analysis (Supplementary table
156 S1, Supplementary note S1). One of us (SCL), as a guest of the Department of Botany,
157 Stockholm University, located Kjellman's type specimens in UPS that are housed in a room
158 separate from the main algal collection. This may explain why earlier investigators were
159 unable to locate them. These specimens, described by F. R. Kjellman between 1877 and
160 1889 were later received on loan by PWG; specimens described by M. H. Foslie between
161 1891 and 1908 were examined by VP or PWG. Most of the specimens had their type
162 localities along the Norwegian coast but some of them were described from Svalbard,
163 Scotland, Greenland, Canada and USA (Kjellman, 1883; 1889; Foslie, 1891; 1895; 1896;
164 1900; 1905a, b; 1908). In addition, 440 recent collections from Norway, Svalbard,
165 Greenland, and the Atlantic and Pacific coasts of Canada and USA have also been
166 sequenced (Supplementary table S2). Most of these specimens were collected subtidally in
167 coralline algal beds (known as maerl or rhodolith beds) or as crusts, and they are preserved
168 in NCU, TRH, SANT, UBC and UNB (see collection details in Supplementary table S2).

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

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

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

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

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

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

233

234 **Results**

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

238 The *rbcL* alignment comprised 121 sequences of variable length resulting in 81
239 unique DNA sequences ranging from 205 to 313 bp, with 114 variable sites. Both ML and
240 Bayesian analyses resolved the type specimens and historical collections with moderate to
241 full support in different Hapalidiales lineages encompassing species of *Lithothamnion*,
242 *Phymatolithon* and *Clathromorphum*, Fig. 1). Most of the type specimens and historical
243 collections sequenced were situated within lineages represented by the lectotype of
244 *Lithothamnion glaciale* Kjellman (0-3 bp differences, up to 1.14 % divergence -uncorrected
245 p-distance-), followed by the lectotype of *L. soriferum* Kjellman (0-1 bp differences, up to
246 0.41% divergence) and then the neotype of *L. tophiforme* (0-2 bp, up to 0.68% divergence)
247 (Fig. 1). Three type specimens were placed in the genus *Phymatolithon* (Fig. 1,
248 Supplementary table S1): the holotype of *Lithothamnion scabriusculum* Foslie was
249 positioned within a clade encompassing collections of *P. rugulosum* W.H.Adey (1-3 bp
250 differences; 0.3-1% divergence); the lectotype of *L. squarulosum* f. *palmatifidum* Foslie
251 was resolved within a clade represented by the neotype of *P. calcareum* (2 bp differences,
252 0.9% divergence); the holotype of *Lithothamnion lenormandii* f. *squamulosum* (Foslie)
253 Cotton was identical in sequence to the isotype of *P. squamulosum* (Foslie) W.H.Adey,
254 Hernández-Kantún & P.W.Gabrielson. Another two lectotypes (*L. coalescens* Foslie and *L.*
255 *evanescens* Foslie) and one historical collection of *Clathromorphum circumscriptum*
256 (Strömfelt) Foslie from Norway were identical in sequence to the epitype of *C.*
257 *circumscriptum* (0 bp differences, Fig. 1); the infraspecific variation within *C.*
258 *circumscriptum* ranged up to 13 bp differences (1.3% uncorrected p-distance) and it
259 increased up to 14 bp differences (1.4%) after comparison with two further *rbcL* sequences
260 obtained from recent collections from Alaska (UBC A92115 and UBC A94120, not

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

267 The COI-5P alignment comprised 151 sequences that consisted of 81 unique
268 sequences ranging from 518 to 579 base pairs (bp), with 153 variable sites. The
269 phylogenetic tree obtained from the ML analysis resolved seven fully and two moderately
270 supported lineages (Supplementary fig. S1). Four of these lineages are represented by
271 recent collections of *L. glaciale*, *L. tophiforme* (Esper) Unger, *L. lemoineae* and *L.*
272 *erinaceum* Melbourne & J.Brodie (herein proposed as a synonym of *L. soriferum* Kjellman,
273 see next section below). The remaining three fully supported lineages (as *L. sp. 2* to *L. sp.*
274 *4*) and another two moderately supported lineages (*L. sp.1*, *L. sp. 5*) corresponded to recent
275 collections pertaining to five *Lithothamnion* species that did not return any relevant match
276 with publicly available GenBank sequences (Supplementary fig. S1, Supplementary tables
277 S2 and S3). The highest infral lineage variation (uncorrected p-distance) was recorded in *L.*
278 *glaciale* (up to 2.07 %).

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

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

298 Given the molecular evidence noted above, and in accordance with Article 11.4 of
299 the International Code of Nomenclature for algae, fungi, and plants (ICN, Turland *et al.*,
300 2018), we present the following taxa with the corresponding heterotypic synonyms from
301 the present study. Note that for each taxon below where it is stated "...the lectotype is
302 narrowed..." we are invoking Article 9.17 of the ICN (Turland *et al.* 2018).

303

304

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

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

307 HOMOTYPIC SYNONYMS:

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

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

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

311 LECTOTYPE: S; seven microscope slides apparently from the original material designated
312 by Athanasiadis (2016: 251) as the holotype, but as Strömfelt (1886) designated syntype
313 localities, this material is better called a lectotype. This is a correctible error in accordance
314 with Art. 9.10 of the ICN (Turland *et al.*, 2018).

315 *Comment:* Adey *et al.* (2015b), while designating an epitype for *C. circumscriptum*
316 inadvertently omitted submitting this epitype sequence to GenBank. This has now been
317 rectified: GenBank XXXXXXXXX, an *rbcL*-263 (bp 1172-1434) sequence.

318

319 HETEROTYPIC SYNONYMS:

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

321 *Clathromorphum coalescens* (Foslie) Foslie, 1898b: 8.

322 *Phymatolithon compactum* f. *coalescens* (Foslie) Foslie, 1905a: 8.

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

324 TYPE LOCALITY: Inderøen, Strømmen, Trondheimsfjord, Norway.

325 *Lectotype DNA sequences:* *psbA* and *rbcL*-263 (bp 1172-1434), GenBank XXXXXXXXX
326 and XXXXXXXXX.

327 *Comment:* Following his description, Foslie (1895) transferred the species without
328 comment to *Clathromorphum* (Foslie, 1898b). Later, Foslie (1905a) reduced

329 *Clathromorphum* to a subgenus of *Phymatolithon* and reduced *C. coalescens* to a form of

330 *Phymatolithon*, as *P. compactum* f. *coalescens*. This name was not treated by Lebednik
331 (1977) nor by Adey *et al.* (2015b), but was listed by Athanasiadis (2016) as a synonym of
332 *C. compactum* (Kjellman) Foslie. According to Woelkerling *et al.* (2005), the lectotype of
333 *L. coalescens* is a blue box with five specimens that was earlier designated by Woelkerling
334 (1993: 52) as the lectotype, noting that Foslie (1895: 163) had cited two syntype localities.
335 Upon examination, the box contained four specimens illustrated in Foslie (1895, pl. 19,
336 among figs. 15-20), one of which was sequenced, and herein the lectotype is narrowed to
337 that sequenced specimen (GenBank XXXXXXXXX and XXXXXXXX). Both the *rbcL* and
338 *psbA* sequences obtained are identical to GenBank sequences of *C. circumscriptum*
339 (voucher US 169083), which were confirmed as identical to the epitype (voucher US
340 170939, Adey *et al.*, 2015b: 195).

341

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

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

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

345 TYPE LOCALITY: Port Clarence, Alaska, USA.

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

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

358

359 *Lithothamnion evanescens* Foslie, 1895: 137.

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

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

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

363 TYPE LOCALITY: Marblehead, Massachusetts, USA.

364 *Lectotype DNA sequences:* *psbA* and *rbcL*-263 (bp 1172-1434), GenBank XXXXXXXXX
365 and XXXXXXXXX.

366 *Comment:* Foslie (1895: 137, Pl. 22 figs. 6, 7) cited and illustrated specimens from two
367 syntype localities, Marblehead, Massachusetts, USA collected by F. S. Collins and from
368 Mastervik, Malangen, Norway collected by himself. Foslie transferred the species twice,
369 first, without comment, to *Clathromorphum* (Foslie 1898b), and later to *Phymatolithon*
370 after admitting that *Clathromorphum* should be considered a subgenus of the latter (Foslie,
371 1905a: 87). Lebednik (1977) first proposed that this species was a synonym of *C.*
372 *circumscriptum*, and this was accepted by Athanasiadis (2016). Woelkerling (1993: 87)
373 designated as lectotype a single specimen collected by Collins in Marblehead,
374 Massachusetts and illustrated by both Foslie (1895, Pl. 22, fig 6) and Printz (1929, pl. 41,

375 fig. 13). Woelkerling (1993) justified the selection of this specimen as lectotype because
376 "...it was in better condition and had numerous conceptacles". Both *rbcL* and *psbA*
377 sequences obtained for this lectotype specimen are identical to GenBank sequences of *C.*
378 *circumscriptum* (voucher US 169083), which was confirmed as identical to the epitype
379 (voucher US 170939, Adey *et al.*, 2015b: 195).

380

381 *Historical collection:*

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

386

387 *Recent collections:*

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

392

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

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

395 TYPE LOCALITY: Mosselbay, Spitsbergen.

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

397 *Comment:* Adey (1970a) made a provisional lectotypification based on "... a Spitzbergen
398 specimen (No. 241, Institute of Taxonomy, Uppsala) collected by Kjellman in 1872-1873."
399 Adey (1970a) further stated that this specimen was not one illustrated by Kjellman (1883)
400 that accompanied the original description. The ICN does not accept provisional lectotypes
401 (Art. 7.11, Turland *et al.* 2018). Chamberlain & Irvine (1994), repeated Adey's (1970a)
402 lectotypification, thus making it acceptable, but stated that they did not see the specimen.

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

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

418

419 HETEROTYPIC SYNONYMS:

420 *Lithothamnion apiculatum* f. *connatum* Foslie, 1895: 54, pl. 15, figs. 9-13 (as '*connata*').
421 LECTOTYPE: TRH B20-2669, 12.vii.1893, no habitat data, leg. H.H. Gran.
422 TYPE LOCALITY: Drøbak, Norway.
423 *Lectotype DNA sequence: rbcL-293* (bp 1172-1464), GenBank XXXXXXXXX.
424 *Comment:* Woelkerling (1993) located four of five specimens as part of the protologue of *L.*
425 *apiculatum* f. *connatum* and designated these lectotype. They have been illustrated by
426 Foslie (1895, pl. 15, figs. 9-12) and by Printz (1929, pl. 21, figs. 11-15) under the name *L.*
427 *colliculosum* f. *pusilla*. One of these four specimens, branched and epilithic on a pebble
428 (among the specimens illustrated as figs. 9-11, Foslie 1895, pl. 15) was sequenced, and
429 herein this lectotype is narrowed to that specimen.
430
431 *Lithothamnion battersii* Foslie, 1896: 1, pl. 1, figs. 1-5.
432 HOLOTYPE: TRH C10-3098, viii.1891, leg. E. Batters.
433 TYPE LOCALITY: Cumbrae, Scotland.
434 *Holotype DNA sequence: rbcL-293* (bp 1172-1464), GenBank XXXXXXXXX.
435 *Comment:* The holotype collection comprises five individuals illustrated by Foslie (1896,
436 pl. 1, figs. 1-5); the specimen sequenced is depicted in Foslie's (1896) figure 2. Based on
437 morpho-anatomy, Chamberlain & Irvine (1994: 182) and Athanasiadis (2016: 217)
438 correctly listed *L. battersii* as a synonym of *L. glaciale*.
439
440 *Lithothamnion colliculosum* Foslie, 1891: 43, pl. 3, fig. 1.
441 LECTOTYPE: TRH B11-2311, 8.ix.1890, leg. M. H. Foslie (designated by Woelkerling,
442 1993: 53).

443 TYPE LOCALITY: Skorpen, Kvænanen, Norway.

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

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

457

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

459 LECTOTYPE: TRH B20-2706, 12.vii.1898, leg. H. H. Gran (designated by Woelkerling
460 1993: 185).

461 TYPE LOCALITY: Drøbak, Norway.

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

463 *Comment:* We sequenced one of the 14 specimens comprising the lectotype, which is
464 located separately within a blue box with label "Prep. 76-77". The lectotype is narrowed
465 herein to the sequenced specimen. Based on morpho-anatomy Athanasiadis (2016: 224)

466 listed *L. colliculosum* f. *pusillum* as *Incertae Sedis*; DNA sequence data has confirmed the
467 placement of the species in *L. glaciale*.

468

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

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

471 1900: 13.

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

473 1993: 60-61).

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

475 2005: 424).

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

477 *Comment:* Foslie (1895: 142-144, pl. 20, figs. 1-6) described and illustrated this species

478 based on six individuals from a single locality, and he compared the species to two other

479 species that he named in the same publication, *L. dehiscens* Foslie and *L. nodulosum* Foslie.

480 Later, Foslie (1900) reduced *L. congregatum* to a form of *L. nodulosum*. The sequenced

481 specimen is illustrated in Foslie (1895, pl. 20, fig. 2), and the lectotype is narrowed herein

482 to that sequenced specimen. Based on morpho-anatomy Athanasiadis (2016: 224) listed *L.*

483 *congregatum* as *Incertae Sedis*; DNA sequence data has confirmed the placement of the

484 species in *L. glaciale*.

485

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

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

488 1993: 195).

489 TYPE LOCALITY: Røberg (now Raudberget), Norway (Woelkerling *et al.*, 2005: 413).
490 *Lectotype DNA sequence: rbcL-293* (bp 1172-1464), GenBank XXXXXXXXX.
491 *Comment:* Woelkerling (1993: 195-196) located and designated as the lectotype four of the
492 original 12 specimens included by Foslie (1895, pl. 16, figs. 14-17) in the original
493 protologue of this form. The specimen sequenced had a green label “Prep. 100-101”; it
494 resembled the specimen illustrated in Foslie (1895, pl. 16, fig. 16). The lectotype is here
495 narrowed herein to this single sequenced.
496
497 *Lithothamnion dimorphum* Foslie, 1895: 68, pl. 10, figs. 1-6.
498 HOMOTYPIC SYNONYM: *Lithothamnion fornicatum* f. *dimorphum* (Foslie) Foslie,
499 1905a: 38.
500 LECTOTYPE: TRH B25-2773, 10.vii.1894, 0-5.5 m depth on sandy and stony bottom, leg.
501 M. H. Foslie (designated by Woelkerling, 1993: 75).
502 TYPE LOCALITY: Frøjen (now Frøya), Rottingsundet, Trondeland, Norway (Woelkerling
503 *et al.*, 2005: 375).
504 *Lectotype DNA sequence: rbcL-293* (bp 1172-1464), GenBank XXXXXXXXX.
505 *Comment:* Foslie (1895, pl. 10, figs. 1-6) illustrated six specimens belonging to this species,
506 but did not designate a holotype. Woelkerling (1993: 74-75) designated as the lectotype
507 four of the six specimens depicted in figs. 1, 3, 5 and 6 (Foslie, 1895, pl. 10). The lectotype
508 is narrowed herein to the Foslie 1895, pl. 10, fig. 3 specimen that was sequenced. Based on
509 morpho-anatomy, Athanasiadis (2016: 225) listed *L. dimorphum* as *Incertae Sedis*; DNA
510 sequence data have confirmed the placement of the species in *L. glaciale*.
511

512 *Lithothamnion divergens* Foslie, 1895: 96, pl. 16, figs. 43-50.
513 HOMOTYPIC SYNONYMS: *Lithothamnion ungeri* f. *divergens* (Foslie) Foslie, 1900: 11;
514 *Lithothamnion tophiforme* f. *divergens* (Foslie) Foslie, 1905a: 51.
515 HOLOTYPE: C11-3167, 8.ix.1890, leg. M. H. Foslie.
516 TYPE LOCALITY: Kvaenangen, Skørpen (now Skorpa), Norway (Woelkerling *et al.*,
517 2005: 438).
518 *Holotype DNA sequence*: rbcL-293 (bp 1172-1464), GenBank XXXXXXXXX.
519 *Comment*: The holotype material comprised two boxes (one round and one quadratic) with
520 seven specimens and fragments (Woelkerling, 1993: 80; Woelkerling *et al.*, 2005: 438).
521 The sequenced specimen is located in the round box with the green tag “Lith. Mon. pl. 20,
522 f. 8” and illustrated in Foslie (1895, pl. 16, fig. 48) and Printz (1929, pl. 20, fig. 8). As
523 ~~allowed by Art. 9.17 of the ICN (Turland *et al.*, 2018), the holotype is here narrowed to the~~
524 ~~one sequenced specimen.~~ Based on morpho-anatomy, Athanasiadis (2016: 226) listed *L.*
525 *divergens* as *Incertae Sedis*; DNA sequence data confirm the placement of the species in *L.*
526 *glaciale*.
527
528 *Lithothamnion fornicatum* f. *sphaericum* Foslie, 1900: 12 (as '*sphaerica*').
529 HOLOTYPE: TRH B26-2789, 20.vii.1894, no habitat data, leg. M. H. Foslie.
530 TYPE LOCALITY: Skjørn, Dalsøren (now Stjørna, Daleøra), Trondheimsfjorden, Norway
531 (Woelkerling *et al.*, 2005: 380).
532 *Holotype DNA sequence*: rbcL-293 (bp 1172-1464), GenBank XXXXXXXXX.
533 *Comment*: Foslie (1900) only provided a reference to a previously published figure (Foslie
534 1895, pl. 12, fig. 1) for the protologue of this form, but Woelkerling (1993: 205) considered

535 this a validly published name. We sequenced the same individual rhodolith cited by Foslie
536 (1900) and illustrated in Foslie (1895, pl. 12, fig. 1).

537

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

539 LECTOTYPE: TRH B25-2777, 6.vii.1894, leg. M. H. Foslie (designated by Woelkerling,
540 1993: 91).

541 TYPE LOCALITY: Bejan (now Beian), Beiskjaeret, Norway (Woelkerling *et al.*, 2005:
542 377).

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

544 *Comment:* Foslie (1895, pl. 5, figs. 1-7) illustrated seven individual rhodoliths that
545 according to Woelkerling (1993) came from two collections from neighboring localities on
546 successive days. Woelkerling (1993: 91) designated as the lectotype collection nine
547 specimens comprising two of those illustrated in the protologue (Foslie, 1895, pl. 5, figs. 5
548 and 7) and seven other specimens. The lectotype is narrowed herein to the sequenced
549 specimen that is marked with label “nr. 2”, which is cited as part of the lectotype in
550 Woelkerling *et al.* (2005: 377).

551

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

553 LECTOTYPE: TRH B27-2805, 15.viii.1890, leg. M. H. Foslie (designated by Woelkerling,
554 1993: 95).

555 TYPE LOCALITY: Tromsø, Norway.

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

557 *Comment:* Foslie (1895) based this form on collections from several localities in Norway,
558 but did not designate a type. Woelkerling (1993) designated the specimen illustrated by
559 Foslie (1895, pl. 7, fig. 3) as the lectotype of this form. According to Woelkerling *et al.*
560 (2005), the lectotype has two green tags, and this was the specimen from which the DNA
561 sequence was obtained.

562

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

564 LECTOTYPE: TRH B8-2153, 12.vi.1892, leg. unknown (designated by Printz, 1929, pl.
565 22, fig. 5 legend).

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

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

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

573

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

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

577 LECTOTYPE: TRH C6-3037, 6.vi.1894, leg. M. H. Foslie (designated by Woelkerling,
578 1993: 109; further information in Woelkerling *et al.*, 2005: 419).

579 TYPE LOCALITY: Rotvold [now Rotvoll], Trondshemsfjord, Norway (Woelkerling *et*
580 *al.*, 2005: 419).

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

582 *Comment*: Foslie (1895) proposed *Lithothamnion gracilescens* for the coralline that Unger
583 (1858: 19) had called *Lithothamnion byssoides*, but Kjellman (1883: 120) already had
584 named this entity *Lithothamnion ungeri*. Foslie (1895: 90) listed three syntype localities,
585 Madal, Dröbak and Rotvold, and from the last location illustrated eight individuals (Foslie
586 1895, pl. 15, figs. 20-27). Later, Foslie (1900) without comment reduced *L. gracilescens* to
587 a form of *L. nodulosum* as *L. nodulosum* f. *gracilescens*. The specimen sequenced
588 corresponds to Foslie (1895, pl. 15, fig. 24), to which the lectotype is narrowed. Based on
589 morpho-anatomy Athanasiadis (2016: 228) listed *L. gracilescens* as *Incertae Sedis*; DNA
590 sequence data have confirmed the placement of the species in *L. glaciale*.

591

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

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

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

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

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

598 *Comment*: Kjellman (1883) did not designate a type specimen for his new species. In UPS
599 there appears to be only one individual rhodolith with a label in Kjellman's hand and with
600 the specific locality of Karlsøy cited in the protologue of *L. intermedium*, although two

601 individuals are illustrated by Kjellman (1883, pl. 4, figs. 1, 2). Thus, we designate UPS
602 A648805 as the lectotype.

603

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

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

606 Woelkerling, 1993: 107).

607 TYPE LOCALITY: Honningsvaag (now Honningsvåg), Finnmark, Norway (Woelkerling

608 *et al.*, 2005: 434).

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

610 *Comment:* Woelkerling (1993: 107) located two of the four specimens illustrated by Foslie

611 (1891, pl. 3, fig. 3). The specimen sequenced is illustrated in Foslie (1891, pl. 3, fig. 3,

612 second specimen from the left), and it is this specimen to which the lectotype is narrowed

613 herein. Athanasiadis (2016: 234) lists as *Incertae Sedis*; DNA sequence data have

614 confirmed the placement of the species in *L. glaciale*.

615

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

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

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

619 2005: 428).

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

621 *Comment:* Woelkerling (1993: 229) considered the material in the Foslie herbarium

622 illustrated by Printz (1929, pl. 22, figs. 6-13) to be the holotype, and we agree. The

623 specimen sequenced is marked with a green tag "pl. 27, fig. 9", but the specimen

624 corresponds to the plate 22, figure 9 in Printz (1929), as was noted by Woelkerling *et al.*
625 (2005: 428). Based on morpho-anatomy, Athanasiadis (2016: 235) listed *L. tusterense* as
626 *Incertae Sedis*; DNA sequence data have confirmed the placement of the species in *L.*
627 *glaciale*.

628

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

630 LECTOTYPE: TRH C8-3077, 6.ix.1897, leg. M. H. Foslie. Woelkerling (1993: 233)
631 designated as lectotype the specimens illustrated by Printz (1929, pl. 33, figs. 12, 13 and
632 15).

633 TYPE LOCALITY: Svolvær, Lofoten, Norway.

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

635 *Comment:* Foslie (1905b) based this species on two collections, one dead, excavated from
636 Vardø, Norway, the other living from Lofoten, Svolvær, Norway. Adey & Lebednik (1967:
637 77) examined material in TRH under this name, but did not designate a lectotype; this was
638 done by Woelkerling (1993: 233). The specimen sequenced corresponds to the one depicted
639 in Printz (1929, pl. 32, fig. 12), and the lectotype is narrowed herein to this specimen.

640 Based on morpho-anatomy, Athanasiadis (2016: 223) listed *L. vardoense* as *Incertae Sedis*;
641 DNA sequence data have confirmed the placement of the species in *L. glaciale*.

642

643 *Historical collections:*

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

646 TRH B10-2305, as *Lithothamnion glaciale f. subfastigiatum* (as '*subfastigiata*').
647 Bekkarfjord, Alten [now Alta], Norway, 21.viii.1897, leg. M. H. Foslie. *DNA sequence*:
648 *rbcL*-293 (bp 1172-1464), GenBank XXXXXXXXX. *Comment*: The largest fragment in the
649 collection was sequenced. The sequence was identical to the lectotype sequence of
650 *Lithothamnion colliculosum f. pusillum*, shown herein as a heterotypic synonym of *L.*
651 *glaciale*. *L. glaciale f. subfastigiatum* is considered a superfluous substitute name for
652 *Lithothamnion varians f. varians* Foslie (Woelkerling *et al.*, 2005: 306); the lectotype of *L.*
653 *varians f. varians* (TRH C23-3649) was DNA-extracted but failed to amplify (see
654 Supplementary note S1).

655

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

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

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

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

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

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

667

668

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

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

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

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

673 XXXXXXXXX and XXXXXXXXX.

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

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

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

677 1-4). In the figure legends, Kjellman refers to the figure 1 specimen as young (ungt), the

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

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

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

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

682 syntype localities Tromsö, Carlsö, Maasö, Magerö, Honningsvaag and Lebesby, the last

683 two localities based on specimens sent to Kjellman by Foslie; the syntype corresponding to

684 the latter locality –Lebesby– was also sequenced (TRH C13-3185, see below). The three

685 specimens in UPS were found in a single envelope (Supplementary fig. S4A) with the

686 locality "Norway. Finnmark: Hammerfest, Måsö [Måsöya]". Following Article 9.3

687 (Turland et al. 2018) we herein designate these three specimens as the lectotype of *L.*

688 *soriferum*.

689 The identical *rbcL-263* sequences of all three UPS specimens are an exact match to

690 GenBank sequences of the recently described *Lithothamnion erinaceum* (Melbourne *et al.*,

691 2017). Following Article 11.4 of the ICN (Turland *et al.*, 2018), the correct name is the

692 combination of the final epithet of the earliest legitimate name of the taxon at the same
693 rank. Consequently, *L. soriferum* has nomenclatural priority over *L. erinaceum*, and it is the
694 correct name for this taxon. Further information about the heterotypic synonym *L.*
695 *erinaceum* is in the entry below.

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

698 TYPE LOCALITY: Lebesby, Finmarken (now Finnmark), Norway (Woelkerling *et al.*,
699 2005: 441).

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

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

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

711

712 HETEROTYPIC SYNONYMS:

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

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

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

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

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

725

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

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

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

729 *Holotype DNA sequences:* GenBank KX828452 (*psbA*) and KX828509 (COI-5P)
730 (Melbourne *et al.*, 2017); GenBank MH697546 and MH697547 (*rbcL*, Hofman & Heesch
731 2018).

732 *Comment:* According to Melbourne *et al.* (2017), collections from Northern Ireland,
733 Iceland, Norway and British Columbia provided in Pardo *et al.* (2014) as *Lithothamnion* sp.
734 2 corresponded to *L. erinaceum*. Based on DNA sequences, these collections are also
735 assigned to *L. soriferum*, as well as the remaining specimens from the UK identified as
736 *Lithothamnion* sp. in Melbourne *et al.* (2017, Table S1). Additionally, GenBank records

737 from Norway identified as *L. erinaceum* (specimens “NCCA” in Supplementary Table S3)
738 correspond to *L. soriferum* (Anglés d’Auriac *et al.*, 2019).
739
740 *Lithothamnion fornicatum* Foslie, 1891: 38, pl. 2 (bottom specimen).
741 LECTOTYPE: TRH B21-2712, 20.ix.1890, leg. unknown (designated by Adey & Lebednik
742 1967: 71).
743 TYPE LOCALITY: Melangen [now Malangen], Mestervik, Tromsø county, Norway
744 (Woelkerling *et al.*, 2005: 366).
745 *Lectotype DNA sequence: rbcL-293* (bp 1172-1464), GenBank XXXXXXXX.
746 *Comment:* Foslie (1891) described and illustrated three specimens from the same locality.
747 Adey (1970c) noted that the lectotype, designated by Adey & Lebednik (1967: 71),
748 comprised two sets of specimens and that the selected set had a specimen pictured in the
749 original description, but Adey (1970c) did not indicate which of the three originally
750 pictured specimens is the designated lectotype. Woelkerling (1993: 97) and Woelkerling *et*
751 *al.* (2005: 366) provided information about the lectotype specimen illustrated in Foslie
752 (1891, pl. 2, bottom specimen) and marked with green tag “Præp. 151”. Based on morpho-
753 anatomy, Athanasiadis (2016: 228) listed *L. fornicatum* as *Incertae Sedis*; DNA sequence
754 data have confirmed the placement of the species in synonymy with *L. soriferum*.
755
756 *Lithothamnion granii* (Foslie) Foslie, 1900: 11.
757 BASIONYM: *Lithothamnion flabellatum* f. *granii* Foslie, 1895: 98, pl. 17, figs. 1-7, pl. 22,
758 fig. 1.

759 HOMOTYPIC SYNONYMS: *Lithothamnion glaciale* var. *granii* (Foslie) Rosenvinge,
760 1917: 222, figs. 138-142, pl. 3, fig. 4; pl. 4: figs. 1-4; *Lithothamnion glaciale* f. *granii*
761 (Foslie) Foslie 1905a: 10.

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

764 TYPE LOCALITY: Drøbak, Norway.

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

766 *Comment*: The specimen sequenced is located in a large, round blue box; the label indicates
767 illustrations in Foslie (1895, pl. 17, fig. 3 and pl. 22, fig. 1) and Printz (1929, pl. 18, fig.
768 15). Foslie (1895: 98, pl. 17, figs. 1-7) described this new form, listed numerous syntype
769 localities and illustrated seven specimens. Later, Foslie (1900) elevated this form to specific
770 rank. Adey & Lebednik (1967) lectotypified the specimens collected by Gran, who is
771 honored by the form name. Subsequent to the original description, Foslie named five
772 additional forms, f. *robustum* (Foslie, 1895), f. *grandifrons*, f. *sphaericum* (Foslie, 1900),
773 and f. *obcrateriforme* and f. *tuberculatum* (Foslie, 1905a). We have not sequenced type
774 material of any of these forms, hence they are not listed as synonyms. Based on morpho-
775 anatomy, Athanasiadis (2016: 228) listed *L. granii* as *Incertae Sedis*; DNA sequence data
776 have confirmed the placement of the species in synonymy with *L. soriferum*.

777

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

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

781 LECTOTYPE: TRH C5-2999, 18.vii.1894, leg. M. H. Foslie (designated by Woelkerling,
782 1993: 158).

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

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

786 *Comment:* We sequenced one of the three rhodoliths comprising the lectotype from
787 Brekstad, Norway, and the sequence was identical to *L. soriferum*. The specimen sequenced
788 is preserved in a round, red box; it is illustrated in Printz (1929, pl. 25, fig. 2) and not in pl.
789 21 as marked on the box (see Woelkerling *et al.*, 2005: 414). The lectotype is narrowed
790 herein to the sequenced specimen. Based on morpho-anatomy, Athanasiadis (2016: 228)
791 listed *L. nodulosum* as *Incertae Sedis*; DNA sequence data have confirmed the placement of
792 the species in synonymy with *L. soriferum*.

793

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

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

796 TYPE LOCALITY: The islet in front of the lighthouse, Røvær, Norway (Woelkerling *et al.*
797 2005: 323).

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

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

804 located separately within a blue, round box that corresponds to the piece illustrated in plate
805 4, figure 8 (Printz (1929)).

806

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

808 LECTOTYPE: TRH C11-3161, 5.viii.1882, leg. M. H. Foslie (designated by Woelkerling,
809 1993: 79).

810 TYPE LOCALITY: Tromsø, Norway.

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

812 *Comment:* Woelkerling *et al.* (2005: 437) noted that there was one specimen in the
813 lectotype collection with a green tag: “Lith. Mon. pl. 20, f. 9” (corresponding to Printz
814 1929, pl. 20, fig. 9), and another specimen with the annotation, “Specimen matches Foslie
815 1891a, pl. 3, fig. 2, lower left”. Previously, Woelkerling (1993: 79) designated as lectotype
816 element the collection containing this latter specimen because no further type material had
817 been found at that time. The specimen selected for sequencing was the specimen with the
818 green tag “Lith. Mon. pl. 20, f. 9” (corresponding to Printz, 1929, pl. 20, fig. 9) among the
819 five rhodoliths contained in the lectotype collection. The lectotype is narrowed herein to the
820 sequenced specimen. Based on morpho-anatomy, Athanasiadis (2016: 228) listed
821 *L.soriferum* f. *divaricatum* as *Incertae Sedis*; DNA sequence data have confirmed the
822 placement of the taxon in *L. soriferum*.

823

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

825 HOMOTYPIC SYNONYMS: *Lithothamnion calcareum* f. *uncinatum* (Foslie) Foslie,
826 1897: 9; *Lithothamnion norvegicum* f. *uncinatum* (Foslie) Foslie, 1900: 13.

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

828 TYPE LOCALITY: Kragerø, Norway.

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

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

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

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

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

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

835

836 *Historical collection:*

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

838 *263* (bp 1172-1434), GenBank XXXXXXXXX (Supplementary table S1).

839

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

841 BASIONYM: *Millepora polymorpha* f. *tophiformis* Esper, 1789: pl. XV [Millepora]

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

843 1970c).

844 TYPE LOCALITY: Julianehaab, Greenland.

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

846 *Comment:* We sequenced the neotype designated by Adey *et al.* (2005), and the GenBank

847 sequences used in Adey *et al.* (2015b) are in agreement with the neotype sequence.

848

849 HETEROTYPIC SYNONYMS:

850 *Lithothamnion alcicorne* Kjellman, 1883: 121, pl. 5, figs. 1-8.

851 HOMOTYPIC SYNONYMS:

852 *Lithothamnion soriferum* f. *alcicorne* Foslie, 1891: 41, pl. 3, fig. 4.

853 *Lithothamnion tophiforme* f. *alcicorne* Foslie, 1895: 147 (as '*alcicornis*').

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

855 TYPE LOCALITY: Tromsø, Norway.

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

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

858 *tophiforme*. Kjellman (1883: 122) stated that this species was from Tromsø and that Foslie

859 was the collector. Woelkerling *et al.* (2005: 443) called TRH C13-3203 syntype material.

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

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

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

863 *tophiforme*.

864

865 *Historical collection:*

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

867 *DNA sequence: rbcL-293* sequence (bp 1172-1464), GenBank XXXXXXXXX; identical to

868 the neotype sequence of *L. tophiforme*.

869 *Comment:* This collection is topotype material of *Lithothamnion norvegicum* (Areschoug)

870 Kjellman (1883: 122, basionym: *Lithothamnion calcareum* var. *norvegicum* Areschoug,

871 1875: 4). The box contains a large collection of rhodoliths but the specimen sequenced is

872 located separately within a small box marked "Prep. 522".

873 Areschoug (1875:4) cited Wittrock as the collector *L. calcareum* var. *norvegicum*,
874 but he did not illustrate material, nor indicate a type. We have been unable to locate any
875 material in either L or UPS where other Areschoug material is located. Eleven collections
876 of Foslie's in TRH are listed under *L. norvegicum* (Woelkerling et al. 2005: 407-408), but
877 only the sequenced specimen is topotype material. A collection by Wittrock is in TRH (C3-
878 2985) and illustrated in Printz (1929, pl. 16, figs. 37-38) but the date of collection and
879 habitat data are lacking, making it difficult to know if this is type material. Woelkerling &
880 Verheij (1995: 67) noted syntype material is present in L. Both the material in TRH and in
881 L needs to be sequenced to understand the correct application of *L. norvegicum*.

882

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

884

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

886 *Lithothamnion squarrulosum* f. *palmatifida* Foslie, 1899: 6.

887 LECTOTYPE: TRH C1-2892, 12.v.1893, leg. L. K. Rosenvinge; designated by

888 Woelkerling *et al.* (2005: 398).

889 TYPE LOCALITY: Fladen, østl. (= Eastern) Kattegat, Denmark (Woelkerling *et al.* 2005:

890 398).

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

892 XXXXXXXXX, respectively.

893 *Comment:* Collection consisted of several rhodoliths. The specimen tagged with an

894 unwritten green label was selected for DNA sequencing. The *rbcL* sequence differed by 2

895 bp from the neotype sequence of *P. calcareum*, while the *psbA* sequences were identical
896 (neotype specimen BM000712373, Supplementary table S3).

897

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

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

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

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

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

903 *Comment*: The largest fragment preserved in a small box marked '520' (further information
904 in Woelkerling *et al.* 2005: 493) was selected for DNA sequencing. Identical *rbcL*

905 sequences were obtained independently by VP and by PWG/JRH, which differed by 1-3 bp

906 from the GenBank sequences of *P. rugulosum* (vouchers US 170942 and BM000659095)

907 collected in Gulf of Maine and Helgoland, Germany, respectively (Adey *et al.* 2015b). By

908 the rule of priority (Art. 11.4 of the ICN, Turland *et al.*, 2018), this name must be adopted

909 for *P. rugulosum*.

910

911 HETEROTYPIC SYNONYM:

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

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

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

915

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

917 **P.W.Gabrielson**

918 BASIONYM: *Lithothamnion squamulosum* Foslie, 1895:183.
919 HOLOTYPE: TRH B5-1962, vii. 1894, leg. P. Boye.
920 TYPE LOCALITY: Sogn, Sulen (now Sula), indre (= inner), Stensund (now Steinsund),
921 Norway (Woelkerling *et al.* 2005: 265).
922 *Holotype DNA sequences: psbA* and *rbcL-293* (bp 1172-1464), GenBank XXXXXXXXX
923 and XXXXXXXXX, respectively.
924 *Comment:* The collection comprises a larger box with two smaller boxes, one square and
925 one round (Woelkerling *et al.*, 2005: 265). The specimen in the rounded box with the
926 annotation “Prep. 65” was sequenced. Recently this taxon was transferred to *Phymatolithon*
927 according to the molecular data obtained from an isotype preserved in BM (BM000044670,
928 Box 434, Adey *et al.*, 2018). The DNA sequencing of the holotype confirms this result; the
929 *rbcL* sequences of both type collections were identical.
930
931 *Recent collections:*
932 Norway: Krøttøya (Troms) and Averøya. Intertidal to subtidal (9 m depth), encrusting on
933 cobble, pebbles and shells, and on hard substrata. Specimens with uniporate (gametangial
934 or carposporangial) and multiporate conceptacles. *DNA sequences: psbA* (Supplementary
935 table S2).
936
937 N.B. We have not dealt with *Lithothamnion sonderi* Hauck in this paper as we have not
938 sequenced the type material, even though the species is thought to be widespread in
939 crustose forms at low light levels in the NE Atlantic, from Nordland (Norway) to North
940 Spain (Chamberlain & Irvine, 1994).

941

942 **Discussion**

943 Since DNA sequences from the first type specimens of geniculate (Gabrielson *et al.*, 2011)
944 and non-geniculate (Sissini *et al.*, 2014) corallines were published, it has become
945 increasingly clear that the primary method to unequivocally apply a historical name is to
946 obtain DNA sequences from the type material to compare them to sequences from other
947 historical or more recently collected specimens (Martone *et al.*, 2012; Hind *et al.*, 2014a;
948 2014b; 2015; Hernández-Kantún *et al.*, 2015a; 2016; Richards *et al.*, 2017; 2018;
949 Gabrielson *et al.*, 2018; 2019; Peña *et al.*, 2018; Jeong *et al.*, 2020; Maneveldt *et al.*, 2020;
950 Puckree-Padua *et al.*, 2020). Herein, we have applied that methodology to the numerous
951 species and infraspecific names of Arctic and Subarctic non-geniculate corallines published
952 by Kjellman (1883; 1889) and later by Foslie (1891; 1895; 1896; 1899; 1900; 1905a, b;
953 1908) and others.

954 With the exception of the *Lithothamnion tophiforme* (Unger, 1858), first published
955 as *Millepora polymorpha* var. *tophiformis* Esper (1789), the oldest names applicable to
956 Arctic and Subarctic non-geniculate corallines are those of Kjellman (1877; 1883; 1889).
957 By sequencing type material, Adey *et al.* (2015b) confirmed the application of two of
958 Kjellman's names, *L. compactum* Kjellman (1883) to *Clathromorphum*, and *L. loculosum*
959 Kjellman (1889) to *Neopolyporolithon*, and showed that a third, *Lithothamnion foecundum*
960 Kjellman (1883), currently placed in *Leptophytum* W.H.Adey, does not belong in that
961 genus, but its generic position remains unresolved. Lectotype material of the oldest name,
962 *Lithophyllum arcticum* Kjellman (1877), collected at Uddebay, Novaya Zemlya, Russia,
963 was shown to be an earlier available name for *Neopolyporolithon loculosum* (Kjellman)

964 W.H.Adey, P.W.Gabrielson, G.P.Johnson & Hernández-Kantún, namely *N. arcticum*
965 (Kjellman) P.W.Gabrielson, S.C.Lindstrom & Hughey (Gabrielson *et al.*, 2019).
966 *Lithothamnion flavescens* Kjellman (1883) was transferred to *Leptophytum* by
967 Athanasiadis (2016), but this was based on morpho-anatomy, which has been shown to
968 be problematic in correctly placing non-geniculate species in a genus (Hind *et al.*, 2016;
969 2018; Gabrielson *et al.*, 2019). Of the remaining six Kjellman names, five are treated
970 herein, *L. alcicorne*, *L. durum*, *L. glaciale*, *L. intermedium* and *L. soriferum*. Attempts to
971 amplify *L. ungeri* Kjellman (1883) were unsuccessful. Thirty-five type specimens of
972 *Lithothamnion* species and infraspecific taxa described by Foslie were sequenced. Below
973 we discuss the systematics of the Arctic and Subarctic *Lithothamnion* species that we
974 recognize, including *L. lemoineae*, and one of the species of *Clathromorphum*, *C.*
975 *circumscriptum*, for which we found an additional synonym. Distributions, habits and
976 habitat data for each species are updated, including range maps for the *Lithothamnion*
977 species.

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

983 The habit and habitat of *C. circumscriptum* are provided by Adey *et al.* (2015b), and
984 the sequenced specimens confirm this information. The species is reported to be circum
985 Arctic ranging south to the Subarctic in both the Atlantic and Pacific Oceans based on
986 morpho-anatomy and its distinct habit (Adey, 1965; Adey *et al.*, 2013; 2015a, b). In the

987 NW Atlantic Subarctic, *C. circumscriptum* is generally more abundant at depths of less
988 than 10 m on moderately exposed rocky shores (Steneck, 1978; Adey & Hayek, 2011).
989 DNA sequences confirm its presence in Greenland, but material from the Russian Arctic
990 and NW Pacific Ocean has not been sequenced. DNA sequences from the western Gulf of
991 Alaska are from specimens collected in mid (GenBank MT732997) and high intertidal
992 pools (MT733001). Other mid pool (MT732990) and low intertidal collections
993 (MT732992, MT732993, MT732996) from this area represent an undescribed species of
994 *Clathromorphum*. Records based on morpho-anatomy from SE Alaska may also represent
995 an undescribed species.

996 *Lithothamnion glaciale*. There is no doubt that the lectotype specimen designated
997 herein is the one illustrated by Kjellman (1883, pls. 2, 3), despite having listed multiple
998 syntype localities. The partial *rbcL* sequence from the lectotype differs by 1 bp from all
999 other specimens that thus far have been sequenced, including one from Spitzbergen. DNA
1000 sequencing also shows that eighteen specific and infraspecific *Lithothamnion* taxa later
1001 named by Foslie are heterotypic synonyms of *L. glaciale*. *Lithothamnion intermedium*,
1002 described in the same publication as *L. glaciale* (Kjellman, 1883), was listed most recently
1003 by Athanasiadis (2016) as *Incertae Sedis*. Kjellman provided three syntype localities for *L.*
1004 *intermedium*, but he himself only collected the specimen at Karlsøy (Carlsö); specimens
1005 from the other two localities (Tromsø and Vadsø) were collected by Foslie. In UPS only
1006 two specimens could be located, one from Karlsøy, collected by Kjellman and with a label
1007 in his handwriting, and the other collected by Foslie from Mestervik, Tromsø. The
1008 Kjellman specimen from Karlsøy we have designated as the lectotype; its sequence differs
1009 by 1 bp from the sequence of the *L. glaciale* lectotype. By DNA sequence the specimen

1010 collected by Foslie is *L. soriferum*. *Lithothamnion glaciale* and *L. intermedium* were
1011 published at the same time and are the same species so either name can be used for this
1012 species. We selected *L. glaciale* because of its long-standing use by the coralline research
1013 community and because the lectotype material is homotypic, whereas *L. intermedium*
1014 mostly has been ignored.

1015 The habit and habitat of *L. glaciale* were described by Adey (1966a) and Adey *et al.*
1016 (2005) based primarily on NW Atlantic material identified by morpho-anatomy.
1017 Specimens ranged from epilithic crusts to free living rhodoliths. More recently, encrusting
1018 epilithic forms of *L. glaciale* have been reported to be very common from the low intertidal
1019 to the photic limit (Adey & Hayek, 2011). Most collections, however, are from the low
1020 intertidal to a depth of ~15 m, which is more a reflection of collection limits than the
1021 species' true vertical distribution. Numerous studies in the past two decades have
1022 documented the presence of rhodoliths throughout the North Atlantic and Arctic at depths
1023 of ~3 to 50 m, and while most studies have assumed *L. glaciale* as the forming species,
1024 little to no corroborative DNA sequencing work has been carried out as part of these studies
1025 (Halfar *et al.*, 2000; Blake and Maggs, 2003; Kamenos & Law, 2010; Gagnon *et al.*, 2012;
1026 Teichert *et al.*, 2012; 2014; Adey *et al.*, 2015a; Millar & Gagnon, 2018; Schoenrock *et al.*,
1027 2018b; Bélanger & Gagnon, 2020; Teed *et al.*, 2020). Although this assumption is
1028 legitimate given the ubiquity of *L. glaciale* in both oceans, morphological deviations from
1029 the norm in a few *L. glaciale* rhodoliths from Newfoundland and Labrador suggests that
1030 rhodoliths may also include other species of corallines such as *L. tophiforme* and *C.*
1031 *compactum* (D. Bélanger & P. Gagnon, unpublished data). In Norway, Anglés d'Auriac *et*

1032 al. (2019) reported plurispecific maerl mainly composed of *L. glaciale* and associated
1033 species of *Phymatolithon* and *Lithophyllum*.

1034 We confirm by DNA sequencing the presence of *L. glaciale* throughout the North
1035 Atlantic (Fig. 2). We have not confirmed many of the Arctic Ocean reports. The
1036 observation of uniporate conceptacles (mostly carposporangial) and multiporate
1037 tetra/bisporangial conceptacles in our collections from Norway, confirmed the common
1038 occurrence of gametophytes and tetra/bisporophytes for this species, as is suggested in the
1039 literature (e.g., Chamberlain & Irvine, 1994).

1040 In the North Pacific this species was first reported by Saunders (1901: 442) based
1041 on specimens collected in Prince William Sound and further west at Kukak Bay and the
1042 Shumagin Islands and identified by Kjellman. We have not confirmed by DNA sequencing
1043 the identity of these specimens. Recently, however, Bringloe & Saunders (2019) reported
1044 this species from Nome, Alaska, USA (Bering Strait), and we have sequenced specimens
1045 from Malcolm Island, central British Columbia, Canada south to Monterey County,
1046 California, USA (Fig. 2). In the NE Pacific, only encrusting epilithic specimens were
1047 found, although they may completely cover pebbles so that they appear to be rhodoliths.
1048 We cannot confirm reports based on morpho-anatomy from Japan and Arctic Russia, but
1049 likely *L. glaciale* is present in those areas as well. Reports of this species from any tropical
1050 and warm temperate regions as found on AlgaeBase (Guiry & Guiry, 2020) are highly
1051 improbable. Reports from the Subantarctic (Heydrich, 1900; Lemoine, 1913) need to be
1052 confirmed.

1053 *Lithothamnion lemoineae*. Melbourne *et al.* (2017) provided a *psbA* sequence from
1054 the holotype of *L. lemoineae* from the NW Atlantic (Maine, USA) to unequivocally link

1055 DNA sequences from field-collected material to the name. Based on DNA sequenced
1056 specimens, we expand the habit of *L. lemoineae* from encrusting epilithic to epiphytic, to
1057 epizoic on shells, and as rhodoliths. The species can also occur in the intertidal, as well as
1058 in the shallow subtidal to 12 m depth. In the NW Atlantic Subarctic, *L. lemoineae* often
1059 dominates rock on exposed shores (Adey & Hayek, 2011), particularly at 10-15 m depth
1060 (R. Steneck, *pers. obs.*).

1061 Melbourne *et al.* (2017) found that specimens from England, thought to be *L.*
1062 *lemoineae* based on morpho-anatomy (Chamberlain & Irvine, 1994), were not that species
1063 based on DNA sequencing. However, based on DNA sequenced material, we corroborated
1064 a recent record of *L. lemoineae* from the same region in the NE Atlantic (Svalbard,
1065 Norway; Hofmann & Heesch, 2018), and likewise Bringloe & Saunders (2019) have the
1066 first confirmed record from the NE Pacific at Nome, Alaska, USA. Here, we confirm its
1067 occurrence on Kodiak Island, Gulf of Alaska (GenBank MT733005), where it occurred on
1068 low intertidal bedrock. The report of this species from the NW Pacific by Lee (2008) needs
1069 to be verified by DNA sequencing. We also confirm the species distribution in the NW
1070 Atlantic from Labrador, Canada to Maine, USA (Fig. 3).

1071 *Lithothamnion soriferum*. We located in UPS three specimens of *L. soriferum* in an
1072 envelope with a label in Kjellman's handwriting and from one of the cited localities, Carlsö
1073 (now Karlsøy). These appear to have been illustrated and published by Kjellman (1883, pl.
1074 1, figs. 1-4) with some artistic license. This is similar to what we found for *L. durum*
1075 (Kjellman, 1889) and *L. glaciale* (Kjellman, 1883), and in all of these examples the
1076 specimens are convincing matches to the illustrations. DNA sequences from type
1077 specimens of five species and infraspecific taxa later named by Foslie are all exact matches

1078 to the lectotype specimens of *L. soriferum*. The recently described *L. erinaceum*
1079 (Melbourne *et al.*, 2017) also is a heterotypic synonym of *L. soriferum*. Since being
1080 published, *L. soriferum* has had a checkered history, sometimes being recognized as a
1081 distinct species (Foslie, 1905; Zinova, 1955) but mostly it has been considered a synonym
1082 of *L. tophiforme* (Foslie, 1895; Lund, 1959; Jaasund, 1965; Lee, 1969; Adey, 1970a;
1083 Vinogradova, 2010). Interestingly, Adey *et al.* (2005), in a detailed examination of *L.*
1084 *tophiforme*, did not mention *L. soriferum*, and, most recently, Athanasiadis (2016) treated
1085 the species as *Incertae Sedis*.

1086 Based on DNA sequences, *L. soriferum* is a distinct species and occurs as an
1087 epilithic, epiphytic or epizoic (specimen on a worm tube) crust or as a free-living rhodolith.
1088 Specimens are primarily subtidal to 27 m depth, but we have one occurrence in the low
1089 intertidal as an epilithic crust. In contrast to *L. glaciale*, gametangial plants have not been
1090 observed in any of the collections. Only multiporate tetra/bisporangial conceptacles were
1091 observed, as it is indicated in the type collections of two heterotypic synonym (*L. breviaxe*
1092 and *L. granii*, Woelkerling *et al.*, 2005) and in the literature (Melbourne *et al.*, 2017).

1093 The species is widespread in the central and eastern North Atlantic (Greenland,
1094 Iceland, UK, Norway), but there is no evidence of its occurrence in the NW Atlantic; in the
1095 NE Pacific there are sporadic records from the Aleutian Islands (Robinson *et al.*, 2017) and
1096 Prince William Sound (Konar *et al.*, 2006), Alaska, USA south to Gwaii Haanas, British
1097 Columbia, Canada (Fig. 4). For having such a widespread distribution, this species appears
1098 uncommon compared to *L. glaciale*. In the first report of *L. soriferum* from the NE Pacific
1099 (Konar *et al.*, 2006), this species was misidentified as *Phymatolithon calcareum* based on
1100 morpho-anatomy. This appears to be so because the cell types in the cross-section image

1101 (Konar *et al.*, 2006, fig. 3B) were misidentified. The figure clearly shows flared epithallial
1102 cells that are not characteristic of any *Phymatolithon* species, but that are found in
1103 *Lithothamnion* species. All reports of *P. calcareum* outside boreal NE Atlantic and the
1104 Mediterranean Sea waters based on morpho-anatomy are doubtful and need to be confirmed
1105 by DNA sequences.

1106 *Lithothamnion tophiforme*. The sequence of the neotype specimen, TRH C13-3203,
1107 designated by Adey *et al.* (2005), confirms the identity of the specimen used by Adey *et al.*
1108 (2015b) to represent this species. Adey (1970a) reported this species to be both encrusting,
1109 especially on shells or shell fragments, and also as free-living rhodoliths. All of the
1110 sequenced specimens to date have been rhodoliths. Adey *et al.* (2005) considered *L.*
1111 *tophiforme* an Arctic species, but also stated that its abundance in the high Arctic is
1112 unknown, a situation that remains unchanged. They also noted that it is found only in
1113 colder waters below 10 m depth and at temperatures below 10° C, and the sequenced
1114 specimens confirm this pattern as all were collected below 15 m depth. All of the recently
1115 collected sequenced specimens are from the NW Atlantic, from Newfoundland, Canada
1116 northward (Fig. 5). The neotype specimen is the only confirmed specimen from Greenland,
1117 and only two historical specimens from the 19th century are from Norway, where the
1118 species was not found recently in an extensive collection effort presented herein.

1119 In the NW Atlantic Subarctic, *L. tophiforme* rhodoliths commonly co-occur with *L.*
1120 *glaciale* rhodoliths, while dominating at depths >25 m (Adey *et al.*, 2015a). In rhodolith
1121 beds where both species occur, thalli of *L. tophiforme* and *L. glaciale* sometimes merge,
1122 forming plurispecific rhodoliths with a characteristic color mosaic where *L. tophiforme*
1123 generally presents a more brownish-orangy color than *L. glaciale* (D. Bélanger & P.

1124 Gagnon, unpublished data). Our sequenced specimens of *L. tophiforme* presented a variety
1125 of shapes and sizes, from a few centimetre-long twig-like thalli, to large (>10 cm across)
1126 branching spheroidal rhodoliths. A few specimens presented a distinct growth form with
1127 fanned-shaped branches. The phenotypic plasticity of *L. tophiforme* highlights the
1128 importance of DNA sequencing for identification.

1129

1130 *Identifying non-geniculate coralline algae to species.* These Arctic and Subarctic
1131 *Lithothamnion* species exemplify the difficulties of identifying non-geniculate coralline
1132 species using morpho-anatomy. DNA sequencing has revealed that by the first decade of
1133 the 20th Century, 30 specific and infraspecific names had been given to three species: *L.*
1134 *glaciale*, *L. soriferum* and *L. tophiforme*. Recently, based on morpho-anatomy, the vast
1135 majority of these were listed as *Incertae Sedis* by Athanasiadis (2016) including, for
1136 example *L. alvicorne*, *L. breviaxe*, and *L. soriferum*. In the over 100 years since these had
1137 been named and examined by numerous coralline morpho-anatomists, their identity could
1138 not be determined with any certainty. And there remain another 21 species or infraspecific
1139 taxa of *Lithothamnion* named by Foslie, 20 from Norway and one from Scotland from
1140 which we were unable to amplify DNA using PCR. It is highly unlikely, however, that any
1141 of these names would apply, due to the extensive sequencing of Norwegian specimens
1142 reported herein and the rule of priority. With the exception of *L. lemoineae*, which has
1143 never been recorded from Norway, the applied *Lithothamnion* names predate any of those
1144 published by Foslie.

1145 Further complicating the naming of specimens without DNA sequencing is that all
1146 of these species can occur either as encrusting corallines attached to a substrate or as

1147 unattached rhodoliths -encrusting a core or not - sometimes occurring singly, but also in
1148 beds. *Lithothamnion lemoineae* previously had only been reported to occur as an epilithic
1149 crust, whereas *L. soriferum* (also as *L. erinaceum*) had not been known as an epilithic crust.
1150 In some regions, species can have restricted morphologies, for example in Norway *L.*
1151 *glaciale* is found as an epilithic crust, or as free-living maerl, whereas in the NE Pacific it
1152 has so far only been reported as an epilithic crust. And three of the four species, *L. glaciale*,
1153 *L. lemoineae* and *L. soriferum*, can occur from the intertidal to, at minimum, 12 m depth.

1154 The finding by DNA sequencing of four Arctic and Subarctic *Lithothamnion*
1155 species that had been named as multiple specific and infraspecific taxa using morpho-
1156 anatomy is clearly opposite the cryptic diversity commonly recorded in temperate
1157 corallines (e.g., Pardo *et al.*, 2014; 2017; Hernández-Kantún *et al.*, 2015a, b; Peña *et al.*,
1158 2015a, b; Richards *et al.*, 2018; Pezsolesi *et al.*, 2019). However, this plethora of specific
1159 and infraspecific names in the Arctic and Subarctic regions was primarily the work of
1160 Foslie, who, as illustrated in the taxonomic results, changed his mind numerous times about
1161 which taxa should be recognized and at what rank. In tropical regions, DNA sequencing of
1162 non-geniculate corallines has shown that some species are widely distributed, whereas most
1163 have local distributions (Sissini *et al.*, 2014; Peña *et al.*, 2014b; Hernández-Kantún *et al.*
1164 2016; Gabrielson *et al.*, 2018; Maneveldt *et al.*, 2019).

1165 In the Arctic and Subarctic additional species of *Lithothamnion* and
1166 *Clathromorphum* need to be recognized based on the DNA sequencing reported herein
1167 (Supplementary table S2). It is also likely that the Arctic and Subarctic *Lithothamnion*
1168 species will need to be transferred to a new genus, as the generitype of *Lithothamnion*, *L.*
1169 *muelleri* Lenormand ex Rosanoff, belongs in a different clade (Yeong *et al.*, 2020).

1170 It is critical that in this time of rapid ocean warming and acidification,
1171 particularly in polar regions, that we have a firm understanding of the taxa currently present
1172 in order to document future changes in their habitats and distributions. Importantly, the
1173 biogeography of coralline algae appears especially sensitive to ocean thermogeography
1174 (Adey & Steneck, 2001; Adey & Hayek, 2011). The relevance of non-geniculate coralline
1175 algae in these regions as ecosystem engineers cannot be overstated, whether occurring as
1176 encrusting species attached primarily to rock substratum (Freiwald & Henrich, 1994; Adey
1177 *et al.*, 2005; Adey *et al.*, 2015a) or as free-living maerl (Pardo *et al.*, 2014; Teichert, 2014;
1178 Teed *et al.*, 2020). As polar seas warm and become increasingly acidified, these coralline
1179 algal species will either be forced to live at lower depths, where they will be limited by the
1180 availability of photosynthetically active radiation through the water column, or they will
1181 become extinct. DNA barcoding of organisms in these habitats, coupled with DNA
1182 sequencing of type and historical specimens, provides the foundation to document these
1183 imperiled species.

1184

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1199 **Supplementary information**

1200 **Supplementary Note 1.** Type collections & historical specimens DNA-extracted but
1201 unsuccessfully sequenced for *psbA* and *rbcL*.

1202 **Supplementary Table S1.** Type collections and historical specimens sequenced in the
1203 study.

1204 **Supplementary Table S2.** Collection and vouchering details for the recent specimens
1205 sequenced in the study. For each species, specimens are sorted by collection areas: NE
1206 Atlantic, NW Atlantic and NE Pacific.

1207 **Supplementary Table S3.** List of GenBank accession numbers used in this study with
1208 details of locality information and references.

1209 **Supplementary Figure S1.** Maximum Likelihood (ML) tree of COI-5P included in the
1210 present study. Bootstrap ML values >50% shown for each node. Scale bar: 0.05
1211 substitutions per site.

1212 **Supplementary Figure S2.** Phylogenetic tree inferred from RAxML and Bayesian
1213 inference of *psbA* sequences included in the present study. Bootstrap ML values >50% and
1214 posterior probabilities >0.50 from Bayesian inference shown for each node. Scale bar: 0.02
1215 substitutions per site.

1216 **Supplementary Figure S3.** Morpho-anatomy of *Lithothamnion glaciale*, UPS A-000202.
1217 Fig. A. Thallus habit and herbarium labels including label handwritten by Kjellman. Fig. B.
1218 Vertical fracture of protuberance showing radial construction and location of overgrown
1219 and buried conceptacle (black arrow). Fig. C. Vertical fracture of protuberance with
1220 conceptacle (black arrow) overgrown by a secondary hypothallus (arrowheads). Fig. D.
1221 Magnified view of secondary hypothallus (bracket) over conceptacle roof. Fig. E.
1222 Perithallus with cell fusions (white arrows). Fig. F. Perithallus (lower bracket), intercalary
1223 meristem (middle bracket, *), and a single-layered epithallus (upper bracket) of flared cells
1224 (e), one with cell roof intact (white arrow). Scale bars: Figs. B-C = 100 μm ; Figs. D-F = 10
1225 μm .

1226 **Supplementary Figure S4.** Morpho-anatomy of *Lithothamnion soriferum*, UPS A-648809.
1227 Fig. A. Thallus habit of specimens and herbarium label handwritten by Kjellman. Figs. B-
1228 D. Vertical fractures of protuberance showing radial construction. Fig. E. Magnified view
1229 of secondary hypothallus (arrowhead, bracket) over the thallus surface of the older growth
1230 layer. Fig. F. Perithallus (lower bracket) with cell fusions (white arrows), intercalary
1231 meristem (middle bracket, *), and epithallus (upper bracket). Figs. G-H. Magnified view of
1232 meristematic cells (*) and a single-layered epithallus of flared cells (e), one with cell roof
1233 intact (white arrow, Fig. H). Scale bars: Fig. A = 2 cm. Figs. B-D = 100 μm . Figs. E-H = 10
1234 μm .

1235

1236 **Disclosure statement**

1237 No potential conflict of interest was reported by the authors.

1238

1239 **Author Contributions**

1240 V. Peña & P.W. Gabrielson: original concept; V. Peña, P.W. Gabrielson, L. Le Gall & J.R.
1241 Hughey: DNA sequencing types; J.L. Richards: morpho-anatomy of type specimens; V.
1242 Peña, P. W. Gabrielson, L. Le Gall, S. C. Lindstrom & G. W. Saunders: DNA sequencing
1243 of contemporary collections. L. Le Gall: distribution maps; E. Rinde: led the field sampling
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1248 Kamenos & P. W. Gabrielson: writing; V. Peña, D. Bélanger, P. Gagnon, L. Le Gall, G.W.
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1253

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1263

1264 **References**

1265 Adey, W.H. (1964). The genus *Phymatolithon* in the Gulf of Maine. *Hydrobiologia*, **24**:
1266 377–420.

1267 Adey, W.H. (1965). The genus *Clathromorphum* in the Gulf of Maine. *Hydrobiologia*, **26**:
1268 539–573.

1269 Adey, W.H. (1966a). The genera *Lithothamnion*, *Leptophytum* (nov. gen.) and
1270 *Phymatolithon* in the Gulf of Maine. *Hydrobiologia*, **28**: 321–370.

1271 Adey, W.H. (1966b). Distribution of saxicolous crustose corallines in the northwestern
1272 North Atlantic. *Journal of Phycology*, **2**: 49–54.

1273 Adey, W.H. (1970a). The crustose corallines of the northwestern North Atlantic, including
1274 *Lithothamnium lemoineae* n. sp. *Journal of Phycology*, **6**: 225–229.

1275 Adey, W.H. (1970b). Some relationships between crustose corallines and their substrate.
1276 *Soc. Scientia Islandica*, **2**: 21–25.

1277 Adey, W.H. (1970c). A revision of the Foslie crustose coralline herbarium. *Det Kongelige*
1278 *Norske Videnskabers Selskabs Skrifter*, **1**: 1–46.

1279 Adey, W.H. (1971). The sublittoral distribution of crustose corallines on the Norwegian
1280 coast. *Sarsia*, **46**: 41–58.

1281 Adey W.H. (1973). Temperature control of reproduction and productivity in a subarctic
1282 coralline alga. *Phycologia*, **12**: 111–118.

- 1283 Adey, W.H. & Adey, P.J. (1973). Studies of the biosystematics and ecology of the epilithic
1284 crustose Corallinaceae of the British Isles. *British Phycological Journal*, **8**: 343–407.
- 1285 Adey, W.H. & Hayek, L.-A.C. (2011). Elucidating marine biogeography with macrophytes:
1286 Quantitative analysis of the North Atlantic supports the thermogeographic model and
1287 demonstrates a distinct Subarctic region in the Northwestern Atlantic. *Northeastern*
1288 *Naturalist*, **18**: 1–128.
- 1289 Adey, W.H. & Lebednik, P. (1967). *Catalog of the Foslie Herbarium*. Kongelige Norske
1290 Videnskabers Selskab Museet, Trondheim.
- 1291 Adey, W.H. & McKibbin, D. (1970). Studies of the maerl species of the Ria de Vigo.
1292 *Botanica Marina*, **8**: 100–106.
- 1293 Adey, W.H. & Steneck, R. (2001). Thermogeography over time creates biogeographic
1294 regions: a temperature/space/time–integrated model and an abundance-weighted test for
1295 benthic marine algae. *Journal of Phycology*, **37**: 677–698.
- 1296 Adey, W.H., Chamberlain, Y.M. & Irvine, L.M. (2005). An SEM-based analysis of the
1297 morphology, anatomy and reproduction of *Lithothamnion tophiforme* (Esper) Unger
1298 (Corallinales, Rhodophyta), with a comparative study of associated North Atlantic
1299 Arctic/Subarctic Melobesioideae. *Journal of Phycology*, **41**: 1010-1024.
- 1300 Adey, W.H., Halfar, J. & Williams, B. (2013). Biological, physiological and ecological
1301 factors controlling high magnesium carbonate formation and a precision
1302 Arctic/Subarctic marine climate archive: the coralline genus *Clathromorphum* emend
1303 Adey. *Smithsonian Contributions to Marine Science*, **40**: 1–41.

- 1304 Adey, W.H., Halfar, J., Humphreys, A., Suskiewicz, T., Belanger, D., Gagnon, P. & Fox,
1305 M. (2015a). Subarctic rhodolith beds promote longevity of crustose coralline algal
1306 buildups and their climate archiving potential. *Palaios*, **30**: 281-293.
- 1307 Adey, W.H., Hernández-Kantún, J.J., Johnson, G. & Gabrielson, P.W. (2015b). DNA
1308 sequencing, anatomy and calcification patterns support a monophyletic, subarctic,
1309 carbonate reef-forming *Clathromorphum* (Hapalidiaceae, Corallinales, Rhodophyta).
1310 *Journal of Phycology*, **51**: 189–203.
- 1311 Adey, W. H., Hernández-Kantún, J.J., Gabrielson, P.W., Nash, M.C. & Hayek, L.-A.C.
1312 (2018). *Phymatolithon (Melobesioideae, Hapalidiales) in the Boreal–Subarctic*
1313 *Transition Zone of the North Atlantic: A Correlation of Plastid DNA Markers with*
1314 *Morpho-Anatomy, Ecology, and Biogeography*. The Smithsonian Institution.
- 1315 Adey, W.H., Lindstrom, S.C., Hommersand, M.H. & Müller, K.M. (2008). The
1316 biogeographic origin of Arctic endemic seaweeds: a thermogeographic view. *Journal of*
1317 *Phycology*, **44**: 1384–1394.
- 1318 Adey W.H., Masaki, T. & Akioka, H. (1976). The distribution of crustose corallines in
1319 eastern Hokkaido and the biogeographic relationships of the flora. *Bulletin of the*
1320 *Faculty of Fisheries, Hokkaido University*, **4**: 303-313.
- 1321 Amado-Filho, G. M., Maneveldt, G. W., Pereira-Filho, G. H., Manso, R. C. C., Bahia, M.
1322 B., Barros-Barreto, M. B. & Guimaraes, S. M. P. B. (2010). Seaweed diversity
1323 associated with a Brazilian tropical rhodolith bed. *Ciencias Marinas*, **36**: 371-391.
- 1324 Anglés d’Auriac, M.B., Le Gall, L., Peña, V., Hall-Spencer, J.M., Steneck, R.S.,
1325 Fredriksen, S., Gitmark, J., Christie, H., Husa, V., Grefsrud, E.S. & Rinde, E. (2019)

1326 Efficient coralline algal *psbA* mini barcoding and High Resolution Melt (HRM) analysis
1327 using a simple custom DNA preparation. *Scientific Reports*, **578**: 578.

1328 Areschoug, J.E. (1875). Observationes phycologicae. Particula tertia. De algis nonnullis
1329 scandinavicis et de conjunctione Phaeozoosporarum *Dictyosiphonis hippuroidis*. *Nova*
1330 *Acta Regiae Societatis Scientiarum Upsaliensis, Series 3*, **10**(1): 1-36.

1331 Athanasiadis, A. (2016). *Phycologia Europaea Rhodophyta Vol. I*. Thessaloniki: Published
1332 and distributed by the author.

1333 Bélanger, D. & Gagnon, P. (2020) Low growth resilience of subarctic rhodoliths
1334 (*Lithothamnion glaciale*) to coastal eutrophication. *Marine Ecology Progress Series*,
1335 **642**: 117-132.

1336 Blake, C. & Maggs, C. (2003). Comparative growth rates and internal banding periodicity
1337 of of maerl species (Corallinales, Rhodophyta) from northern Europe. *Phycologia*, **42**:
1338 606-612.

1339 Bringloe, T.T. & Saunders, G.W. (2019). DNA barcoding of the marine macroalgae from
1340 Nome, Alaska (Northern Bering Sea) reveals many trans-Arctic species. *Polar Biology*,
1341 **42**: 851–864.

1342 Brodie, J., Williamson, C., Smale, D., Kamenos, N., Mieszkowska, N., Santos, R., Cunliffe,
1343 M., Steinke, M., Yesson, C., Anderson, K., Asnaghi, V., Brownlee, C., Burdett, H.,
1344 Burrows, M., Collins, S., Donohue, P., Harvey, B., Foggo, A., Noisette, F., Nunes, J.,
1345 Ragazzola, F., Raven, J., Schmidt, D., Suggett, D., Teichberg, M. & Hall-Spencer, J.
1346 (2014). The future of the northeast Atlantic benthic flora in a high CO₂ world. *Ecology*
1347 *and Evolution*, **4**:2787-2798.

- 1348 Chan, P., Halfar, J., Adey, W.H., Lebednik, P.A., Steneck, R.S., Norley, C.J.D. &
1349 Holdsworth D.W. (2020). Recent density decline in wild-collected subarctic crustose
1350 coralline algae reveals climate change signature. *Geology*, **48**: 226-230.
- 1351 Chamberlain, Y.M. & Irvine, L.M. (1994). Melobesioideae Bizzozero. In *Seaweeds of the*
1352 *British Isles. Volume 1. Rhodophyta Part 2B Corallinales, Hildenbrandiales* (Irvine,
1353 L.M. & Chamberlain, Y.M. editors), 159-234. London: HMSO.
- 1354 Copeland, A., Edinger, E., Devillers, R., Bell, T., LeBlanc, P. & Wroblewski, J. (2013)
1355 Marine habitat mapping in support of Marine Protected Area management in subarctic
1356 fjord: Gilbert Bay, Labrador, Canada. *Journal of Coastal Conservation*, **17**: 225-237.
- 1357 Darriba, D., Taboada, G.L., Doallo, R. & Posada D. (2012). jModelTest 2: more models,
1358 new heuristics and parallel computing. *Nature Methods*, **9**: 772.
- 1359 Esper, E.J.C. (1789). Die Pflanzthiere. In *Abbildungen nach der Natur mit Farben*
1360 *erleuchtet nebst Beschreibungen*. Erster Theil. Part 4: 169-196. Nürnberg: Raspe.
- 1361 Foslie, M. (1891). Contribution to the knowledge of the marine algae of Norway. II.
1362 Species from different tracts. *Tromsø Museums Aarshefter*, **14**: 36–58.
- 1363 Foslie, M. (1895). The Norwegian forms of *Lithothamnion*. *Det Kongelige Norske*
1364 *Videnskabers Selskabs Skrifter*, **1894**: 29–208.
- 1365 Foslie, M. (1896). New or critical *Lithothamnia*. *Det Kongelige Norske Videnskabers*
1366 *Selskabs Skrifter*, **1895**: 1–10.
- 1367 Foslie M. (1897). On some *Lithothamnia*. *Det Kongelige Norske Videnskabers Selskabs*
1368 *Skrifter*, **1897**: 1–20.
- 1369 Foslie, M. (1898a). Systematical survey of the *Lithothamnia*. *Det Kongelige Norske*
1370 *Videnskabers Selskabs Skrifter*, **1898**(2):1-7.

- 1371 Foslie, M. (1898b). List of species of the Lithothamnia. *Det Kongelige Norske*
1372 *Videnskabers Selskabs Skrifter*, **1898**(3): 1-11.
- 1373 Foslie, M. (1899). Some new or critical Lithothamnia. *Det Kongelige Norske Videnskabers*
1374 *Selskabs Skrifter*, **1898**(6): 1-19.
- 1375 Foslie, M. (1900). Revised systematical survey of the Melobesieae. *Det Kongelige Norske*
1376 *Videnskabers Selskabs Skrifter*, **1900**: 1–22.
- 1377 Foslie, M. (1905a). Remarks on northern lithothamnia. *Det Kongelige Norske Videnskabers*
1378 *Selskabs Skrifter*, **1905** (3): 1–138.
- 1379 Foslie, M. (1905b). *Lithothamnion vardöense* a new alga. *Det Kongelige Norske*
1380 *Videnskabers Selskabs Skrifter*, **1905**: 1–4.
- 1381 Foslie, M. (1908). Algologiske notiser V. *Det Kongelige Norske Videnskabers Selskabs*
1382 *Skrifter*, **1908**:1–20.
- 1383 Foster, M. (2001) Rhodoliths: between rocks and soft places. *Journal of Phycology*, **37**:
1384 659-667.
- 1385 Freiwald, A. & Henrich, R. (1994). Reefal coralline algal build-ups within the Arctic
1386 Circle: morphology and sedimentary dynamics under extreme environmental
1387 seasonality. *Sedimentology*, **41**: 963-984.
- 1388 Gabrielson, P.W., Miller, K.A. & Martone, P.T. (2011). Morphometric and molecular
1389 analyses confirm two species of *Calliarthron* (Corallinales, Rhodophyta), a genus
1390 endemic to the northeast Pacific. *Phycologia*, **50**: 298-316.
- 1391 Gabrielson, P.W., Hughey, J.R., & Diaz-Pulido, G. (2018). Genomics reveals abundant
1392 speciation in the coral reef building alga *Porolithon onkodes* (Corallinales, Rhodophyta).
1393 *Journal of Phycology*, **54**: 429–434.

1394 Gabrielson, P.W., Lindstrom, S.C. & Hughey, J.R. (2019). *Neopolyporolithon loculosum* is
1395 a junior synonym of *N. arcticum* comb. nov. (Hapalidiales, Rhodophyta), based on
1396 sequencing type material. *Phycologia*, **58**: 229-233.

1397 Gagnon, P., Matheson, K. & Stapleton, M. (2012). Variation in rhodolith morphology and
1398 biogenic potential of newly discovered rhodolith beds in Newfoundland and Labrador
1399 (Canada). *Botanica Marina*, **55**: 85-99.

1400 Gouy, M., Guindon, S., Gascuel, O. (2010). SeaView Version 4: a multiplatform graphical
1401 user interface for sequence alignment and phylogenetic tree building. *Molecular Biology
1402 and Evolution*, **27**: 221-224.

1403 Guiry M.D. & Guiry G.M. (2020). AlgaeBase. World-wide electronic publication, National
1404 University of Ireland, Galway. <http://www.algaebase.org>; searched on 6 October 2020.

1405 Halfar, J., Adey, W.H., Kronz, A., Edinger, E. & Fitzhugh, W. (2013). Arctic sea-ice
1406 decline archived by multicentury annual resolution record from crustose coralline algal
1407 proxy. *Proceedings of the National Academy of Sciences U.S.A.*, **110**: 19737-19741.

1408 Halfar, J., Zack, T., Kronz, A. & Zachos C. (2000). Growth and high-resolution
1409 paleoenvironmental signals of rhodoliths (coralline red algae): A new biogenic archive.
1410 *Journal of Geophysical Research*, **105**: 107-116.

1411 Hernández-Kantún, J.J., Rindi, F., Adey, W.H., Heesch, S., Peña, V., Le Gall, L. &
1412 Gabrielson, P.W. (2015a). Sequencing type material resolves the identity and
1413 distribution of the generitype *Lithophyllum incrustans*, and related European species *L.*
1414 *hibernicum* and *L. bathyporum* (Corallinales, Rhodophyta) *Journal of Phycology*, **51**:
1415 791-807.

- 1416 Hernández-Kantún, J.J., Riosmena-Rodriguez, R., Hall-Spencer, J.M., Peña, V., Maggs,
1417 C.A. & Rindi, F. (2015b). Phylogenetic analysis of rhodolith formation in the
1418 Corallinales (Rhodophyta). *European Journal of Phycology*, **50**: 46–61.
- 1419 Hernández-Kantún, J.J., Gabrielson, P.W., Hughey, J.R., Pezsolesi, L., Rindi, F., Robinson,
1420 N.M., Peña, V., Riosmena-Rodriguez, R., Le Gall, L. & Adey, W.H. (2016).
1421 Reassessment of branched *Lithophyllum* spp. (Corallinales, Rhodophyta) in the
1422 Caribbean Sea with global implications. *Phycologia*, **55**: 609–635.
- 1423 Heydrich, F. (1900). Les Lithothamniées de l'Expédition Antarctique. *Bulletin de la Classes*
1424 *des Sciences de l'Académie royale de Belgique*, **1900**: 560-566.
- 1425 Hind, K.R., Gabrielson, P.W., Lindstrom S.C. & Martone, P.T. (2014a). Misleading
1426 morphologies and the importance of sequencing type specimens for resolving coralline
1427 taxonomy (Corallinales, Rhodophyta): *Pachyarthron cretaceum* is *Corallina officinalis*.
1428 *Journal of Phycology*, **50**: 760-764.
- 1429 Hind, K.R., Gabrielson, P.W. & Saunders, G.W. (2014b). Molecular-assisted alpha
1430 taxonomy reveals pseudocryptic diversity among species of *Bossiella* (Corallinales,
1431 Rhodophyta) in the eastern Pacific Ocean. *Phycologia*, **53**: 443-456.
- 1432 Hind, K.R., Miller, K.A., Young, M., Jensen, C., Gabrielson, P.W. & Martone, P.T. (2015).
1433 Resolving cryptic species of *Bossiella* (Corallinales, Rhodophyta) using contemporary
1434 and historical DNA. *American Journal of Botany*, **102**: 1-19.
- 1435 Hind K.R., Gabrielson, P.W., Jensen, C.P. & Martone, P.T. (2016). *Crusticorallina* gen.
1436 nov., a non-geniculate genus in the subfamily Corallinoideae (Corallinales,
1437 Rhodophyta). *Journal of Phycology*, **52**: 929-941.

- 1438 Hind, K. R., Gabrielson, P.W., Jensen, C.P. & Martone, P.T. (2018). Evolutionary reversals
1439 in *Bossiella* (Corallinales, Rhodophyta): first report of a coralline genus with both
1440 geniculate and nongeniculate species. *Journal of Phycology*, **54**:788-798.
- 1441 Hofmann, L.C. & Heesch, S. (2018). Latitudinal trends in stable isotope signatures and
1442 carbon-concentrating mechanisms of northeast Atlantic rhodoliths. *Biogeosciences*, **15**:
1443 6139–1649.
- 1444 Hughey, J. & Gabrielson, P.W. (2012). Comment on "Acquiring DNA sequence data from
1445 dried archival red algae (Florideophyceae) for the purpose of applying available names
1446 to contemporary genetic species: a critical assessment". *Botany*, **90**:1191-1194.
- 1447 Hughey J.R., Silva P.C. & Hommersand M.H. (2001). Solving taxonomic and
1448 nomenclatural problems in Pacific Gigartinaceae (Rhodophyta) using DNA from type
1449 material. *Journal of Phycology*, **37**: 1091–1109.
- 1450 Jaasund, E. (1965). Aspects of the marine algal vegetation of North Norway. *Botanica*
1451 *Gothoburgensia*, **4**: 5-174.
- 1452 Jeong, S.Y., Nelson, W., Sutherland, J.E., Peña, V., Le Gall, L., Díaz-Pulido, G., Won,
1453 B.Y. & Cho, T.O. (2020). Corallinapetrales and Corallinapetraceae: a new order and
1454 family of coralline red algae including *Corallinapetra gabrieli* comb. nov. *Journal of*
1455 *Phycology* (in press). DOI: 10.1111/jpy.13115
- 1456 Jørgensbye, H.I.Ø. & Halfar, J. (2017). Overview of coralline red algal crusts and rhodolith
1457 beds (Corallinales, Rhodophyta) and their possible ecological importance in Greenland.
1458 *Polar Biology*, **40**: 517-531.
- 1459 Kamenos N.A. & Law, A. (2010). Temperature controls on coralline algal skeletal growth.
1460 *Journal of Phycology*, **46**: 331-335.

- 1461 Kamenos, N.A., Burdett, H.L., Aloisio, E., Findlay, H.S., Martin, S., Longbone, C., Dunn,
1462 J., Widdicombe, S. & Calosi, P. (2013). Coralline algal structure is more sensitive to
1463 rate, rather than the magnitude, of ocean acidification. *Global Change Biology*, **19**:
1464 3621-3628.
- 1465 Kamenos, N.A., Perna, G., Gambi, M.C., Micheli, F. & Kroeker, K.J. (2016). Coralline
1466 algae in a naturally acidified ecosystem persist by maintaining control of skeletal
1467 mineralogy and size. *Proceedings of the Royal Society B: Biological Sciences*, **283**:
1468 20161159.
- 1469 Kendrick, M.R., Huryn, A.D., Bowden, W.B., Deegan, L.A., Findlay, R.H., Hershey, A.E.,
1470 Peterson, B.J., Beneš, J.P. & Schuettet, E.B. (2018). Linking permafrost thaw to shifting
1471 biogeochemistry and food web resources in an arctic river. *Global Change Biology*, **24**:
1472 5738– 5750.
- 1473 Kjellman, F.R. (1877). Bidrag till Kännedomen om Kariska hafvets Algvegetation.
1474 *Öfversigt af Kongl. Vetenskaps-Akademiens Forhandlingar*, **2**: 3–30.
- 1475 Kjellman, F.R. (1883). Norra Ishafvets algflora. *Vega-expeditionens Vetenskapliga*
1476 *Iakttagelser*, **3**: 1-431.
- 1477 Kjellman, F.R. (1889). Om Beringhafvets algflora. *Kongl. Svenska Vetenskaps-Akademiens*
1478 *Handlingar*, **23**: 1–58.
- 1479 Konar, B., Riosmena-Rodriguez, R. & Iken, K. (2006). Rhodolith bed: a newly discovered
1480 habitat in the North Pacific Ocean. *Botanica Marina*, **49**: 355-359.
- 1481 Lebednik, P. (1977 '1976'). The Corallinaceae of Northwestern North America. I.
1482 *Clathromorphum* Foslie emend. Adey. *Syesis*, **9**: 59–112.
- 1483 Lee, Y.P. (2008). *Marine algae of Jeju*. Academy Publication, Seoul.

- 1484 Lemoine, M. (1913). Mélobésiées. Revision des Mélobésiées antarctiques. In *Deuxième*
1485 *Expédition Antarctique Française (1908-1910) commandée par le Dr. Jean Charcot,*
1486 *Sciences Naturelles: Documents Scientifiques, Botanique* (Masson et Cie, editors) vol. 1,
1487 1-67. Paris.
- 1488 Lindstrom, S.C. & Fredericq, S. (2003). *rbcL* gene sequences reveal relationships among
1489 north-east Pacific species of *Porphyra* (Bangiales, Rhodophyta) and a new species, *P.*
1490 *aestivalis*. *Phycological Research*, **51**: 211-224.
- 1491 Lund, S. (1959). The marine algae of East Greenland. I. Taxonomic Part. *Meddelser om*
1492 *Grønland*, **156**: 1-247.
- 1493 Maneveldt, G.W., Gabrielson, P.W., Townsend, R.A. & Kangwe, J. (2019). *Lithophyllum*
1494 *longense* (Corallinales, Rhodophyta): a species with a widespread Indian Ocean
1495 distribution. *Phytotaxa*, **419**: 149–68.
- 1496 Maneveldt, G.W., Jeong, S.Y., Cho, T.O., Hughey, J.R. & Gabrielson, P.W. (2020).
1497 Reassessment of misapplied names, *Phymatolithon ferox* and *P. repandum*
1498 (Hapalidiales, Corallinophycidae, Rhodophyta) in South Africa, based on DNA
1499 sequencing of type and recently collected material. *Phycologia*, **59**: 449–455.
- 1500 Martin S. & Hall-Spencer J.M. (2017). Effects of Ocean Warming and Acidification on
1501 Rhodolith/Maërl Beds. In *Rhodolith/Maërl Beds: A Global Perspective* (Riosmena-
1502 Rodríguez R., Nelson W. & Aguirre J. editors), 55-85. Springer International Publishing,
1503 Cham.
- 1504 Martone, P.T., Lindstrom, S.C., Miller, K.A. & Gabrielson, P.W. (2012). *Chiharaea* and
1505 *Yamadaia* (Corallinales, Rhodophyta) represent reduced and recently derived articulated
1506 coralline morphologies. *Journal of Phycology*, **48**: 859-868.

1507 McCoy, S.J. & Kamenos, N.A. (2018). Coralline algal skeletal mineralogy affects grazer
1508 impacts. *Global Change Biology*, **24**: 4775–4783.

1509 Melbourne, L.A., Hernández-Kantún, J.J., Russell, S. & Brodie, J. (2017). There is more to
1510 maerl than meets the eye: DNA barcoding reveals a new species in Britain,
1511 *Lithothamnion erinaceum* sp. nov. (Hapalidiales, Rhodophyta). *European Journal of*
1512 *Phycology*, **52**: 166-178.

1513 Millar, K. & Gagnon, P. (2018). Mechanisms of stability of rhodolith beds:
1514 sedimentological aspects. *Marine Ecology Progress Series*, **594**: 65-83.

1515 Miller, M.A., Pfeiffer, W., Schwartz, T. (2010). Creating the CIPRES Science Gateway for
1516 inference of large phylogenetic trees. *Proceedings of the Gateway Computing*
1517 *Environment Workshop (GCE)* 1–8.

1518 Nelson W.A. (2009). Calcified macroalgae – critical to coastal ecosystems and vulnerable
1519 to change: a review. *Marine and Freshwater Research*, **60**: 787-801.

1520 Pardo, C., Lopez, L., Peña, V., Hernández-Kantún, J., Le Gall, L., Bárbara, I. & Barreiro,
1521 R. (2014). A multilocus species delimitation reveals a striking number of species of
1522 coralline algae forming maerl in the OSPAR maritime area. *PLoS ONE*, **9**: e104073.

1523 Pardo, C., Barbara, I., Barreiro, R. & Peña, V. (2017). Insights into species diversity of
1524 associated crustose coralline algae (Corallinophycidae, Rhodophyta) with Atlantic
1525 European maerl beds using DNA barcoding. *Anales del Jardín Botánico de Madrid*, **74**:
1526 e059.

1527 Pearce, C.M. & Scheibling R.E. (1990). Induction of metamorphosis of larvae of the green
1528 sea urchin, *Strongylocentrotus droebachiensis*, by coralline red algae. *Biological*
1529 *Bulletin*, **179**: 304-3011.

- 1530 Peña, V., Bárbara, I., Grall, J., Maggs, C.A. & Hall-Spencer, J.M. (2014a). The diversity of
1531 seaweeds on maerl in the NE Atlantic. *Marine Biodiversity*, **44**: 533-551.
- 1532 Peña, V., Rousseau, F., De Reviers, B. & Le Gall, L. (2014b). First assessment of the
1533 diversity of coralline species forming maerl and rhodoliths in Guadeloupe, Caribbean
1534 using an integrative systematic approach. *Phytotaxa*, **190**: 190–215.
- 1535 Peña, V., Pardo, C., López, L., Carro, B., Hernández-Kantún, J., Adey, W.H., Bárbara, I.,
1536 Barreiro, R. & Le Gall, L. (2015a). *Phymatolithon lusitanicum* sp. nov. (Hapalidiales,
1537 Rhodophyta): the third most abundant maerl-forming species in the Atlantic Iberian
1538 Peninsula. *Cryptogamie, Algologie*, **36**: 429-459.
- 1539 Peña, V., De Clerck, O., Afonso-Carrillo, J., Ballesteros, E., Bárbara, I., Barreiro, R. & Le
1540 Gall, L. (2015b). An integrative systematic approach to species diversity and distribution
1541 in the genus *Mesophyllum* (Corallinales, Rhodophyta) in Atlantic and Mediterranean
1542 Europe. *European Journal of Phycology*, **50**: 20-36.
- 1543 Peña, V., Hernández-Kantún, J.J., Adey, W.H. & Le Gall, L. (2018). Assessment of
1544 coralline species diversity in the European coasts supported by sequencing of type
1545 material: the case study of *Lithophyllum nitorum* (Corallinales, Rhodophyta).
1546 *Cryptogamie Algologie*, **39**: 123-137.
- 1547 Pezolesi, L., Peña, V., Le Gall, L., Gabrielson, P.W., Kaleb, S., Hughey, J.R., Rodondi,
1548 G., Hernández-Kantún, J., Falace, A., Basso, D., Cerrano, C. & Rindi, F. (2019).
1549 Mediterranean *Lithophyllum stictiforme* (Corallinales, Rhodophyta) is a genetically
1550 diverse species complex: implications for species circumscription, biogeography and
1551 conservation of coralligenous habitats. *Journal of Phycology*, **55**: 473–492.

1552 Printz, H. (1929). *Contributions to a monograph of the Lithothamnia*. After the author's
1553 death collected and edited by Henrik Printz. Trondhjem [Trondheim]: Aktietrykkeriet.

1554 Puckree-Padua, C.A., Gabrielson, P.W., Hughey, J.R. & Maneveldt, G.W. (2020). DNA
1555 sequencing of type material reveals *Pneophyllum marlothii* comb. nov. from South
1556 Africa and *P. discoideum* comb. nov. (Chamberlainoideae, Corallinales, Rhodophyta)
1557 from Argentina. *Journal of Phycology* (in press). DOI: 10.1111/jpy.13047-20-081.

1558 QGIS.org (2020). QGIS Geographic Information System. QGIS Association.
1559 <http://www.qgis.org>

1560 Richards, J.L., Sauvage, T., Schmidt, W.E., Fredericq, S., Hughey, J.R. & Gabrielson, P.W.
1561 (2017). The coralline genera *Sporolithon* and *Heydrichia* (Sporolithales, Rhodophyta)
1562 clarified by sequencing type material of their generitypes and other species. *Journal of*
1563 *Phycology*, **53**:1044-1059.

1564 Richards, J.L., Gabrielson, P.W., Hughey, J.R. & Freshwater, D.W. (2018). A re-evaluation
1565 of subtidal *Lithophyllum* species (Corallinales, Rhodophyta) from North Carolina, USA,
1566 and the proposal of *L. searlesii* sp. nov. *Phycologia*, **57**: 318–330.

1567 Riosmena-Rodríguez, R., Nelson, W. & Aguirre, J. (2017). *Rhodolith/maërl beds: a global*
1568 *perspective*. Springer International Publishing, Cham.

1569 Robinson, N.M., Fernández-García, C., Riosmena-Rodríguez, R., Rosas-Alquicira, E.F.,
1570 Konar, B., Chenelot, H., Jewett, S.C., Melzer, R.R., Meyer, R., Försterra, G.,
1571 Häussermann, V. & Macaya, E.C. (2017). Eastern Pacific. In *Rhodolith/Maërl Beds: A*
1572 *Global Perspective* (Riosmena-Rodríguez, R., Nelson, W. & Aguirre, J. editors), 319-
1573 333. Springer International Publishing, Cham.

- 1574 Ronquist, F. & Huelsenbeck, J. (2003). MrBayes 3: Bayesian phylogenetic inference under
1575 mixed models. *Bioinformatics*, **19**: 1572–1574.
- 1576 Rosenvinge, L.K. (1917). The marine algae of Denmark Part II. Rhodophyceae II
1577 (Cryptonemiales). *Kongelige Danske Videnskabernes Selskabs Skrifter, 7. Række,*
1578 *Naturvidenskabelig og Matematisk Afdeling*, **7**: 153-284.
- 1579 Rowley, R.J. (1989). Settlement and recruitment of sea urchins (*Strongylocentrotus* spp.) in
1580 a sea-urchin barren ground and a kelp bed: are populations regulated by settlement or
1581 post-settlement processes? *Marine Biology*, **100**: 485-494.
- 1582 Saunders, De A. (1901). Papers from the Harriman Alaska Expedition XXV. The algae.
1583 *Proceedings of the Washington Academy of Sciences*, **3**: 391-486.
- 1584 Saunders, G.W. & McDevit, D.C. (2012). Methods for DNA Barcoding Photosynthetic
1585 Protists Emphasizing the Macroalgae and Diatoms. *In DNA Barcodes : Methods and*
1586 *Protocols* (Kress, W.J. & Erickson, D.L., editors), 207-222. Methods in Molecular
1587 Biology Series. Humana Press.
- 1588 Saunders, G.W. & Moore, T.E. (2013). Refinements for the amplification and sequencing
1589 of red algal DNA barcode and RedToL phylogenetic markers: a summary of current
1590 primers, profiles and strategies. *Algae*, **28**:31-43.
- 1591 Schoenrock, K.M., Bacquet, M., Pearce, D., Rea, B.R., Schofield, J.E., Lea, J., Mair, D. &
1592 Kamenos, N. (2018a). Influences of salinity on the physiology and distribution of the
1593 Arctic coralline algae, *Lithothamnion glaciale* (Corallinales, Rhodophyta). *Journal of*
1594 *Phycology*, **54**: 690-702.

1595 Schoenrock K.M., Vad, J., Muth, A., Pearce, D.M., Rea, B.R., Schofield, J.E. & Kamenos,
1596 N.A. (2018b). Biodiversity of kelp forest and coralline algae habitats in southwestern
1597 Greenland. *Diversity*, **10**: 117.

1598 Sissini, M.N., Oliveira M.C., Gabrielson, P.W., Robinson, N.M., Okolodkov, Y.B.,
1599 Riosmena-Rodriguez, R. & Horta, P.A. (2014). *Mesophyllum erubescens* (Corallinales,
1600 Rhodophyta)--so many species in one epithet. *Phytotaxa*, **190**: 299-319.

1601 Stamatakis, A. (2014). RAxML Version 8: A tool for phylogenetic analysis and post-
1602 analysis of large phylogenies. *Bioinformatics*, **30**: 1312–1313.

1603 Steneck, R.S. (1978). *Factors influencing the distribution of crutose coralline algae*
1604 *(Rhodophyta, Corallinaceae) in the Damariscotta River Estuary, Maine*. Thesis.
1605 University of Maine, USA.

1606 Steneck, R.S. (1982). A limpet-coralline alga association: adaptations and defenses between
1607 a selective herbivore and its prey. *Ecology*, **63**: 507-522.

1608 Strömfelt, H.F.G. (1886). Einige für die Wissenschaft neue Meeresalgen aus Island.
1609 *Botanisches Zentralblatt*, **26**: 172-173.

1610 Tamura, K., Stecher, G., Peterson, D., Filipiński, A., Kumar, S. (2013). MEGA6: Molecular
1611 Evolutionary Genetics Analysis version 6.0. *Molecular Biology and Evolution*, **30**:
1612 2725–2729.

1613 Teed, L., Bélanger, D., Gagnon, P. & Edinger, E. (2020). Calcium carbonate (CaCO₃)
1614 production of a subpolar rhodolith bed: Methods of estimation, effect of bioturbators,
1615 and global comparisons. *Estuarine and Coastal Shelf Science*, **242**: 106822.

1616 Teichert, S. (2014). Hollow rhodoliths increase Svalbard's shelf biodiversity. *Scientific*
1617 *Reports*, **4**: 6972.

1618 Teichert, S., Woelkerling, W., Rüggeberg, A., Wisshak, M., Piepenburg, D., Meyerhöfer,
1619 M., Form, A., Büdenbender, J. & Freiwald, A. (2012). Rhodolith beds (Corallinales,
1620 Rhodophyta) and their physical and biological environment at 80° 31' in Nordkappbukta
1621 (Nordaustlandet, Svalbard Archipelago, Norway). *Phycologia*, **51**: 371-390.

1622 Teichert, S., Woelkerling, W., Rüggeberg, A., Wisshak, M., Piepenburg, D., Meyerhöfer,
1623 M., Form, A. & Freiwald, A. (2014). Arctic rhodolith beds and their environmental
1624 controls (Spitsbergen, Norway). *Facies*, **60**: 15-37.

1625 Turland, N. J., Wiersema, J. H., Barrie, F. R., Greuter, W., Hawksworth, D.L., Herendeen,
1626 P.S., Knapp, S., Kusber, W.-H., Li, D.-Z., Marhold, K., May, T.W., McNeill, J., Monro,
1627 A.M., Prado, J., Price, M.J. & Smith, G.F. (eds.) (2018). *International Code of*
1628 *Nomenclature for algae, fungi, and plants (Shenzhen Code) adopted by the Nineteenth*
1629 *International Botanical Congress Shenzhen, China, July 2017*. Regnum Vegetabile 159.
1630 Glashütten: Koeltz Botanical Books.

1631 Unger, F. (1858). Beiträge zur näheren Kenntniss des Leithakalkes, namentlich der
1632 vegetabilischen Einschlüsse und der Bildungsgeschichte desselben. *Denkschriften der*
1633 *Kaiserlichen Akademie der Wissenschaften [Wein], Mathematisch-*
1634 *naturwissenschaftliche Klasse*, **14**: 13-35.

1635 Vinogradova, K.L. (2010). Taxonomic review of the Corallinales (Rhodophyta) in the
1636 northern Russian seas. *Botanicheskii Zhurnal (St. Petersburg)*, **95**: 667-681.

1637 Walvoord, M.A. & Striegl, R.G. (2007). Increase groundwater to stream discharge from
1638 permafrost thawing in the Yukon River Basin: Potential impacts on lateral export of
1639 carbon and nitrogen. *Geophysical Research Letters*, **34**: L12402.

- 1640 Wassmann, P., Duarte, C.M., Agustí, S. & Sejr, M.K. (2011). Footprints of climate change
1641 in the Arctic marine ecosystem. *Global Change Biology*, **17**: 1235–1249.
- 1642 Williams, B., Chan, P.T.W., Halfar, J., Hargan, K. & Adey, W. (2020). Arctic crustose
1643 coralline alga resilient to recent environmental change. *Limnology and Oceanography*.
1644 (in press). DOI: 10.1002/lno.11640.
- 1645 Woelkerling, W.J. (1993). Type collections of Corallinales (Rhodophyta) in the Foslie
1646 Herbarium (TRH). *Gunneria*, **67**:1–289.
- 1647 Woelkerling, W.J. & Verheij, E. (1995). Type collections of nongeniculate corallines
1648 (Rhodophyta) in the Rijksherbarium (L), Leiden University, The Netherlands. *Blumea*,
1649 **40**: 33–90.
- 1650 Woelkerling, W.J., Gustavsen, G., Myklebost, H.E., Prestø, T. & Såstad, S.M. (2005). The
1651 coralline red algal herbarium of Mikael Foslie: revised catalogue with analyses.
1652 *Gunneria*, **77**: 1-625.
- 1653 Wynne, M.J. (1995). F. R. Kjellman. *Phycological Newsletter*, **31**: 2-3, available at
1654 www.psaalgae.org
- 1655 Zinova, A.D. (1955). *Opredelitel burykh vodoroslej severnykh morej SSSR [Determination*
1656 *book of the red algae of the northern seas of the USSR]*. Akad. Nauk SSSR, Moscow &
1657 Leningrad.
- 1658

1659 **Figure legends**

1660 **Figure 1.** Phylogenetic tree inferred from maximum likelihood (ML) and Bayesian
1661 inference of *rbcL* sequences included in the present study. Bootstrap ML values >60% and
1662 posterior probabilities >0.60 from Bayesian inference shown for each node. Scale bar: 0.05
1663 substitutions per site.

1664 **Figure 2:** Distribution map of *Lithothamnion glaciale* obtained for collections analyzed in
1665 the molecular studies, type collections and historical specimens.

1666 **Figure 3:** Distribution map of *Lithothamnion lemoineae* obtained for collections analyzed
1667 in the molecular studies, type collections and historical specimens.

1668 **Figure 4:** Distribution map of *Lithothamnion soriferum* obtained for collections analyzed in
1669 the molecular studies, type collections and historical specimens.

1670 **Figure 5:** Distribution map of *Lithothamnion tophiforme* obtained for collections analyzed
1671 in the molecular studies, type collections and historical specimens.