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## Reinstatement of *Corallina chilensis* (Corallinaceae, Rhodophyta) based on DNA sequencing of the type material collected by Darwin

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### ABSTRACT

To determine whether *Corallina chilensis* is a distinct species or a variety (i.e. *C. officinalis* var. *chilensis*) of the generitype of *Corallina*, molecular phylogenetic analyses were performed using *psbA*, COI-5P, *rbcl*, or some combination of these gene regions from 75 voucher specimens representing *Corallina* collections from around the world. Names were applied by comparing these DNA sequences with sequences obtained from type specimens, including a 263 bp *rbcl* sequence from an isotype of *C. chilensis* collected by Darwin (*C. Darwin 2151*) from Valparaiso, Chile. DNA sequences from the *C. chilensis* isotype matched unnamed coralline DNA sequences from British Columbia, Canada, and previously published DNA sequences from the northeast and southeast Pacific. The clade containing the isotype of *C. chilensis* was distinct from *C. officinalis* specimens in phylogenetic analyses. Although morphologically variable, fronds of *C. chilensis* from British Columbia populations matched Kützing's original description of *C. officinalis* var. *chilensis*. These data support the conclusion that *C. chilensis* is a distinct species, not a variety of *C. officinalis*, and is distributed in both hemispheres. While this study strongly supported *C. chilensis* as a distinct species, phylogenetic relationships among *Corallina* species remain elusive because individual gene trees are not congruent.

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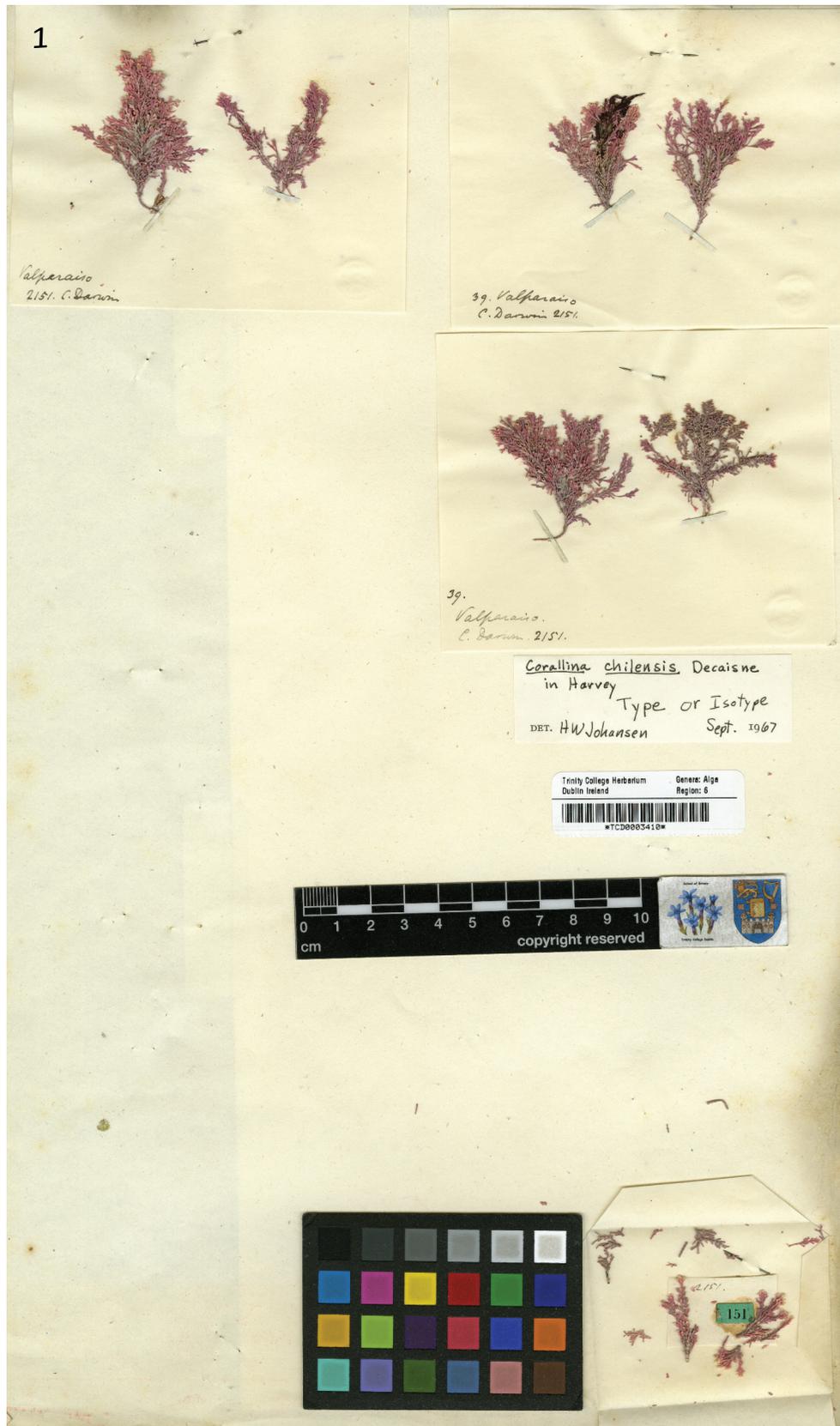
COI-5P; *Corallina officinalis* var. *chilensis*; Distribution range; Majority-rule tree; *psbA*; *rbcl*

## INTRODUCTION

Geniculate coralline algae in subfamilies Metagoniolithoideae, Lithophylloideae, and Corallinoideae are notoriously challenging to identify because they have few diagnostic characters and a high degree of morphological variation. This morphological variation has led to instances where one name has been applied to multiple species (Gabrielson *et al.* 2011; Brodie *et al.* 2013; Hind & Saunders 2013a; Hind *et al.* 2014b, 2015; Janot & Martone 2018) or where multiple names have been applied to the same species (Walker *et al.* 2009; Hind *et al.* 2014a, 2015; Bustamante *et al.* 2019). Consequently, historical taxonomic delineations based primarily on morpho-anatomy have required significant and ongoing updates. In the last decade, DNA sequence data have been used to designate boundaries between geniculate coralline species, and have in turn suggested which morpho-anatomical characters, if any, may be useful for differentiating species (Gabrielson *et al.* 2011; Martone *et al.* 2012; Hind & Saunders 2013b; Hind *et al.* 2015). Importantly, this current taxonomic process is incomplete without knowing the identity of historical type specimens – that is, without sequencing type specimens – on which names are based (Turland *et al.* 2018, Art. 7.2).

One confusing geniculate coralline species in need of clarification is *Corallina chilensis* Decaisne. William Henry Harvey (1849, p. 103) published the name *C. chilensis*, designating a collection by Charles Darwin (*C. Darwin 2151*) from Valparaiso, Chile as the 'type' collection (Fig. 1) and crediting Joseph Decaisne for the description. Whether Decaisne saw the collection *C. Darwin 2151* is unknown, as it is housed in the Trinity College Herbarium (TCD) in Dublin and Decaisne worked at the Muséum National d'Histoire Naturelle (PC; herbarium acronyms follow Thiers 2022, *Index herbariorum*). Decaisne's description may therefore have been based on the collections of Claudio Gay and Alcide d'Orbigny, two French naturalist contemporaries of Darwin who contributed their collections from Chile to PC. The 'type' collection referred to by Harvey (1849, p. 104) should be regarded as the holotype collection as per Art. 9.1 and Note 1 of the ICN (Turland *et al.* 2018).

Nearly a decade after Harvey's publication, Kützing (1858, p. 32) reduced *C. chilensis* to a variety (as '*C. officinalis chilensis*') now *C. officinalis* var. *chilensis* (Decaisne) Kützing. In his publication *Tabulae Phycologicae* . . ., describing collections loaned to him by 'foreign friends', Kützing (1858) recognized six other varieties of *C. officinalis* Linnaeus in addition to



**Fig. 1.** Holotype collected by Darwin (C. Darwin 2151) in Valparaiso, Chile, housed at Trinity College Herbarium, Dublin, Ireland. The holotype comprises one standard herbarium sheet onto which three smaller sheets, bearing six specimens, and a packet of frond fragments are attached. The sequence generated in this study was taken from an isotype (UC 2085164) most likely sampled from this packet.

*C. officinalis* var. *chilensis*, based on specimens from the North Sea, the Adriatic Sea and the Atlantic Ocean. Following Kützing's reduction of *C. chilensis* to a variety of *C. officinalis*, Yendo (1902) reported *C. officinalis* var. *chilensis* from the northern hemisphere, Botany Beach, British Columbia, Canada. Yendo reported that his Botany Beach specimen matched Kützing's description of *C. officinalis* var. *chilensis* and that he was able to identify the specimen because it was fertile. Unfortunately, most of Yendo's collections of geniculate corallines from both the northwest (Japan) and northeast (British Columbia) Pacific cannot be found.

Not all authors accepted Kützing's (1858) change in rank (see e.g. Foslie 1907; Smith 1944; Papenfuss 1964; Williamson et al. 2015). Both names, *C. chilensis* and *C. officinalis* var. *chilensis*, co-occur in the literature from 1858 onward and have been applied to *Corallina* specimens from South Africa (Silva et al. 1996), the west coast of North America from Baja California, Mexico north through British Columbia, Canada (Setchell & Gardener 1903; Smith 1944; Taylor 1945; Dawson 1953; Abbott & Hollenberg 1976; Williamson et al. 2015; Alejo et al. 2019), from Chile (Ramírez & Santelices 1991; Calderon et al. 2021), from Argentina (Pujals 1963) and from the Falkland Islands (Foslie 1907). In the past six years the name *C. chilensis* has been applied to various collections (Williamson et al. 2015; Alejo et al. 2019; Calderon et al. 2021), but until now, the type of *C. chilensis* has not been sequenced to confirm the correct application of the name. To determine the identity of *C. chilensis*, a partial *rbcl* sequence from an isotype specimen collected by Darwin from Valparaiso, Chile, was amplified and this sequence was compared to DNA from contemporary samples. Sequences of *psbA* (photosystem II protein D1 precursor), COI-5P (cytochrome *c* oxidase subunit 1-5'), and *rbcl* (ribulose 1,5-bisphosphate carboxylase/oxygenase large subunit) were obtained from recent collections to determine at which rank *C. chilensis* should be recognized and to verify its distribution. Inconsistencies between different gene trees in *Corallina* were explored by documenting the position of the generitype, *C. officinalis*, in two additional phylogenetic analyses.

## MATERIAL AND METHODS

Fragments of an isotype specimen (UC 2085164) of *Corallina chilensis* (*C. Darwin 2151*), removed from the holotype (TCD 0003410, although from which individual or envelope the fragments were removed is unknown), were sequenced. Fragments in UC from historical specimens in PC collected by Claudio Gay at Ancud, Isla Chiloe, Chile (UC 2085165), and by d'Orbigny, with no locality provided but assumed to be Patagonia (UC 2085166), were also sequenced (see Table S1). DNA extraction and amplification followed Hughey et al. (2001), as modified in Lindstrom et al. (2011), following the recommendations by Hughey & Gabrielson (2012). A portion of the *rbcl* gene (263 bp) was targeted using the primers F1150cor (Gabrielson et al. 2011) and R-*rbcl*S (Freshwater & Rueness 1994).

*Corallina* specimens (N = 98) were collected between 2000 and 2019 from the Pacific coastline of Canada and the United States, and from Chile, Japan and Taiwan (see Table S1).

Specimens were pressed onto herbarium paper and clean portions of each specimen were removed and preserved in silica for DNA extraction.

At the University of British Columbia (UBC), DNA from contemporary collections was extracted following the red algal extraction protocol described in Hind & Saunders (2013a); and at the University of North Carolina (UNC), Chapel Hill, following Gabrielson et al. (2011). At UBC, the protocol outlined in Hind et al. (2016) was used to amplify and determine variable length sequences of *psbA* (877 bp), COI-5P (664 bp) and *rbcl* (1,334 bp). See Table S2 for primers and sources. At UNC, Chapel Hill, amplification and sequencing of *rbcl* 3' (851 bp), followed Gabrielson et al. (2011).

Other DNA sequences were retrieved from GenBank to obtain outgroups and additional *Corallina* species, including the epitype of *C. officinalis* (Brodie et al. 2013), for the analyses. See Table S1 for collection data, and herbarium and GenBank accession numbers.

DNA sequences were aligned, edited and placed in single-gene alignments using Geneious Prime® 2019.2.3, build 2019-09-24 (Biomatters Ltd., Auckland, New Zealand). Maximum likelihood trees were created in IQ-tree 1.6.12 for MacOSX (Nguyen et al. 2014) for each gene. DNA sequences were partitioned by codon position. Models of sequence evolution for each gene were estimated under Bayesian Information Criterion (BIC) utilizing ModelFinder (Kalyaanamoorthy et al. 2017) implemented in IQ tree (see evolution models in Table S3). Internal node robustness was assessed in IQ tree by 1,000 maximum likelihood bootstrap (BS) replicates and by approximate Likelihood Ratio Tests (aLRT) based Shimodaira-Hasegawa-like procedures (Anisimova 2006). MrBayes (Ronquist et al. 2011) was used to run Bayesian analyses on the three individual gene alignments. Since MrBayes has fewer sequence evolution models available than IQ-tree, ModelFinder in IQ-tree was re-run on each partitioned dataset to determine the optimal sequence evolution models within the MrBayes available subset (see Table S3). Two independent analyses were run on each partitioned dataset with four independent chains. Analyses ran for 4 million generations, sampled every 1,000 generations. The first 10% of the trees were discarded as burn-in, and trees from subsequent generations were saved because the log-likelihoods had plateaued after that point and estimated sample sizes of parameter values exceeded 200 when viewed in Tracer v1.7.1 (Rambaut et al. 2018). Trees were visualized using FigTree v1.4.4 (Rambaut 2018); aLRT values, Maximum Likelihood bootstrap percentages and posterior probabilities were superimposed on Bayesian or Maximum Likelihood tree topologies. Four phylogenetic trees were generated, viz. a *rbcl* gene tree containing the three (short) 263-bp sequences from the historical herbarium specimens, including *C. Darwin 2151*, a *psbA* tree, a COI-5P tree and an *rbcl* tree excluding the 263-bp DNA sequences.

Congruence of the *psbA*, COI-5P and *rbcl* genes of *C. officinalis* was tested by aligning concatenated sequences from all taxa except *C. officinalis*. Sequences of *psbA*, COI-5P and *rbcl* of *C. officinalis* were added as separate OTUs (Operational Taxonomic Units) rather than concatenating the sequences. If the gene genealogies were congruent, it was

predicted that the individual genes from *C. officinalis* would, if resolved, cluster with the same species in the otherwise concatenated gene tree. To confirm that the manual alignment using Geneious Prime was not responsible for incongruences among genes, all concatenated sequences were realigned in MAFFT v7 (Kato 2013). The alignment was partitioned by codon and a GTR gamma + I substitution model was used in generating the concatenated tree. The concatenated gene tree was assembled from 200 replicated searches in RAxML-HPC2 on XSEDE through the CIPRES Science Gateway v3.3 (Miller *et al.* 2010). The alignment was analysed in RAxMLGUI to produce 1,000 bootstrap trees and bootstrap percentages were then overlaid on the most likely tree.

A majority-rule analysis was created for ease of viewing discrepancy across individual gene trees simultaneously in one comprehensive tree instead of having to observe the shifting branches between three individual gene trees. For each *psbA*, COI-5P and *rbcl* gene, 1,000 bootstrap trees were generated in RAxMLGUI 1.5 beta (Silvestro & Michalak 2012), using vouchers listed in Table S1, except for the 1800s materials, or as otherwise noted. For each gene, a 50% majority-rule consensus tree was created from the 1,000 bootstrap trees using PAUP v4.0a, build 167 (Sunderland, Massachusetts, USA; Swofford 2002). A final majority-rule consensus tree was then created in PAUP from the three individual gene majority-rule consensus trees. Short branches, mostly near the bottom of the majority-rule tree or otherwise nonsensically paired with other taxa, were an artifact of missing data. This was confirmed by aligning questionable sequence pairs and counting bp differences. Thus, the positions of short branches were (and should be) generally disregarded.

The 41 specimens used for morpho-anatomical measurements were collected between northern Oregon and northern British Columbia between 2007 and 2017, and all were sequenced (Table S1). Morphological measurements taken for each specimen are summarized in Table 1 and Fig. 2, and all measurements may be found in Table S4.

Photographs were taken of eight specimens from British Columbia, Canada, which represented the range of morphological variability observed across the specimens analysed.

## RESULTS

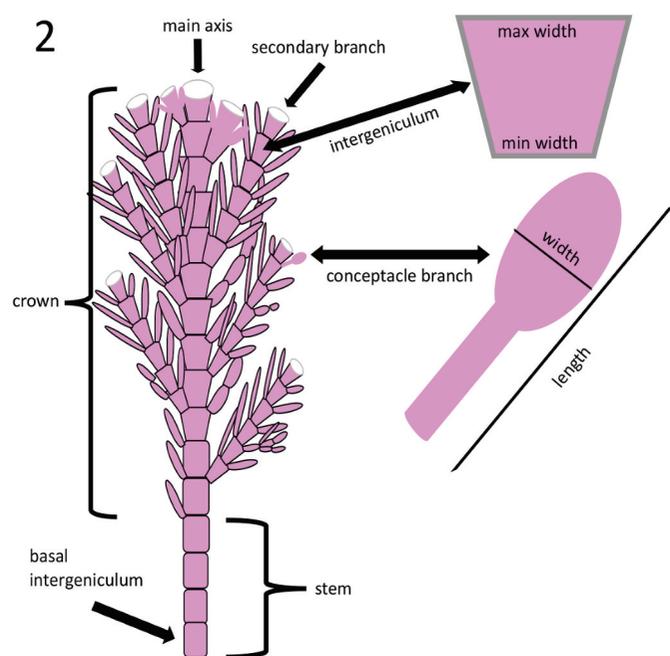
The *rbcl* sequence (263 bp) from isotype fragments (UC 2085164) from the holotype of *C. chilensis*, *C. Darwin 2151*, Valparaiso, Chile (Fig. 1), was distinct from all other *rbcl* type sequences of *Corallina* species thus far recognized (Fig. 3). This sequence was identical over its entire length to the *rbcl* sequence from UBC A89284 collected in British Columbia, Canada (Table S1) from which were also obtained *psbA* (877 bp), COI-5P (664 bp) and *rbcl* (1334 bp) sequences. These latter sequences were used in subsequent analyses to represent *C. chilensis*.

Recent collections from Chile yielded only one specimen confirmed by DNA sequencing (*rbcl* 263 bp) to be *C. chilensis*, NCU 656905 from Playa Cocholgue, Concepción (Table S1). Only two other historical specimens have been confirmed by DNA sequencing to be *C. chilensis*, *C. Darwin 2151* and UC 2085166, the latter fragments originally from a specimen in PC (unnumbered) collected by Alcide d'Orbigny with no locality provided but assumed to be Patagonia (Table S1). The 263 bp *rbcl* sequence from UC 2085165, fragments originally from PC 0028646 collected by Gay from San Carlos de Chiloé (now Ancud, Chile) and labeled '*Corallina chilensis*' by Decaisne, differed by 2 bp over its entire length from the *C. chilensis* isotype (UC 2085164), but was identical to a Chilean sequence of a specimen confirmed to be *C. berteroi* Montagne *ex* Kützing from Curinaco, Chile (GenBank accession: MZ262633).

A total of 232 northeast Pacific *Corallina* collections were included in the analyses, many of them from GenBank (Table S1). Comparisons with UBC A89284 [the specimen with an *rbcl* sequence already linked to the isotype (UC 2085164) sequence of *C. chilensis*] confirmed that 109

**Table 1.** Summary of morphological measurements from *Corallina chilensis* from the northeast Pacific (N = 22). See Fig. 2 for details.

Thallus measurement	Average (mm)	Range (mm)
Fronde width, tallest frond	29.1 ± 15.1	7.2–60.1
Fronde length, tallest frond	50.6 ± 41.1	16.0–115.3
Fronde width, random frond	23.9 ± 11.5	9.0–51.2
Fronde length, random frond	41.3 ± 19.3	14.2–95.2
Crown length	31.5 ± 18.5	11.1–87.2
Stem length	9.9 ± 9.7	0–28.4
Secondary branch length	14.9 ± 8.9	6.5–37.9
Mid intergeniculum, main axis, maximum width	1.62 ± 0.28	1.08–2.05
Mid intergeniculum, main axis, minimum width	0.97 ± 0.20	0.62–1.44
Mid intergeniculum, main axis, length	1.56 ± 0.28	1.23–2.41
Basal intergeniculum, width	1.25 ± 0.32	0.69–1.83
Basal intergeniculum, length	1.28 ± 0.42	0.69–2.32
Mid intergeniculum, secondary branch, maximum width	1.38 ± 0.38	0.89–2.49
Mid intergeniculum, secondary branch, minimum width	0.68 ± 0.17	0.41–1.07
Secondary branch, mid intergeniculum, length	1.64 ± 0.23	1.17–2.02
Conceptacle branch width (widest point)	0.65 ± 0.04	0.61–0.71
Conceptacle branch length	1.52 ± 0.51	0.96–2.54



**Fig. 2.** Diagram of a geniculate coralline thallus, depicting how the morphological measurements (found in Table 1) were obtained.

of these specimens were *C. chilensis*. Collections were confirmed as *C. chilensis* either through phylogenetic tree analyses or BLAST search matches (Table S1). Included among the 109 specimens from the Northern Hemisphere were UBC A94460 and UBC A94461, collected in 2018 from Botanical Beach, BC, where Yendo (1902) reported this species.

*Corallina chilensis* resolved in a lineage with the generitype *C. officinalis* in the *psbA*, COI-5P and *rbcL* trees with strong support, confirming its placement in *Corallina*. *Corallina chilensis* is a distinct species but its inferred phylogenetic relationships with other *Corallina* species differ for each individual gene. In the *psbA* tree (Fig. 4), *C. chilensis* (N = 9) formed a well-supported clade (94.5/73/1) nested within a moderately supported clade (75.5/28/0.75) containing ‘*Corallina* sp. Clade 4’, ‘*Corallina* sp. Clade 5’ and ‘*Corallina* sp. Clade 1’. In the COI-5P tree (Fig. 5), *C. chilensis* (N = 3) formed a well-supported clade (99/96/1), nested within a larger clade containing four other species from the NW Pacific Ocean (Korea and Japan). In the *rbcL* tree (Fig. 6), *C. chilensis* (N = 2) occurred on a well-supported branch (96/99/1) within a polytomy that included the species *C. berteroi*, *C. yendoi* Martone, P.W. Gabrielson, M.S. Calderon & D.E. Bustamante, *C. chamberlainiae* J. Brodie & Mrowicki and *C. crassissima* (Yendo) K.R. Hind & G.W. Saunders.

The branching order among *Corallina* species varied across gene trees (Figs 4–6). Sequences from the generitype, *C. officinalis*, formed well-supported monophyletic clades in all three gene trees, but, like *C. chilensis*, had different sister taxon relationships in each of the three gene trees (Figs 4–6). In the *psbA* tree (Fig. 4), *C. officinalis* was in a larger clade containing *C. berteroi*, *C. yendoi* and *C. chamberlainiae*, but lacking support (77/5/0.64). In the COI-5P tree (Fig. 5), *C. officinalis* was sister to the clade containing *C. vancouveriensis* Yendo with strong support (98/98/1). In the *rbcL* tree (Fig. 6), *C. officinalis* was nested within a clade containing the remainder of the species except for ‘*Corallina* sp. Clade 3’ and

‘*Corallina* sp. Clade 6’ with moderate (88/66/1) branch support. Incongruence was especially evident in the failure of *C. officinalis* sequences to form a single monophyletic group when sequences were added to the otherwise concatenated alignment as separate OTUs (Fig. S1). Instead, each gene provided a different phylogeny, as *C. officinalis* sequences occurred in three different clades in the concatenated tree when only *C. officinalis* sequences were left unconcatenated (Fig. S1). The *psbA* gene from *C. officinalis* was most similar to the *psbA* gene of ‘*Corallina* sp. Clade 2’, the *C. officinalis* COI-5P gene was most similar to the COI-5P genes of *C. vancouveriensis* and ‘*Corallina* sp. Clade 9’; and the *C. officinalis* *rbcL* gene was most similar to the *rbcL* genes of ‘*Corallina* sp. Clade 3’ and ‘*Corallina* sp. Clade 6’. Aside from *C. officinalis*, concatenated species-level groups were monophyletic in the concatenated tree (Fig. S1).

In the majority-rule consensus tree (Fig. S2), most DNA sequences clustered together by species, but relationships among *Corallina* species were unresolved, appearing as a polytomy of 19 clades. The percentages on the branches in the majority-rule consensus tree indicated the frequency that the particular topology appeared across all three individual majority-rule gene trees (e.g. 33% indicated that a branch only appeared in one of the three majority-rule gene trees). Some of the low support values resulted from missing data in one or more genes, but much of the low support resulted from disagreement across genes. There was only one instance where all three gene trees agreed and that was with respect to the clustering of three outgroups (Fig. S2).

Sequenced specimens used for morphological analyses (N = 41) were morphologically variable (Figs 7–14). Fronds were 14.2–95.2 mm in height (Table 1). Basal intergenicula were 0.69–1.83 mm wide, 0.69–2.32 mm long and were devoid of secondary branching (Table 1). Secondary branches occurred further along the main axes forming crowns that were 11.1–87.2 mm long (Table 1). Mid-intergenicula along main axes were on average  $1.6 \pm 0.28$  mm wide at their broadest point, and secondary branch mid-intergenicula were on average  $1.38 \pm 0.38$  mm wide at their broadest point (Table 1). Intergenicula bearing apical conceptacles were on average  $1.52 \pm 0.51$  mm long and on average  $0.65 \pm 0.04$  mm wide at their broadest point (Table 1). The complete list of morphological measurements is in Table S4.

### *Corallina chilensis* Decaisne in Harvey (1849, p. 103)

HOMOTYPIC SYNONYM: *Corallina officinalis* var. *chilensis* Kützing (1858, p. 32).

DESCRIPTION: The following updated description of northeast Pacific populations combines elements from this study with those from former descriptions of *C. chilensis* and *C. officinalis* var. *chilensis*. “Red-violet colour” (Kützing 1858, p. 32). “Articulations of the stem and branches once and half as long as broad, cuneate, simple, the upper [intergenicula] longer and more expanded towards the apex” (Harvey 1849, p. 104). “Branching of axis distichously pinnate and with progressively shorter branches toward apex of axis. Branches tending to lie in one plane and not laterally appressed. A majority of the branches pinnately branched and those toward base of axes often bipinnate” (Smith 1944). “Branching normally strictly distichous, opposite-pinnate, of 1–3 orders, densest in upper parts, the lower portions of main axes usually nude from erosive falling away of older pinnules and branchlets; intergenicula cylindrical at the base, compressed to flatten above . . .” (Dawson 1952, p. 132). Fronds



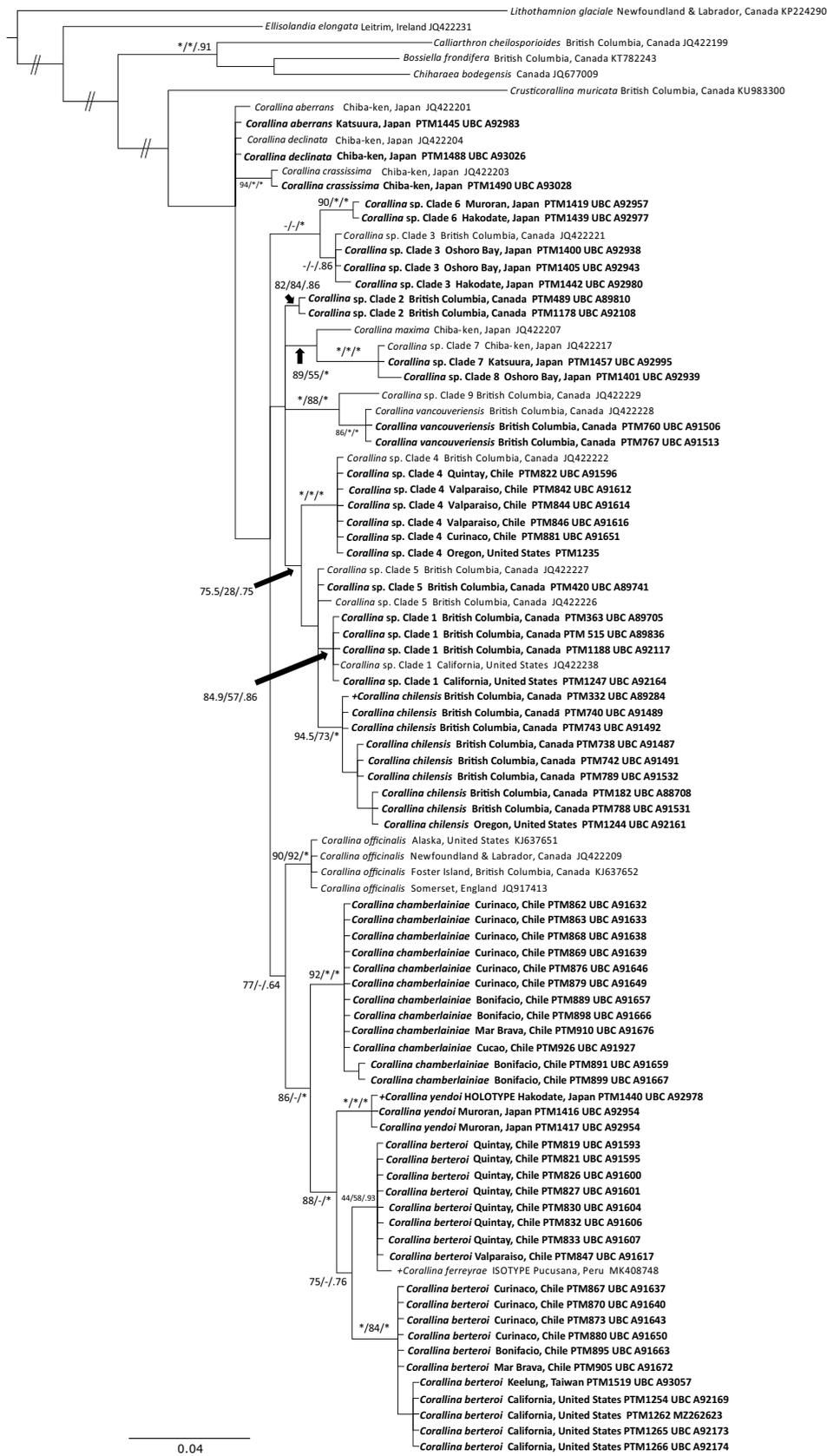
**Fig. 3.** Maximum likelihood *rbcL* tree of *Corallina*, including the sequence from an isotype (UC 2085164) of *C. chilensis*. Short DNA sequences (263 bp) from specimens collected by Darwin, d'Orbigny and Gay were extracted from herbarium material from the 1800s. The first two branch support values are aLRT and Maximum Likelihood bootstrap percentages. The third value is the Bayesian posterior probability. Asterisks (\*) denote values above 95% or 0.95 posterior probability. Dashes (-) denote values less than 50% or 0.50 posterior probability. Addition signs (+) indicate sequences from type material, as well as sequences linked to type material. Sequences prepared for this study are bolded. Scale bar refers to the number of substitutions per site. Collection details may be found in Table S1.

14.2–95.2 mm in height; basal intergenicula  $1.25 \pm 0.32$  mm wide and  $1.28 \pm 0.42$  mm long. Intergenicula on upper main axis  $1.62 \pm 0.28$  mm wide at their broadest point; intergenicula on secondary branches  $1.38 \pm 0.38$  mm wide at their broadest point (this study).

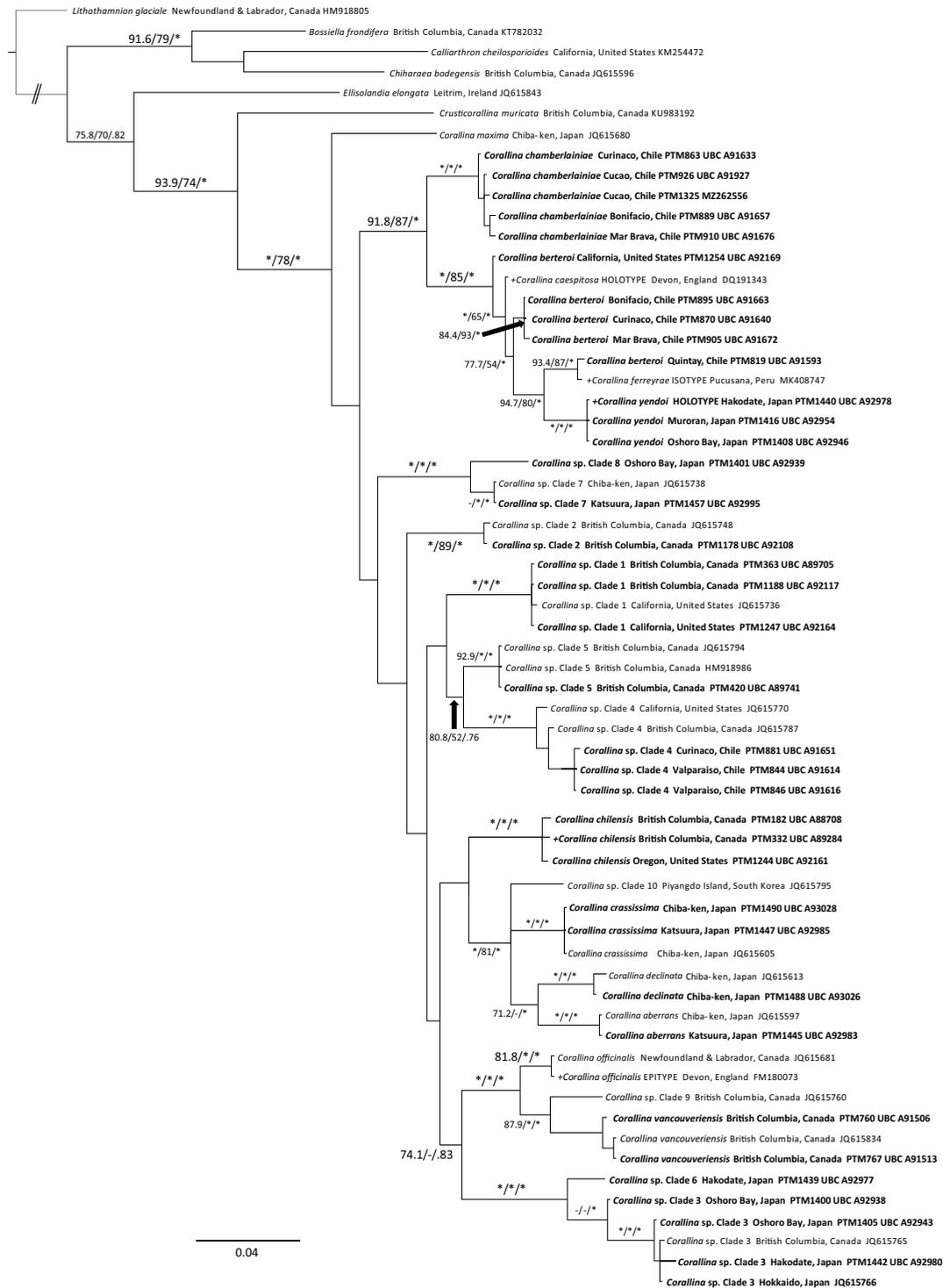
HOLOTYPE: TCD 0003410, Valparaiso, Chile, *C. Darwin* 2151, August–September 1834, comprising a collection of six specimens and fragments in an envelope.

ISOTYPES: UC 2085164, S A6794.

HABITAT: Habitat information of the type collection was not provided by Harvey (1849). The *C. chilensis* specimen from Playa Cocholgue, Concepción, Chile, was collected from the drift, so the habitat in Chile is unclear, but presumably it is the shallow subtidal. The habitat described by Smith (1944: "Growing on rocks between –1.5 ft (below)–0.5 ft (above) tide levels. Also found in tide pools at higher tidal levels.")



**Fig. 4.** Bayesian phylogenetic gene tree of *psbA* sequences of *Corallina* and six outgroups. Branch support values are aLRT/Maximum Likelihood percentages (1,000 bootstraps)/Bayesian posterior probability. Asterisks (\*) denote values above 95% or 0.95 posterior probability. Dashes (-) denote values less than 50% or 0.50 posterior probability. Addition signs (+) indicate sequences from type material, as well as sequences linked to type material. Sequences prepared for this study are bolded. Scale bar refers to the number of substitutions per site. Collection details may be found in Table S1.



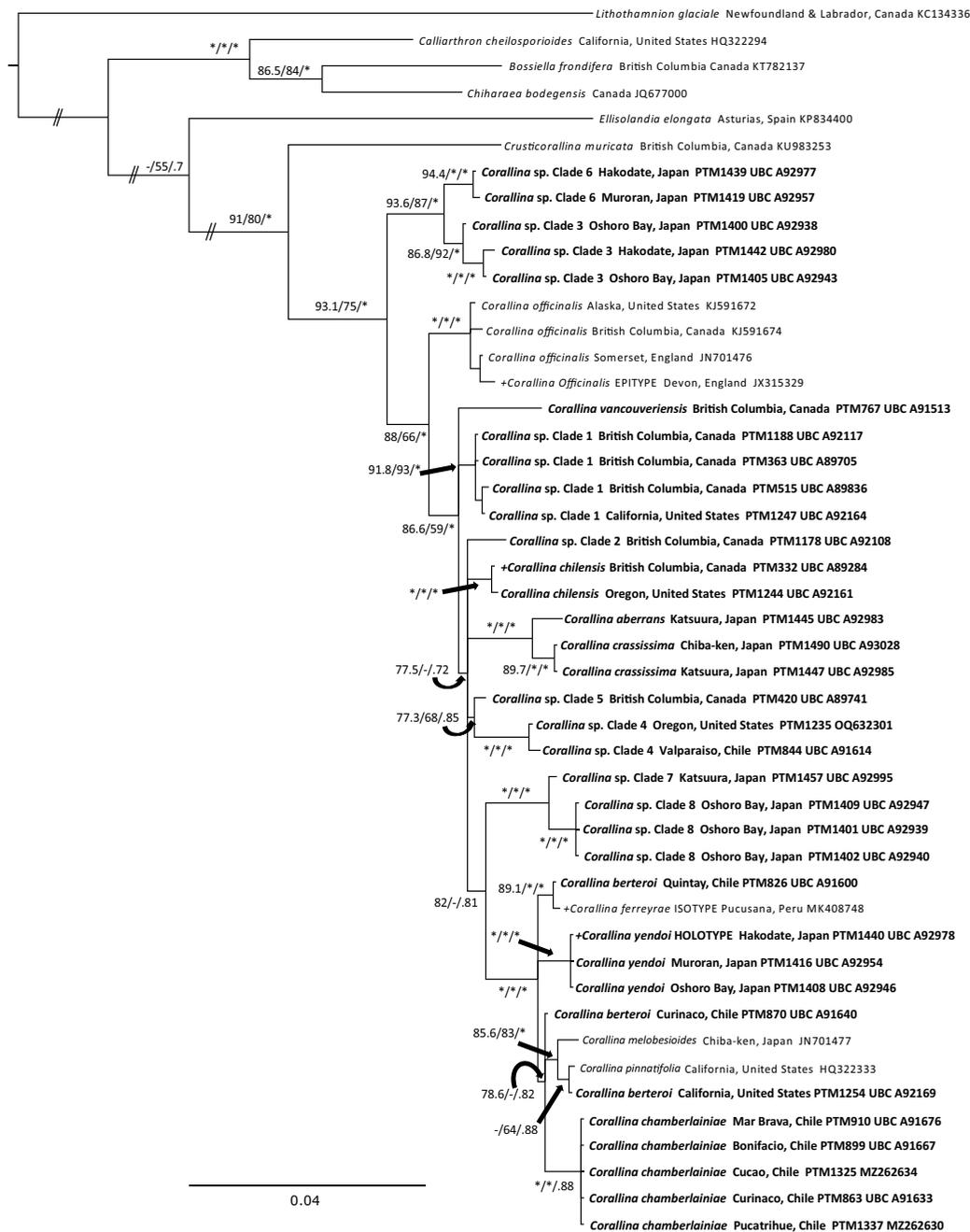
**Fig. 5.** Bayesian phylogenetic gene tree of COI-5P sequences of *Corallina* and six outgroups. Branch support values are aLRT/Maximum Likelihood percentages (1,000 bootstraps)/Bayesian posterior probability. Asterisks (\*) denote values above 95% or 0.95 posterior probability. Dashes (-) denote values less than 50% or 0.50 posterior probability. Addition signs (+) indicate sequences from type material, as well as sequences linked to type material. Sequences prepared for this study are bolded. Scale bar refers to the number of substitutions per site. Collection details may be found in Table S1.

is consistent with habitat observations in this study for northeast Pacific populations.

**DISTRIBUTION:** Based on DNA sequence data (Table S1), *C. chilensis* is confirmed as far north as Haida Gwaii, British Columbia, Canada, in the northeast Pacific. It is found in Washington, Oregon, and California as far south as Laguna Beach, California, USA. In South America, two specimens were found in Paita and Paracas, Peru (Calderon *et al.*

2021). In Chile, it is known from only two localities, Valparaiso and Playa Cocholgue, Concepción.

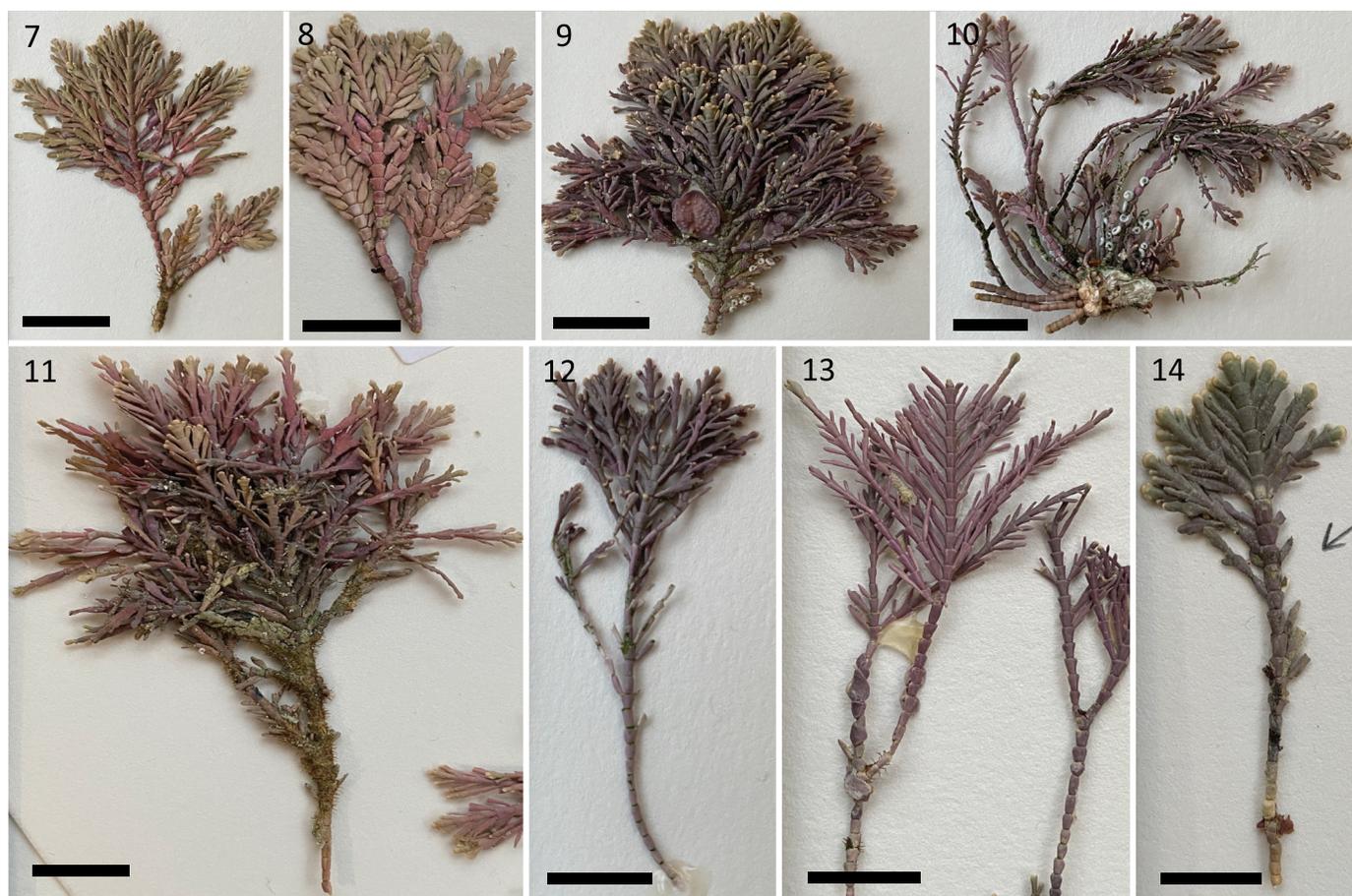
Harvey (1849, p. 103) attributed the name *Corallina chilensis* to Decaisne, and following the description, in Latin, wrote, “*Dne. in Herb. Paris. ined.*”, indicating that Decaisne used this name, but that it was unpublished. Harvey cited two collections, one from Port Famine (*C. Darwin* 1840, Puerto del



**Fig. 6.** Bayesian phylogenetic gene tree of *rbcL* sequences of *Corallina* and six outgroups. Sequences from the 1800s material are not included. Branch support values are aLRT/Maximum Likelihood percentages (1,000 bootstraps)/Bayesian posterior probability. Asterisks (\*) denote values above 95% or 0.95 posterior probability. Dashes (-) denote values less than 50% or 0.50 posterior probability. Addition signs (+) indicate sequences from type material, as well as sequences linked to type material. Sequences prepared for this study are bolded. Scale bar refers to the number of substitutions per site. Collection details may be found in Table S1.

Hambre, Patagonia, Chile) and one from Valparaíso (*C. Darwin 2151*), both collected by Charles Darwin on the *Beagle* expedition. Harvey clearly indicated that the Valparaíso specimens were the type collection of *C. chilensis*. In TCD, there is one standard herbarium sheet (0003410) to which are pinned three small sheets, each bearing two individuals or fronds from individuals, and a packet with fragments of fronds, each labeled ‘Valparaíso *C. Darwin 2151*’. Dawson *et al.* (1964, p. 46) lectotypified the Valparaíso specimens. In September 1967, H.W. Johansen annotated these specimens as ‘Type or Isotype’ (Fig. 1). Porter (1987), in his evaluation of Darwin’s notes on plant collections, considered the mounted

specimens and packet as syntypes, and Port Famine specimens as paratypes. However, because all the *C. Darwin 2151* specimens look similar and are labeled with a single collection number, this sheet is regarded in this study as the holotype of *C. chilensis* as per Art. 9.1 and Note 1 of the ICN (Turland *et al.* 2018). The late Dr. Paul C. Silva, in his *Index Nominum Algarum* (<http://ucjeps.berkeley.edu/CPD/>), noted the lectotypification (“fide Dawson, Acleto and Foldvik”), and clearly identified Darwin as the collector, *C. Darwin 2151* as the type, and the type locality as Valparaíso. Paul Silva also had labeled the tiny packet (UC 2085164) that contains fragments of *C. Darwin 2151* (probably taken from the packet at TCD) as



**Figs 7–14.** *Corallina chilensis* specimens from British Columbia, Canada. Scale bars = 1 cm.

**Fig. 7.** UBC A89284 Calvert Island, Fifth Beach, exposed point, low intertidal.

**Fig. 8.** UBC A89285 Calvert Island, Fifth Beach, exposed point, low intertidal.

**Fig. 9.** UBC A89288 Calvert Island, Fifth Beach, exposed point.

**Fig. 10.** UBC A94461 Botanical Beach, Vancouver Island, mid intertidal below the amphitheater, submerged in tidepool.

**Fig. 11.** UBC A89279 Calvert Island, Fifth Beach, low intertidal tidepool.

**Fig. 12.** UBC A94460 Botanical Beach, Vancouver Island, mid intertidal below the amphitheater, submerged in tidepool.

**Fig. 13.** UBC A91532 Calvert Island, Fifth Beach, mid intertidal tidepool.

**Fig. 14.** UBC A89808 Calvert Island, Fifth Beach channel, subtidal. The arrow indicates where a portion was removed for DNA analysis.

isotype material. The sequence in this study was derived from some of the fragments in this packet.

## DISCUSSION

The application of the name *Corallina chilensis* has now been confirmed by sequencing an isotype in UC. Phylogenetic analyses of three different genes show that it is a distinct species, and not a variety of *C. officinalis* as recorded earlier; however, its relationship to other *Corallina* species remains unresolved. Numerous *Corallina* specimens collected and sequenced in the northeast Pacific were conspecific with the isotype of *C. chilensis* (UC 2085164), *C. Darwin* 2151 from Valparaiso, Chile, as well as with one recently collected specimen from Playa Cocholgue, Concepción, Chile (NCU 656905), and two specimens recently collected in Peru (CNU 025341, CNU 025338; Calderon *et al.* 2021). Thus, as Yendo (1902) proposed, this species occurs in both the northern and southern hemispheres of the eastern Pacific.

Despite efforts to collect specimens from the temperate southeast Pacific, *C. chilensis* appears to be much more

common in the temperate northeast Pacific. Few habitat notes were provided in Harvey (1849), but it may possibly be implied in Harvey's account that the type collection from Valparaiso was not from the upper intertidal zone: "The Port Famine specimens have a starved look, and probably grew near high-water mark. Those from Valparaiso are more developed, and serve for the type of the species." Despite more recent sampling in Valparaiso, Chile, and south to Isla Chiloé, including SCUBA for sampling in the shallow subtidal, only a single unattached specimen from Cocholgue, Concepción, Chile has been found. *Corallina chilensis* appears to be uncommon to rare in the southeast Pacific, despite that being the region of its type locality. DNA sequencing indicates that in the northeast Pacific, *C. chilensis* is fairly common and is regularly found intertidally on rocky shores within its distributional range.

The disjunct distribution of *C. chilensis*, encompassing cold temperate waters of the southeast and northeast Pacific, but not subtropical and tropical waters in-between, is fascinating and deserves further study. Temperature is a major driver of seaweed distributions (van den Hoek 1982, 1984), and the

modern-day distribution of *C. chilensis* may be a remnant of a much wider, continuous distribution dating back to when the Earth was cooler and the tropics were narrower (Thompson *et al.* 2003; Meyer & Wagner 2009), possibly permitting connectivity across hemispheres. In this case, a disjunct distribution could arise as the Earth warmed and populations receded toward the poles. Alternatively, long distance transport across hemispheres via ship ballast/hull or seaweed rafts (Saunders 2014) may have generated a discontinuous distribution directly, although survival during transit through tropical waters is questionable. For the latter, there would be a question of origin: did *C. chilensis* originate in the northeast Pacific, where it is locally abundant, and was subsequently transported to the southern hemisphere, or did *C. chilensis* originate in the southeast Pacific and then get transported to the northern hemisphere, where it flourished and increased in abundance? That other seaweeds have a similarly disjunct distribution across hemispheres – e.g. *Bossia orbigniana* (Decaisne) P.C. Silva (Hind *et al.* 2014b); *Callophyllis variegata* (Bory) Kützinger (Clarkston & Saunders 2013); *Mastocarpus latissimus* (Harvey) S.C. Lindstrom, Hughey & Martone (Lindstrom *et al.* 2011) – shows that this biogeographic pattern is not unique to *C. chilensis*, perhaps lending insight into a shared mechanism. Future work could employ haplotype mapping to explore connectivity between northeast and southeast Pacific populations, estimate a migration or separation timeline, identify founder events and source/sink populations, and perhaps even predict whether this species was once more abundant in the southern hemisphere.

An updated description of southern hemisphere populations is not possible at this time, given so few recent collections from this region, one of which was collected from the drift. Thus, all morphological descriptions in this study were based only on northeast Pacific *C. chilensis* populations. The most unmistakable morphological characteristics of northeast Pacific *C. chilensis* were its distichous branching pattern and large intergenicula (an average of nearly 1.5 mm width and length), particularly on the main axis. Specimens from the northeast Pacific exhibited distichous secondary branching, starting  $\frac{1}{3}$  to  $\frac{1}{2}$  of the distance from the base of the frond, giving them a feather-like appearance. Fronds were bipinnate or tripinnate, and individuals appeared robust or spindly depending on branch thickness and the gap size between branches. Branching in some specimens was irregular resulting in an uneven appearance, whereas others were orderly and symmetrical, but all were distichous.

Inconsistency in reconstructing relationships using different genes was evident in the phylogenetic trees (Figs 4–6). The lack of resolution was explored with respect to *C. officinalis*, the generitype of *Corallina*, and conflict was defined as incongruent branches with more than 70% aLRT, 70% BS, or 0.7 PP support. Since *C. officinalis* had a different sister species in each gene tree with moderate support for different *C. officinalis*/sister combinations, the three gene trees were all in conflict. Overall incongruence was widespread throughout *Corallina*, as exemplified with *C. officinalis* when it was decoupled in the concatenated analysis (Fig. S1) and as demonstrated by the collapsed branches and low consensus

percentage values in the majority-rule consensus of individual gene bootstrap trees (Fig. S2). Although the *psbA*, COI-5P and *rbcL* sequences could not resolve the phylogenetic relationships among species of *Corallina*, the same sequences consistently clustered together in species groups, providing confidence in species delimitations.

While it is common to use concatenated trees in phylogenetic studies (Cranston *et al.* 2009; Hind & Saunders 2013a; Jarvis *et al.* 2014), some researchers advise against concatenation when there is conflict among individual gene trees, as it may produce misleading results (Mossel & Vigoda 2005; Liu & Pearl 2007). Given that the three different genes in this study exhibited distinct evolutionary histories for species within *Corallina*, concatenation was deemed inappropriate for determining phylogenetic relationships and the partially concatenated tree (Fig. S1) was included to illustrate how misleading conclusions may result from concatenation. Furthermore, assuming that each mitochondrial and plastid genome consists of one uniparentally inherited chromosome, congruence would at least be expected between individual mitochondrial or plastid gene genealogies (Janouškovec *et al.* 2013; Muñoz-Gómez *et al.* 2017; Lee *et al.* 2018; Yoshida & Mogi 2019). The discovery of incongruence between the *psbA* and *rbcL* plastid genes, presumably located on the same chromosome, was therefore unexpected.

Incongruence is becoming more commonly documented among non-algal taxa (Moncalvo *et al.* 2006; Bell & Hyvönen 2009; Cranston *et al.* 2009; Moyer *et al.* 2009; Pelsner *et al.* 2010; Jarvis *et al.* 2014). This study corroborates recent findings by Yesson *et al.* (2020), in which mitochondrial and plastid genome phylogenies of *C. officinalis* differed. Other studies of red algal genomes have reported high genomic diversity, transposons, and evidence of horizontal gene transfer and parasitic genetic elements (Janouškovec *et al.* 2013; Lee *et al.* 2016; Muñoz-Gómez *et al.* 2017). Potential causes of such patterns include hybridization or incomplete lineage sorting, particularly among early-diverged lineages after rapid radiation (Lee *et al.* 2016, 2018; Tavares *et al.* 2018), perhaps lending insight into the evolutionary history of *Corallina* species.

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## DISCLOSURE STATEMENT

The authors report no conflicts of interest. The authors alone are responsible for the content and writing of this article.

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## REFERENCES

- Abbott I.A. & Hollenberg G.J. 1976. *Marine algae of California*. Stanford University Press, Stanford, California, USA. 872 pp.
- Alejo I.A., Aleman T.E., Almanza K., Alonso W., Manriquez M.G.A., Armbrister T., Astudillo Y., Batistiana L., Blas Guido J.S., Bustamante D.E. *et al.* 2019. The complete mitochondrial and plastid genomes of *Corallina chilensis* (Corallinales, Rhodophyta) from Tomales Bay, California, USA. *Mitochondrial DNA Part B* 4: 1 1879–1880. DOI: [10.1080/23802359.2019.1614891](https://doi.org/10.1080/23802359.2019.1614891).
- Anisimova M. & Gascuel O. 2006. Approximate likelihood-ratio test for branches: a fast, accurate, and powerful alternative. *Systematic Biology* 55: 539–552. DOI: [10.1080/10635150600755453](https://doi.org/10.1080/10635150600755453).
- Bell N.E. & Hyvönen J. 2010. Phylogeny of the moss class Polytrichopsida (Bryophyta): generic-level structure and incongruent gene trees. *Molecular Phylogenetics and Evolution* 55: 381–398. DOI: [10.1016/j.ympev.2010.02.004](https://doi.org/10.1016/j.ympev.2010.02.004).
- Brodie J., Walker R.H., Williamson C. & Irvine L.M. 2013. Epitypification and redescription of *Corallina officinalis* L., the type of the genus, and *C. elongata* Ellis et Solander (Corallinales, Rhodophyta). *Cryptogamie Algologie* 34: 49–56. DOI: [10.78872/crya.v34.iss1.2013.49](https://doi.org/10.78872/crya.v34.iss1.2013.49).
- Brodie J., Melbourne L., Mrowicki R.J., Brickle P., Russell S. & Scott S. 2021. *Corallina* (Corallinales, Rhodophyta) from Tristan da Cunha and the Falkland Islands: implications for south Atlantic biogeography. *European Journal of Phycology* 56: 94–104. DOI: [10.1080/09670262.2020.1780635](https://doi.org/10.1080/09670262.2020.1780635).
- Broom J.E., Hart D.R., Farr T.J., Nelson W.A., Neill K.F. & Harvey A.S. 2008. Utility of *psbA* and *nSSU* for phylogenetic reconstruction in the Corallinales based on New Zealand taxa. *Molecular Phylogenetics and Evolution* 46: 958–973. DOI: [10.1016/j.ympev.2007.12.016](https://doi.org/10.1016/j.ympev.2007.12.016).
- Bustamante D.E., Calderon M.S. & Hughey J.R. 2019. Conspicuity of the Peruvian *Corallina ferreyrae* with *C. caespitosa* (Corallinales, Rhodophyta) inferred from genomic analysis of the type specimen. *Mitochondrial DNA Part B* 4: 1285–1286. DOI: [10.1080/23802359.2019.1591203](https://doi.org/10.1080/23802359.2019.1591203).
- Calderon M.S., Bustamante D.E., Gabrielson P.W., Martone P.T., Hind K.R., Schipper S.R. & Mansilla A. 2021. Type specimen sequencing, multilocus analyses, and species delimitation methods recognize the cosmopolitan *Corallina berteroii* and establish the northern Japanese *C. yendoii* sp. nov. (Corallinales, Rhodophyta). *Journal of Phycology* 57: 1659–1672. DOI: [10.1111/jpy.13202](https://doi.org/10.1111/jpy.13202).
- Clarkston B.E. & Saunders G.W. 2013. Resolving species diversity in the red algal genus *Callophyllis* (Kallymeniaceae, Gigartinales) in Canada using molecular assisted alpha taxonomy. *European Journal of Phycology* 48: 27–46. DOI: [10.1080/09670262.2013.767943](https://doi.org/10.1080/09670262.2013.767943).
- Cranston K.A., Hurwitz B., Ware D., Stein L. & Wing R.A. 2009. Species trees from highly incongruent gene trees in rice. *Systematic Biology* 58: 489–500. DOI: [10.1093/sysbio/syp054](https://doi.org/10.1093/sysbio/syp054).
- Dawson E.Y. 1953. *Marine red algae of Pacific Mexico*, vol. 17. The University of Southern California Press, Los Angeles, California, USA. 409 pp.
- Dawson E.Y., Acleto C. & Foldvik N. 1964. The seaweeds of Peru. *Beihefte zur Nova Hedwigia* 13: 1–111.
- Foslie M. 1907. Antarctic and subantarctic Corallinales. In: *Wissenschaftliche Ergebnisse der Schwedischen Südpolar-Expedition 1901-1903*, vol. 4:5. (Ed. by O. Nordenskjöld), pp 1–16. Lithographisches Institut des Generalstabs, Stockholm, Sweden.
- Freshwater W.D. & Rueness J. 1994. Phylogenetic relationships of some European *Gelidium* (Gelidiales, Rhodophyta) species, based on *rbcL* nucleotide sequence analysis. *Phycologia* 33: 187–194. DOI: [10.2216/i0031-8884-33-3-187.1](https://doi.org/10.2216/i0031-8884-33-3-187.1).
- Gabrielson P.W., Miller K.A. & Martone P.T. 2011. Morphometric and molecular analyses confirm two distinct species of *Calliarthron* (Corallinales, Rhodophyta), a genus endemic to the northeast Pacific. *Phycologia* 50: 298–316.
- Harvey W.H. 1849. *Nereis Australis or Algae of the Southern Ocean, Part II*. Reeve Brothers, London, UK. 119 pp.
- Hind K.R. & Saunders G.W. 2013a. A molecular phylogenetic study of the tribe Corallineae (Corallinales, Rhodophyta) with an assessment of genus-level taxonomic features and descriptions of novel genera. *Journal of Phycology* 49: 103–114. DOI: [10.1111/jpy.12019](https://doi.org/10.1111/jpy.12019).
- Hind K.R. & Saunders G.W. 2013b. Molecular markers from three organellar genomes unravel complex taxonomic relationships within the coralline algal genus *Chiharaea* (Corallinales, Rhodophyta). *Molecular Phylogenetics and Evolution* 67: 529–540. DOI: [10.1016/j.ympev.2013.02.022](https://doi.org/10.1016/j.ympev.2013.02.022).
- Hind K.R., Gabrielson P.W., Lindstrom S.C. & Martone P.T. 2014a. Misleading morphologies and the importance of sequencing type specimens for resolving coralline taxonomy (Corallinales, Rhodophyta): *Pachyarthron cretaceum* is *Corallina officinalis*. *Journal of Phycology* 50: 760–764. DOI: [10.1111/jpy.12205](https://doi.org/10.1111/jpy.12205).
- Hind K.R., Gabrielson P.W. & Saunders G.W. 2014b. Molecular-assisted alpha taxonomy reveals pseudocryptic diversity among species of *Bossiella* (Corallinales, Rhodophyta) in the eastern Pacific Ocean. *Phycologia* 53: 443–456. DOI: [10.2216/13-239.1](https://doi.org/10.2216/13-239.1).
- Hind K.R., Miller K.A., Young M., Jensen C., Gabrielson P.W. & Martone P.T. 2015. Resolving cryptic species of *Bossiella* (Corallinales, Rhodophyta) using contemporary and historical DNA. *American Journal of Botany* 102: 1912–1930. DOI: [10.3732/ajb.1500308](https://doi.org/10.3732/ajb.1500308).
- Hind K.R., Gabrielson P.W., Jensen C. & Martone P.T. 2016. *Crusticorallina* gen. nov., a non-geniculate genus in the subfamily Corallinoideae (Corallinales, Rhodophyta). *Journal of Phycology* 52: 929–941. DOI: [10.1111/jpy.12449](https://doi.org/10.1111/jpy.12449).
- Hind K., Gabrielson P., Jensen C. & Martone P.T. 2018. Evolutionary reversals in *Bossiella* (Corallinales, Rhodophyta): first report of a coralline genus with both geniculate and non-geniculate species. *Journal of Phycology* 54: 788–798. DOI: [10.1111/jpy.12788](https://doi.org/10.1111/jpy.12788).
- Hughey J.R., Silva P.C. & Hommersand M.H. 2001. Solving taxonomic and nomenclatural problems in Pacific Gigartinales (Rhodophyta) using DNA from type material. *Journal of Phycology* 37: 1091–1109. DOI: [10.1046/j.1529-8817.2001.01048.x](https://doi.org/10.1046/j.1529-8817.2001.01048.x).
- Hughey J.R. & Gabrielson P.W. 2012. Comment on “acquiring DNA sequence data from dried archival red algae (Florideophyceae) for the purpose of applying available names to contemporary genetic species: a critical assessment.” *Botany* 90: 1191–1194. DOI: [10.1139/b2012-102](https://doi.org/10.1139/b2012-102).
- Janot K. & Martone P.T. 2018. Bending strategies of convergently-evolved, articulated coralline algae. *Journal of Phycology* 54: 305–316. DOI: [10.1111/jpy.12639](https://doi.org/10.1111/jpy.12639).
- Janoušková J., Liu S.L., Martone P.T., Carré W., Leblanc C., Collén J. & Keeling P.J. 2013. Evolution of red algal plastid genomes: ancient architectures, introns, horizontal gene transfer, and taxonomic utility of plastid markers. *PLOS One* 8: Article e59001. DOI: [10.1371/journal.pone.0059001](https://doi.org/10.1371/journal.pone.0059001).
- Jarvis E.D., Mirarab S., Aberer A.J., Li B., Houde P., Li C., Ho S.Y.W., Faircloth B.C., Howard J.T., Suh A. *et al.* 2014. Whole-genome analyses resolve early branches in the tree of life of modern birds. *Science* 346 (6215): 1320–1331. DOI: [10.1126/science.1253451](https://doi.org/10.1126/science.1253451).
- Kalyaanamoorthy S., Minh B.Q., Wong T.K.F., von Haeseler A. & Jermini L.S. 2017. ModelFinder: fast model selection for accurate phylogenetic estimates. *Nature Methods* 14: 587–589. DOI: [10.1038/nmeth.4285](https://doi.org/10.1038/nmeth.4285).
- Katoh S. 2013. MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Molecular Biology and Evolution* 30: 772–780. DOI: [10.1093/molbev/mst010](https://doi.org/10.1093/molbev/mst010).

- Kützing F.T. 1858. *Tabulae phycologicae oder Abbildungen der Tange*, vol. 8. Gedruckt auf kosten des Verfassers (in commission by W. Köhne) Nordhausen, Germany. 48 pp, 100 plates.
- Lee J., Kim K.M., Yang E.C., Miller K.A., Boo S.M., Bhattacharya D. & Yoon H.S. 2016. Reconstructing the complex evolutionary history of mobile plasmids in red algal genomes. *Scientific Reports* 6: Article 23744. DOI: 10.1038/srep23744.
- Lee J.M., Song H.J., Park S.I., Lee Y.M., Jeong S.Y., Cho T.O., Kim J.H., Choi H., Choi C.G., Nelson W.A. et al. 2018. Mitochondrial and plastid genomes from coralline red algae provide insights into the incongruent evolutionary histories of organelles. *Genome Biology and Evolution* 10: 2961–2972. DOI: 10.1093/gbe/evy222.
- Lindstrom S.C., Hughey J.R. & Martone P.T. 2011. New, resurrected and redefined species of *Mastocarpus* (Phylloporaceae, Rhodophyta) from the northeast Pacific. *Phycologia* 50: 661–683. DOI:10.2216/10-38.1.
- Liu L. & Pearl D.K. 2007. Species trees from gene trees: reconstructing Bayesian posterior distributions of a species phylogeny using estimated gene tree distributions. *Systematic Biology* 56: 504–514. DOI 10.1080/10635150701429982.
- Martone P.T., Lindstrom S.C., Miller K.A. & Gabrielson P.W. 2012. *Chiharaea* and *Yamadaia* (Corallinales, Rhodophyta) represents reduced and recently derived articulated coralline morphologies. *Journal of Phycology* 48: 859–868. DOI: 10.1111/j.1529-8817.2012.01190.x.
- Meyer I. & Wagner S. 2009. The Little Ice Age in Southern South America: proxy and model based evidence. In: *Past climate variability in South America and surrounding regions from the Last Glacial Maximum to the Holocene* (Ed. by F. Vimeux, F. Sylvestre & M. Khordri), pp 395–412. Springer, New York, USA.
- Miller M.A., Pfeiffer W. & Schwartz T. 2010. Creating the CIPRES science gateway for inference of large phylogenetic trees. In: *Proceedings of the Gateway Computing Environments Workshop (GCE)*, pp 1–8. New Orleans, Louisiana, USA. DOI: 10.1109/GCE.2010.5676129.
- Moncalvo J.M., Nilsson R.H., Koster B., Dunham S.M., Bernauer T., Matheny P.B., Porter T.M., Margaritescu S., Weiß M., Garnica S. et al. 2006. The cantharelloid clade: dealing with incongruent gene trees and phylogenetic reconstruction methods. *Mycologia* 98: 937–948. DOI: 10.3852/mycologia.98.6.937.
- Mossel E. & Vigoda E. 2005. Phylogenetic MCMC algorithms are misleading on mixtures of trees. *Science* 309: 2207–2209. DOI: 10.1126/science.1115493.
- Moyer G.R., Remington R.K. & Turner T.F. 2009. Incongruent gene trees, complex evolutionary processes, and the phylogeny of a group of North American minnows (*Hybognathus* Agassiz 1855). *Molecular Phylogenetics and Evolution* 50: 514–525. DOI: 10.1016/j.ympev.2008.11.002.
- Muñoz-Gómez S.A., Mejía-Franco F.G., Durnin K., Colp M., Grisdale C. J., Archibald J.M. & Slamovits C.H. 2017. The new red algal subphylum Proteorhodophytina comprises the largest and most divergent plastid genomes known. *Current Biology* 27: 1677–1684. DOI: 10.1016/j.cub.2017.04.054.
- Nguyen L.T., Schmidt H.A., von Haeseler A. & Minh B.Q. 2014. IQ-TREE: a fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. *Molecular Biology and Evolution* 32: 268–274. DOI: 10.1093/molbev/msu300.
- Papenfuss G.F. 1964. Catalogue and bibliography of Antarctic and Sub-Antarctic benthic marine algae. In: *Bibliography of the Antarctic Seas, Antarctic Research Series*, vol. 1 (Ed. by M.O. Lee), pp 1–76. American Geophysical Union, Washington D.C., USA.
- Pelser P.B., Kennedy A.H., Tepe E.J., Shidler J.B., Nordenstam B., Kadereit J.W. & Watson L.E. 2010. Patterns and causes of incongruence between plastid and nuclear Senecioneae (Asteraceae) phylogenies. *American Journal of Botany* 97: 856–873. doi: 10.3732/ajb.0900287.
- Porter D.M. 1987. Darwin's notes on Beagle plants. *Bulletin of the British Museum (Natural History), Historical Series* 14: 145–233. [http://darwin-online.org.uk/content/frameset?pageseq=1&itemID=F1827&viewtype=text.]
- Pujals C. 1963. Catálogo de Rhodophyta citadas para la Argentina. *Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Ciencias Botánicas* 3: 1–139.
- Rambaut A. 2018. FigTree, version v1.4.4. <http://tree.bio.ed.ac.uk/software/figtree/> 2018.
- Rambaut A., Drummond A.J., Xie D., Baele G. & Suchard M.A. 2018. Posterior summarization in Bayesian phylogenetics using Tracer 1.7. *Systematic Biology* 67: 901–904. DOI: 10.1093/sysbio/syy032.
- Ramírez M.E. & Santelices B. 1991. *Catálogo de las algas marinas bentónicas de la costa temperada del Pacífico de Sudamérica*. Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile. 437 pp [Monografías Biológicas 5].
- Ronquist F., Teslenko M., van der Mark P., Ayres D.L., Darling A., Höhna S., Larget B., Liu L., Suchard M.A. & Huelsenbeck J.P. 2012. MRBAYES 3.2: efficient Bayesian phylogenetic inference and model selection across a large model space. *Systematic Biology* 61: 539–542. DOI: 10.1093/sysbio/sys029.
- Saunders G.W. 2014. Long distance kelp rafting impacts seaweed geography in the north-east Pacific: the kelp conveyor hypothesis. *Journal of Phycology* 50: 968–974. DOI:10.1111/jpy.12237.
- Setchell W.A. & Gardner N.L. 1903. Algae of northwestern America. *University of California Publications in Botany* 1: 165–418.
- Silva P.C. & Moe R.L. *Index Nominum Algarum*. University Herbarium, University of California, Berkeley, California, USA. <http://ucjeps.berkeley.edu/CPD/>; searched on 1 May 2022.
- Silva P.C., Basson P.W. & Moe R.L. 1996. *Catalogue of the benthic marine algae of the Indian Ocean*. University of California Press, Berkeley, California, USA. 1259 pp.
- Silvestro D. & Michalak M. 2012. raxmlGUI: a graphical front-end for RAXML. *Organisms Diversity and Evolution* 12: 335–337. DOI: 10.1007/s13127-011-0056-0.
- Skottsberg C. 1923. Botanische Ergebnisse der schwedischen Expedition nach Patagonien und dem Feuerlande 1907–1909. IX. Marine algae 2. Rhodophyceae. *Kungliga Svenska Vetenskapsakademiens Handlingar, ser. 4* 63 (8): 1–70.
- Smith G.M. 1944. *Marine algae of the Monterey Peninsula, California*. Stanford University Press, Stanford, California, USA. 622 pp.
- Swofford D.L. 2002. PAUP.\* Phylogenetic analysis using parsimony (\*and other methods), version 4. Sinauer Associates, Sunderland, Massachusetts, USA. <http://phylosolutions.com/paup-test>.
- Tavares A.I., Nicastró K.R., Kolzenburg R., Ragazzola F., Jacinto R. & Zardi G.I. 2018. Isolation and characterization of nine microsatellite markers for the red alga *Corallina officinalis*. *Molecular Biology Reports* 45: 2791–2794. DOI: 10.1007/s11033-018-4353-y.
- Taylor W.R. 1945. *Pacific marine algae of the Allan Hancock Expeditions to the Galapagos Islands*. University of Southern California Press, Los Angeles, California, USA. 528 pp. *Allan Hancock Pacific Expeditions*, vol. 12.
- Thiers B.M. 2022. [Continuously updated electronic resource]. *Index Herbariorum: a global directory of public herbaria and associated staff*. New York Botanical Garden's Virtual Herbarium, New York. <http://sweetgum.nybg.org/ih/>.
- Thompson L.G., Mosley-Thompson E., Davis M.E., Lin P.N., Henderson K. & Mashiotta T.A. 2003. Tropical glacier and ice core evidence of climate change on annual to millennial time scales. *Climatic Change* 59: 137–155. DOI: 10.1023/A:1024472313775.
- Turland N.J., Wiersema J.H., Barrie F.R., Greuter W., Hawksworth D.L., Herendeen P.S., Knapp S., Kusber W.H., Li D.Z., Marhold K. et al. [Eds] 2018. *International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code) adopted by the Nineteenth International Botanical Congress Shenzhen, China, July 2017*. Koeltz Botanical Books, Glashütten, Germany. xxxviii + 254 pp. [Regnum Vegetabile 159] DOI: 10.12705/Code.2018.
- Twist B.A., Neill K.F., Bilewitch J., Jeong S.Y., Sutherland J.E. & Nelson W.A. 2019. High diversity of coralline algae in New Zealand revealed: knowledge gaps and implications for future research. *PLOS One* 14: Article 0225645. DOI: 10.1371/journal.pone.0225645.
- van den Hoek C. 1982. The distribution of benthic marine algae in relation to the temperature regulation of their life histories.

- Biological Journal of the Linnean Society* 18: 81–144. DOI: [10.1111/j.1095-8312.1982.tb02035.x](https://doi.org/10.1111/j.1095-8312.1982.tb02035.x).
- van den Hoek C. 1984. World-wide latitudinal and longitudinal seaweed distribution patterns and their possible causes, as illustrated by the distribution of rhodophyten genera. *Helgoländer Meeresuntersuchungen* 38: 227–257. DOI: [10.1007/BF01997483](https://doi.org/10.1007/BF01997483).
- Walker R.H., Brodie J., Russell S., Irvine L.M. & Orfanidis S. 2009. Biodiversity of coralline algae in the Northeastern Atlantic including *Corallina caespitosa* sp. nov. (Corallinoideae, Rhodophyta). *Journal of Phycology* 45: 287–297. DOI: [10.1111/j.1529-8817.2008.00637.x](https://doi.org/10.1111/j.1529-8817.2008.00637.x).
- Williamson C.J., Walker R.H., Robba L., Yesson C., Russell S., Irvine L.M. & Brodie J. 2015. Toward resolution of species diversity and distribution in the calcified red algal genera *Corallina* and *Ellisolandia* (Corallinales, Rhodophyta). *Phycologia* 54: 2–11. DOI: [10.2216/14-024.1](https://doi.org/10.2216/14-024.1).
- Yendo K. 1902. Corallinae verae of Port Renfrew. *Minnesota Botanical Studies* 2: 711–722.
- Yesson C., Jackson A., Russell S., Williamson C.J. & Brodie J. 2018. SNPs reveal geographical population structure of *Corallina officinalis* (Corallinaceae, Rhodophyta). *European Journal of Phycology* 53: 180–188. DOI: [10.1080/09670262.2017.1402373](https://doi.org/10.1080/09670262.2017.1402373).
- Yesson C., Bian X, Williamson C., Briscoe A.G. & Brodie J. 2020. Mitochondrial and plastid genome variability of *Corallina officinalis* (Corallinales, Rhodophyta). *Applied Phycology* 1: 73–79. DOI: [10.1080/26388081.2020.1827940](https://doi.org/10.1080/26388081.2020.1827940).
- Yoshida Y. & Mogi Y. 2019. How do plastids and mitochondria divide? *Microscopy* 68: 45–56. DOI: [10.1093/jmicro/dfy132](https://doi.org/10.1093/jmicro/dfy132).