RESOLVING SOME OF THE EARLIEST NAMES FOR *CORALLINA* SPECIES (CORALLINALES, RHODOPHYTA) IN THE NORTH PACIFIC BY SEQUENCING TYPE SPECIMENS AND DESCRIBING THE CRYPTIC *C. HAKODATENSIS* SP. NOV. AND *C. PARVA* SP. NOV.[1]

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Partial *rbc*L sequences from type specimens of three of the earliest described *Corallina* species showed that *C. arbuscula* (type locality: Unalaska Island, Alaska, USA) and *C. pilulifera* (type locality: Okhotsk Sea, Russia) are synonymous, with *C. pilulifera* as the taxonomically accepted name and that *C. vancouveriensis* (type locality: Botanical Beach, Vancouver Island, Canada) is a distinct species. To identify molecular species limits and clarify descriptions and distributions of *C. pilulifera* and *C. vancouveriensis*, we sequenced and analyzed portions of one mitochondrial and two plastid genes from historical and recent collections. The single-gene phylogenetic reconstructions support the recognition of both species as distinct, as well as two additional species, *C. hakodatensis* sp. nov. and *C. parva* sp. nov., which are sister to, and often

morphologically indistinguishable from *C. pilulifera* and *C. vancouveriensis*, respectively. DNA sequence data currently illustrate that *C. pilulifera* is found in the cold northern Pacific waters from the Okhotsk Sea of Russia to Hokkaido, Japan, eastward across the Aleutian Islands to Knoll Head, Alaska, and as far south as Nanaimo, British Columbia. *Corallina vancouveriensis* is distributed as far west as Attu Island in the Aleutian Islands to Sitka, Alaska, and southeasterly at numerous sites from British Columbia to the north of Point Conception, California, USA. The cryptic species *C. hakodatensis* and *C. parva* occur sympatrically with their sister species but with narrower ranges. The complex phylogenetic relationships shown by the single gene trees recommend *Corallina* as a model genus to explore coralline algal biogeography, evolution, and patterns of speciation.

Key index words: articulated coralline; COI; coralline red algae; cryptic species; intertidal; North Pacific; *psb*A; *rbc*L; species delimitation; sympatry; temperate

Abbreviations: COI-5P, 5′ end of cytochrome c oxidase 1 gene; *psb*A, photosystem II protein D1; PTP, poisson tree processes

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Corallina (Corallinoideae, Corallinaceae) is a cosmopolitan genus of coralline algae primarily from warm and cold temperate marine waters with reduced diversity in tropical and high latitudes (Guiry and Guiry 2022). It is currently the third most speciose genus of geniculate corallines, after *Amphiroa* and *Jania*, with 31 presently recognized species (Guiry and Guiry 2022). As with many other coralline taxa, *Corallina* taxonomy and systematics are confounded by a lack of informative morphological characters (Robba et al. 2006, Hind et al. 2014). There has been recent interest in clarifying species boundaries and the systematics of this genus using molecular phylogenetic techniques anchored with sequences from type specimens (Hind et al. 2014, Bustamante et al. 2019, Huber 2020, Calderon et al. 2021).

Molecular taxonomic reassessments have been published for *Corallina* species from the NE Atlantic Ocean and Mediterranean Sea (Robba et al. 2006, Walker et al. 2009, Brodie et al. 2013, Williamson et al. 2015, Pardo et al. 2017, Yesson et al. 2018), and more recently from southern hemisphere waters (Brodie et al. 2021, Calderon et al. 2021). Revisions have also occurred in the NE and NW Pacific, where four formerly recognized genera, *Pachyarthron*, *Serraticardia*, *Marginisporum*, and *Yamadaia* were placed in synonymy under *Corallina* by Hind et al. (2014), Hind and Saunders (2013), and Martone et al. (2012), respectively. After *C. officinalis* (Linnaeus 1758), the oldest validly published *Corallina* species were described by Postels and Ruprecht (1840), namely, *C. arbuscula* (type locality: Unalaska Island, Alaska, USA) and *C. pilulifera* (type locality: Okhotsk Sea, Russia). In the NE Pacific, the most commonly collected species is *C. vancouveriensis* (type locality: Botanical Beach, Vancouver Island, British Columbia, Canada), described by Yendo (1902a). Here, we report our results based on sequencing the type specimens of these three species, identify their molecular species limits, clarify their descriptions and biogeographic distributions, and describe two new species that occur sympatrically with and are easily confused with these taxa.

MATERIALS AND METHODS

Specimens. A total of 307 field specimens of *Corallina* species were collected intertidally or in the very shallow subtidal in the NE Pacific (USA: California, Oregon, Washington, Alaska; Canada: British Columbia), the NW Pacific (Japan), as well as more distant locations from which *C. pilulifera* and *C. vancouveriensis* are reported, including Australia (Chapman and Parkinson 1974), Chile (Levring 1945, Ramirez and Santelices 1991), Hong Kong, and Taiwan (Huang 2000, Phang et al. 2016). These specimens were air-dried, or air-dried and placed in silica gel. Type and historical specimens, or fragments from these specimens, were sent from LE, S, and UC; vouchers of field-collected sequenced specimens were deposited in NCU, UBC, or UC; herbarium acronyms follow the online *Index Herbariorum* (Thiers 2022, continuously updated).

Morphological characterization: At least two specimens per clade, representing the geographic range, were assessed for morphological characters. Intergenicular measurements were made on intergenicula at the midpoint of the main axis of a random frond. Measured characters included maximum thallus length (mm), maximum intergeniculum width (μm), minimum intergeniculum width (μm), intergeniculum length (μm), and the ratio of maximum intergeniculum length to maximum intergeniculum width. If conceptacles were present, the external diameter at its widest point was measured (μm). The presence of a crustose base and conceptacle branchlets were also noted.

DNA sequencing and editing. Historical and type material was extracted and amplified separately from field-collected material at two different institutions—the University of North Carolina, Chapel Hill (UNC) and Hartnell College (HC), and these samples were accompanied by negative controls at every step. At UNC, type material and recent collections were extracted following Gabrielson et al. (2011) but modified for type specimens by following the guidelines in Hughey and Gabrielson (2012). At HC, type material was extracted according to Hernandez-Kantún et al. (2015) also following the guidelines proposed by Hughey and Gabrielson (2012). At UBC, recent collections were extracted using a modified protocol for a Promega Wizard® DNA Clean-Up System (Saunders 1993).

Two chloroplast gene markers, *rbc*L and *psb*A, and one mitochondrial marker, COI-5P (hereafter COI), were amplified. DNA amplifications were performed at HC, UBC, and UNC. For type specimens and historical collections, *rbc*L gene sequences were obtained with primer pairs F1150Cor (Sissini et al. 2014)/1460cor (Hernandez-Kantún et al. 2015) or F1150Cor/RbcS-Start (Freshwater and Rueness 1994), yielding fragments trimmed to 263 bp (1172–1434) or 293 bp (1172–1464), respectively; for recent collections, *rbc*L gene

sequences were obtained either with two primer pairs F57-R1150 and F753-RrbcS-Start to produce overlapping fragments, together trimmed to 1383 bp, or with the primers F753/RrbcS-Start and trimmed to 691 bp (772–1464). Sequences of the *psb*A gene and COI were generated only for recent collections; *psb*A gene sequences were obtained using the primers psbAF1 and psbAR2 (Yoon et al. 2002) and COI sequences were obtained using the primers Gaz-F1/Gaz-R2, Gaz-F1/GCorR3, GWSfn/GWSRx (Le Gall and Saunders 2010), or M13F/M13R following Saunders (2005), Saunders and Moore (2013) or Peña et al. (2015). At HC, PCR products were purified and sequenced by Functional Biosciences, Inc. (Madison, WI, USA); at UBC, PCR products were purified using ExoSap-IT™ (Applied Biosystems™, Waltham, MA, USA) and sequenced at the Genome Québec Centre d'Expertise et de Services (Québec, CA); at UNC, PCR products were purified according to Hughey et al. (2001) and sequenced at the DNA Analysis Core Facility, Center for Marine Sciences, University of North Carolina, Wilmington. Sequences were assembled and aligned with either Geneious (v. 7.1.9 or 2020.0.4, Biomatters Ltd., Auckland, New Zealand) or with a combination of CodonCode Aligner® (CodonCode Corporation, Centerville, MA, USA) or with Sequencher (Gene Codes Corp., Ann Arbor, MI, USA) and SeaView version 4 (Gouy et al. 2010) or Sequence Alignment Editor (http://tree.bio.ed.ac.uk/software/seal/). In total, 312 new sequences were generated and deposited in the Barcode of Life Data Systems (BOLD project "CRLNA", http://www.boldsystems.org; Ratnasingham and Hebert 2007) and GenBank www.ncbi.nlm.nih.gov/genbank/ (Table S1 in the Supporting Information).

Phylogenetic analyses. Sequences were aligned with *Crusticorallina painei* and *Ellisolandia elongata* sequences, the latter specified as an outgroup, and with other *Corallina* sequences available on GenBank with default settings of the MUSCLE algorithm and manually corrected in Geneious (v. 2020.0.4, Biomatters Ltd., Auckland, NZ). To determine the best model of sequence evolution for each gene alignment (*rbc*L = 1334 bp; *psb*A = 851 bp; COI = 664 bp), JModelTest2 on XSEDE (v 2.1.6) was used. Individual gene trees were estimated using maximum likelihood and Bayesian Inference methods via RaxML-HPC2 on XSEDE (v. 8.2.12) and MrBayes on XSEDE (3.2.7a), respectively, also via the CIPRES gateway (Miller et al. 2010). Maximum likelihood tree estimations were run for 1,000 bootstrap generations and using default parameters. Bayesian inferred tree estimates were run for 5,000,000 generations with sampling every 1,000 generations and a burn-in value of 0.10. Convergence was confirmed using Tracer v.1.7.2 (Rambaut et al. 2018) by assessing the likelihood score landscape and effective sample size.

Species delimitation. A combination of methods was used to assess species delimitation: Automatic Barcode Gap Discovery (ABGD; Puillandre et al. 2012), a Poisson Tree Processes (PTP) model, a Bayesian implementation of the PTP (bPTP) model (Zhang et al. 2013), and a General Mixed Yule Coalescent (GMYC) model (Fujisawa and Barraclough 2013). Each analysis was run for each gene for a total of 12 species delimitation analyses on a reduced representation alignment, without type sequences (due to their comparatively reduced length and/or absence in the gene data set) but maintaining as much of the sequence diversity in the master alignment as possible. This reduced alignment also included only species for which phylogenetic boundaries had been established using type sequences to ensure that inter- and intraspecific differences were as precise as possible. ABGD was performed without outgroup sequences through the web interface (https://bioinfo.mnhn.fr/abi/public/abgd/abgdweb.html) using the model Kimura-2-parameters and 50 screening steps, variability (P) was set between 0.001 (P_{min}) and 0.1 (P_{max})

whereas the relative gap width (X) and the Nb bins (for distance distribution) to 1 and 20, respectively (Tineo et al. 2020). Poisson Tree Processes (PTP) and bPTP were performed on the web server (http://species.h-its.org/) using the above-generated rooted ML tree as input, setting 500,000 MCMC generations, thinning value of 100, a burn-in of 10%, and removing the outgroup to improve species delimitation.

The input ultrametric trees for GMYC species delimitation analyses were constructed by Bayesian analysis in BEAST2 v.2.6.3 (Drummond et al. 2012) via the CIPRES Science Gateway with the GTR model. The relaxed clock log normal molecular clock model (Drummond et al. 2006) and the coalescent exponential population prior were used. Markov Chain Monte Carlo was run for 50 million generations, sampling every 1,000 generations. Output log files were visualized in Tracer v.1.7.2 (Rambaut et al. 2018) for assessing the stationary state of parameters based on values of estimate-effective sample size (ESS). Twenty-five percent of trees were removed as burn-in, and the remaining trees were summarized in a single tree (ultrametric maximum clade credibility tree) by TreeAnnotator v.2.0.2 (Drummond et al. 2012). Both single-threshold and multi-threshold GMYC analyses were performed using the web interface (www.species.h-its.org/gmyc/).

RESULTS

Corallina phylogeny and species delimitation. Fragments at the 3′-end of the targeted *rbc*L gene locus were generated for the type specimens of *Corallina arbuscula* (296 bp), *C. pilulifera* (263 bp), and *C. vancouveriensis* (263 bp), as well as for the forms *C. officinalis* f. *multiramosa* (263 bp) and *C. vancouveriensis* f. *densa* (263 bp) that were previously synonymized with *C. vancouveriensis* (Setchell and Gardner 1903). The topologies among the reconstructed gene trees were incongruent: the COI and *rbc*L gene trees had poorly resolved deeper nodes, and the position of clades varied across all three trees (Figs. S1–S3 in the Supporting Information). Thus, we have chosen to show only the *rbc*L gene tree topology in the main figure as a visual backbone for the species delimitation analyses, given that a portion of this locus was sequenced for the historical and type specimens. Bayesian reconstructions resulted in an abundance of polytomies; therefore, only maximum likelihood reconstructions with bootstrap support values are provided in the main and supplemental figures. Despite topology incongruences between gene loci, both identically aligned *rbc*L sequences and phylogenetic analyses support the synonymy of *C. arbuscula* and *C. pilulifera* (Figs. 1, S1–S3).

Sequences from specimens identified as *Corallina pilulifera* and *C. vancouveriensis* segregated consistently with other unidentified specimens into four clades, all of which were supported by strong bootstrap values (Figs. 1, S1–S3). The inclusion of type specimens confirmed the correct identification of one of the clades for each pair as the authentic *C. pilulifera* and *C. vancouveriensis*. *Corallina pilulifera* and its sister clade were 2.41% different on average in sequence identity across the targeted gene loci
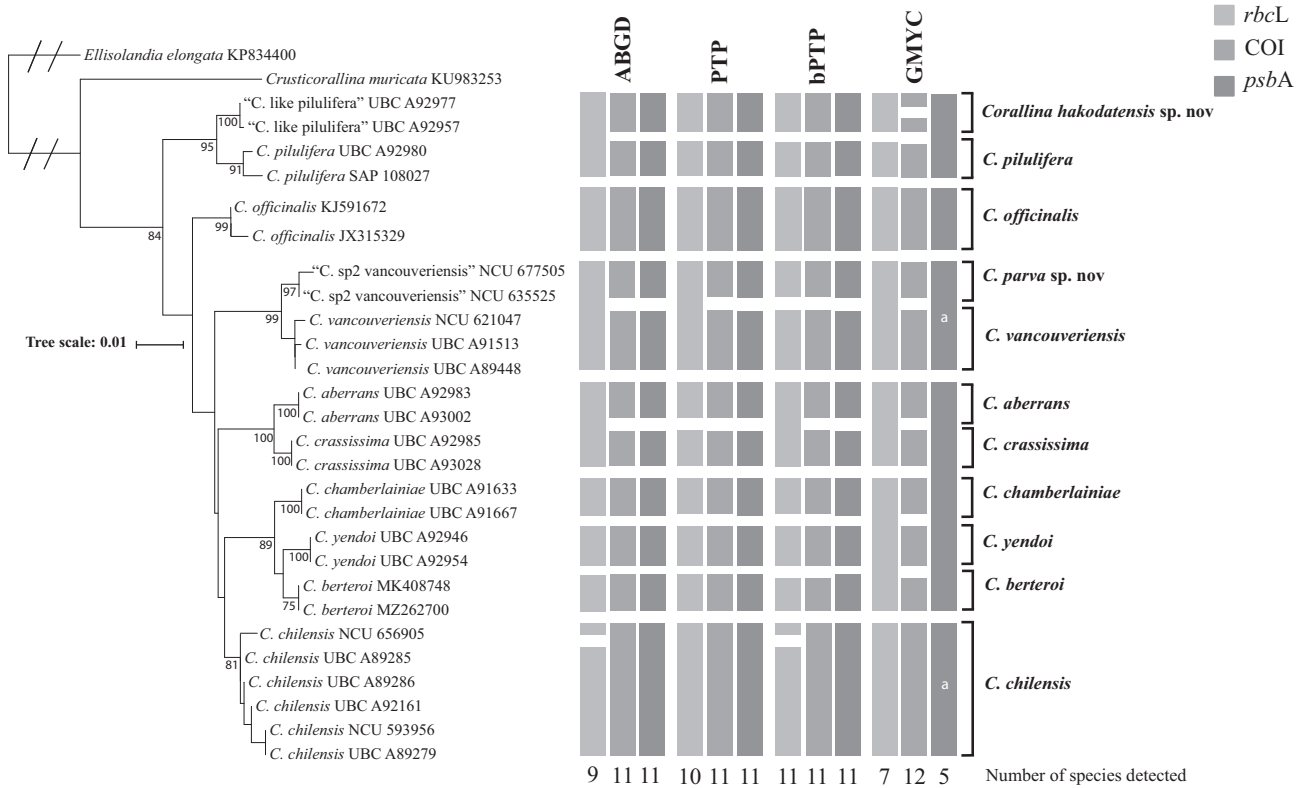
FIG. 1. Maximum likelihood phylogenetic reconstruction of the *rbc*L gene tree with species delimitation analyses. Nodal values represent bootstrap support; only values >70 are shown. Tree scale represents the number of substitutions per site. The numbers below each gene and species delimitation method represent the number of species within the tree supported by the analysis. Lowercase notations within the gray bars represent lineages that were lumped into single entities in the COI or *psb*A gene trees.

(Table 1). *Corallina vancouveriensis* and its sister clade were 1.84% different on average (Table 1). Furthermore, these two pairs of sister clades were supported as four distinct entities by the species delimitation analyses: 10 of 12 analyses supported *C. pilulifera* as distinct from its sister clade, and 8 of 12 supported *C. vancouveriensis* as distinct from its sister clade (Fig. 1). GMYC single-threshold analyses consistently lumped species, particularly those that had previously been described as distinct (e.g., *C. berteroi*, *C. chamberlainiae*, and *C. yendoi*); thus, only the multi-threshold results are presented (Fig. 1). The strong support for these four clades justifies amending the descriptions of *C. pilulifera* and *C. vancouveriensis* and providing the descriptions of two new species, one each sister to *C. pilulifera* and *C. vancouveriensis*.

TABLE 1. Range of percent differences in sequence data among the targeted loci for *Corallina hakodatensis*, *C. parva*, *C. pilulifera*, and *C. vancouveriensis*.

	*rbc*L	*psb*A	COI
C. hakodatensis-C. pilulifera	1.33–1.48	0.47–0.59	4.79–6.66
C. parva-C. vancouveriensis	0.59–1.04	0.59–0.85	3.39–4.90

Morphological assessment and taxonomy: Morphology summaries for previously described species include characters provided by the species authorities (included in quotes), along with additional details provided by our specimens with DNA-confirmed identifications. Sequenced specimens that document the distribution of each species are listed from west to east and north to south in each species description below. For a complete list of sequenced specimens, see Table S1. The distributions of each taxon below are based solely on sequenced specimens and not on the literature, as nearly all of the historically named species are reported from localities where they likely do not occur (see Discussion).

***Corallina pilulifera* Postels & Ruprecht 1840: 20, pl. XL, fig. 101**.

Holotype: LE (no accession no.), Okhotsk Sea, no date, no habitat data, leg. I. Redowsky (Fig. S4A in the Supporting Information).

Homotypic synonym: *Corallina officinalis* f. *pilulifera* (Postels & Ruprecht) Setchell & N.L.Gardner 1903: 366.

Heterotypic synonyms: *Corallina arbuscula* Postels & Ruprecht 1840: 20, pl. XL, fig. 102, *Corallina pilulifera* f. *arbuscula* (Postels & Ruprecht) Yendo 1905: 30.

Lectotype (designated herein): S A2604, Unalaska Island (as Unalaschka), no date, no habitat data, leg. Dr. Mertens (Fig. S4, B and C).

Diagnostic DNA sequences: *psb*A (OP703060–OP703064), *rbc*L (OP702980–OP702998), and COI (OP689502–OP689513) were used to recognize this species.

Morphology (amended from original description by Postels and Ruprecht 1840 in quotes): Erect geniculate fronds 1 to at least 4 cm in length emerging from a small, crustose holdfast; "most often corymbose and stipitate with terete" to sub-terete main axes, "becoming more compressed towards the apices", with or without solitary intergenicula below first determinate branch; "distal intergenicula quite compressed, cuneate, and terminally enlarged"; conceptacles axial and stipitate, globose or somewhat deltoid or rhomboid, rarely giving rise to one or two solitary intergenicula (Fig. 2).

Habitat: Epilithic, low intertidal (can be found under kelp), mid-high intertidal pools.

Distribution: Russia: Okhotsk Sea (LE no accession no.); Japan: Muroran (UBC A92960), Hakodate (UBC A92980), Oshoro Bay (UBC A92941); United States: Sledge Island, Alaska (UNB GWS042368); Unalaska Island, Alaska (S A2604), Sanak Island, Alaska (UBC A90539), Kinzarof Lagoon, Cold Bay, Alaska (UBC A88799), Knoll Head, Alaska (UBC A94122); Canada: Calvert Island, BC (UBC A89665), Nanaimo, BC (UNB GWS006466); (Fig. 3).

Comments: DNA sequencing of the lectotype of *Corallina arbuscula* and the holotype of *Corallina pilulifera* showed that these taxa are conspecific. Thus, *C. arbuscula* is herein a heterotypic synonym of *C. pilulifera* based on Yendo's (1905) inclusion of *C. arbuscula* as a form of *C. pilulifera*, and in compliance with ICN Article 11.4 (Turland et al. 2018).

Corallina pilulifera looks strikingly different depending on which side of the Pacific Ocean basin the specimen is collected: in Japan, *C. pilulifera* is routinely corymbose and pinnate, while in Alaska and British Columbia, *C. pilulifera* can look tangled and sparsely branched (Fig. 2, A and D). This difference is largely reflected in their gross morphology, but it is notable that specimens from the eastern Pacific often exhibit measurements in the upper limits of intergenicular and conceptacle features (Fig. 4).

Of the five *Corallina* species described by Postels and Ruprecht (1840: 20, *Corallina arbuscula*, *C. cretacea*, *C. frondescens*, *C. pilulifera*, and *C. tuberculosa*), only *C. pilulifera* was not collected on the *Seniavin*
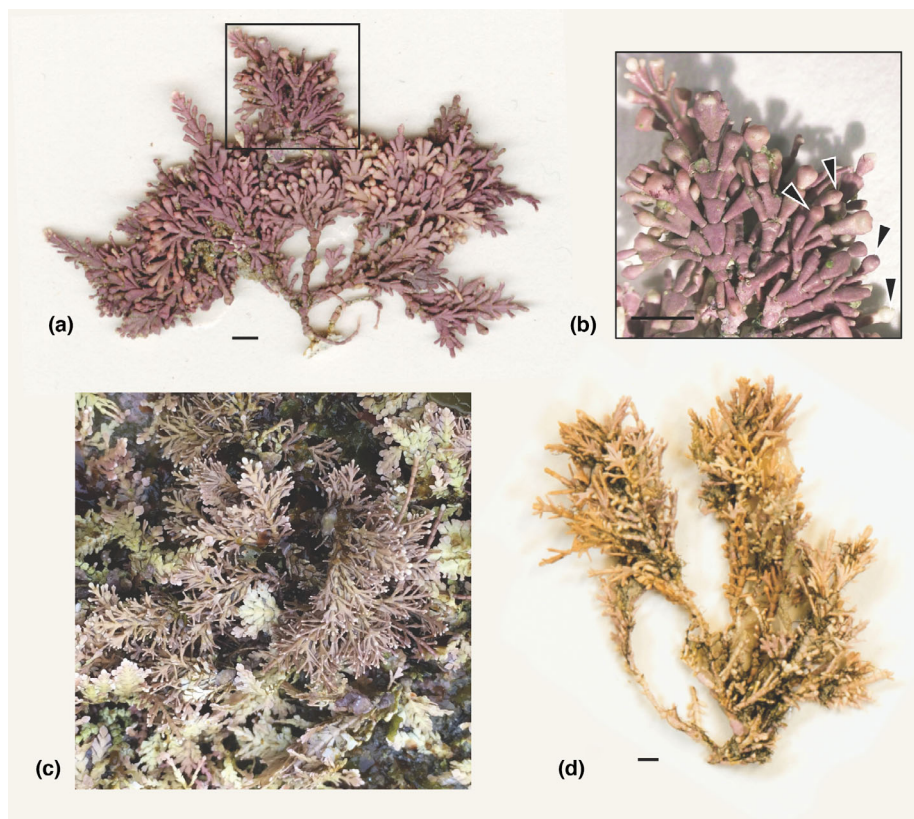

FIG. 2. Habit of *Corallina pilulifera*. (a) Muroran, Hokkaido, Japan, upper-mid intertidal, UBC A92961; (b) Inset magnification of intergenicula and conceptacles (arrowheads), UBC A92961; (c) Calvert Island, British Columbia, Canada, lower intertidal, UBC A93931; (d) Cold Bay, Kinzarof Lagoon, Alaska, upper subtidal, UBC A88799. All scale bars = 2 mm.
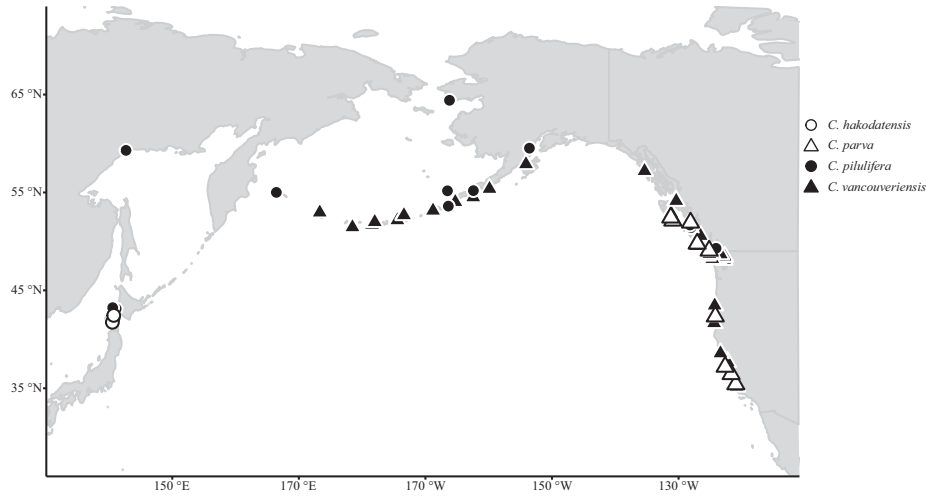
FIG. 3. Distribution map of *Corallina hakodatensis, C. parva, C. pilulifera,* and *C. vancouveriensis* records supported by molecular-assisted identification.
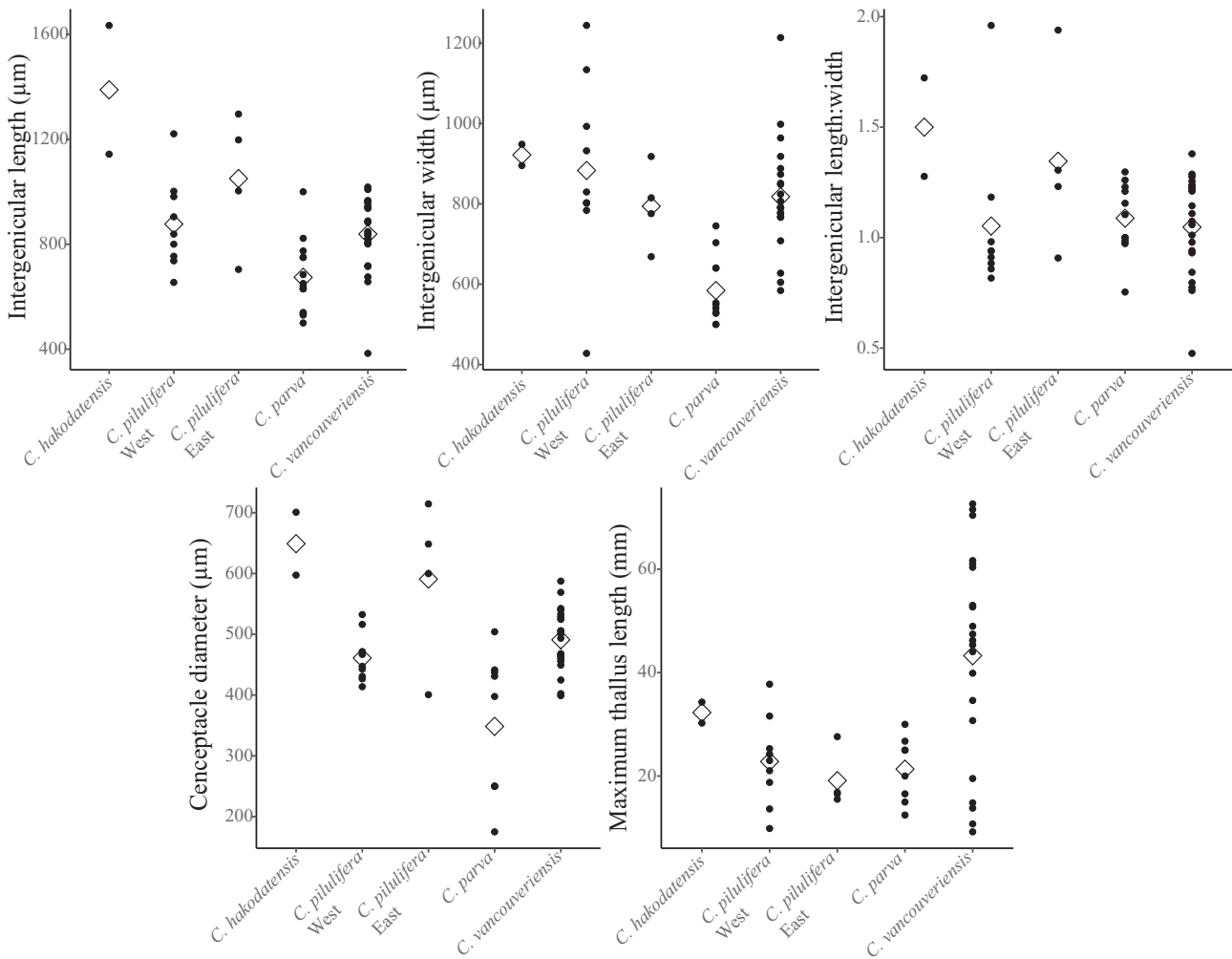

FIG. 4. Comparison of primary morphometric characters between *Corallina hakodatensis, C. parva, C. pilulifera,* and *C. vancouveriensis*. Solid circles represent raw data, unfilled diamonds represent species means. "East" and "West" refer to the side of the Pacific Ocean basin from which *C. pilulifera* was collected.

expedition of 1826–1829. The original specimen label (Fig. S4B) reads "Corallina pilulifera Post. et Rupr., Mare Okhotsk, Herb. M.B., leg. Redowsky". In the original protologue, Postels and Ruprecht (1840) wrote, "*Vidimus specimina ex Herbario M. de Bieberstein inscripta patria* "Sibiria transbaicalensis "(*an mare Ochotense*?)". The collector of the specimen, Ivan Ivanovich Redowsky (1774–1807), was a Lithuanian botanist who explored Siberia and the Kamchatka Peninsula (https://plants.jstor.org/stable/10.5555/al.ap.person.bm000326090). This specimen, later deposited in LE, was found in the herbarium of Baron Friedrich August Marschall von Bieberstein, an avid collector of land plants from the Crimean and Caucasian regions of Russia in the late 18th and early 19th centuries. The designation in Postels and Ruprecht (1840) "*Sibiria transbaicalensis*" refers to the locality as Transbaikalia where the far-eastern region of Siberia meets the Sea of Okhotsk.

Corallina hakodatensis Martone & R.M.Wade sp. nov. Figure 5.

Holotype (designated herein): UBC A92977, May 19, 2015, Cape Tachimachi, Hakodate, Hokkaido, Japan (41.745, 140.722), mid-intertidal pool.

Isotype: SAP 115643, May 19, 2015, mid-intertidal pool.

Paratype: UBC A92957, Muroran, Japan, May 18, 2015, low intertidal.

Etymology: The species epithet signifies that the type is from the port city of Hakodate on the island of Hokkaido in Japan.

Habitat: Marine, low- to mid-intertidal zones, including tidepools.

Distribution: Southern Hokkaido, Japan: Muroran (UBC A92957) and Hakodate (UBC 92977; Fig. 3).

Diagnostic DNA sequences: *psb*A (OP703056–OP703057), *rbc*L (OP702975–OP702976), and COI (OP689494–OP689495) were used to recognize this species.

Description: Erect fronds ~3 cm in length; often corymbose and stipitate; intergenicula of main axis subterete at base, becoming more compressed, sometimes palmate, toward the distal portions of the thallus; palmate intergenicula may give rise to up to six secondary intergenicula, which may also be palmate, giving a winged appearance; conceptacles primarily axial and sometimes shortly stipitate, globose to ovate, sometimes somewhat cordate (Fig. 5).

Comments: This species can be found growing sympatrically with *Corallina pilulifera* in Japan but may be less abundant. For example, during a collection trip to Hokkaido and Honshu specifically to collect coralline algae, only two *C. hakodatensis* specimens were collected versus 10 *C. pilulifera* specimens. From two specimens, it is difficult to provide reliable characters that distinguish *C. hakodatensis* from *C. pilulifera* because the ranges of measurements for the two species largely overlap (Fig. 4). *Corallina*

hakodatensis can appear more elongated, particularly in its second-order intergenicula (range of intergenicular length *C. hakodatensis* = 1.14–1.63 mm; *C. pilulifera* = 0.65–1.30 mm). *Corallina hakodatensis* also exhibits conceptacle diameters in the upper range for the two species (range of mean conceptacle diameter for *C. hakodatensis* = 0.60–0.70 mm; *C. pilulifera* = 0.40–0.72 mm). Lastly, the winged appearance of one of the *C. hakodatensis* specimens due to its palmate second-order intergenicula (Fig. 5, C and D) is striking and was never observed in *C. pilulifera* specimens. However, more collections of *C. hakodatensis* are needed to document its range of morphological variation.

Corallina vancouveriensis Yendo 1902: 719, pl.LIV: fig. 3; pl. LV: figs. 1, 2; pl. 56, figs. 16, 17.

Lectotype (designated herein): UC 564666, Botany Beach, near Port Renfrow, British Columbia, Canada no habitat data, July 1901, Yendo (Fig. S5A in the Supporting Information).

Homotypic synonym: Corallina vancouveriensis f. vancouveriensis Yendo, as *C. vancouveriensis* f. *typica* Yendo (1902a: 719, pl. LIV, fig. 3, pl. LVI, fig. 16).

Heterotypic synonyms: Corallina aculeata Yendo (1902a: 720, pl. LV, fig. 3, pl. LVI, figs. 18, 19); *Corallina vancouveriensis* f. *densa* Yendo (1902a: 719, Pl. LV, fig. 1, Pl. LVI, fig. 17); lectotype (designated herein): UC 564667, Botany Beach, near Port Renfrow, Vancouver Island, British Columbia, Canada, July 1901, no habitat data, leg. K. Yendo (Fig. S5B); *Corallina officinalis* f. *multiramosa* Setchell & N.L.Gardner (1903: 366), lectotype (designated herein): UC 1456186, Uyak Bay, Kodiak Island, Alaska, USA, 1899, epilithic, lowermost intertidal and on edges of tide pools higher in the intertidal, leg. W.A. Setchell & A.A. Lawson (Fig. S5C).

Habitat: Epilithic in the low to high intertidal zones, including tidepools, sometimes in high energy areas, such as surge channels, can be often found under kelp in the low intertidal zone.

Distribution: United States: Alaska: Aleutian Islands: Attu Island (UBC A90567), Atka Island (NCU 594342), Rat Island (NCU 601353), Amchitka Island (UBC A90566), Umnak Island (NCU 601352), Tigalda Island (NCU 591434), Sanak Island (UBC A94127); Shumagin Islands (FH 00258857), Uyak Bay, Kodiak Island (UC 1456186), Sitka (no voucher, SCL 15395); Canada: British Columbia: Haida Gwaii (UNB GWS031477), Calvert Island (UBC A89274), Vancouver Island (UBC A88682); United States: Washington: Strait of Juan de Fuca (NCU 621047); San Juan Island (NCU 585602, Cor.van.22vii08), Whidbey Island (UBC A88624); Oregon: Coos Bay (NCU 635514); Brookings (NCU 625523); California: San Mateo County; (KAM MB-C-01-09; Fig. 3).

Diagnostic DNA sequences: *psb*A (OP703066–OP703075), *rbc*L (OP703006–OP703033), and COI (OP689514–OP689515) were used to recognize this species.
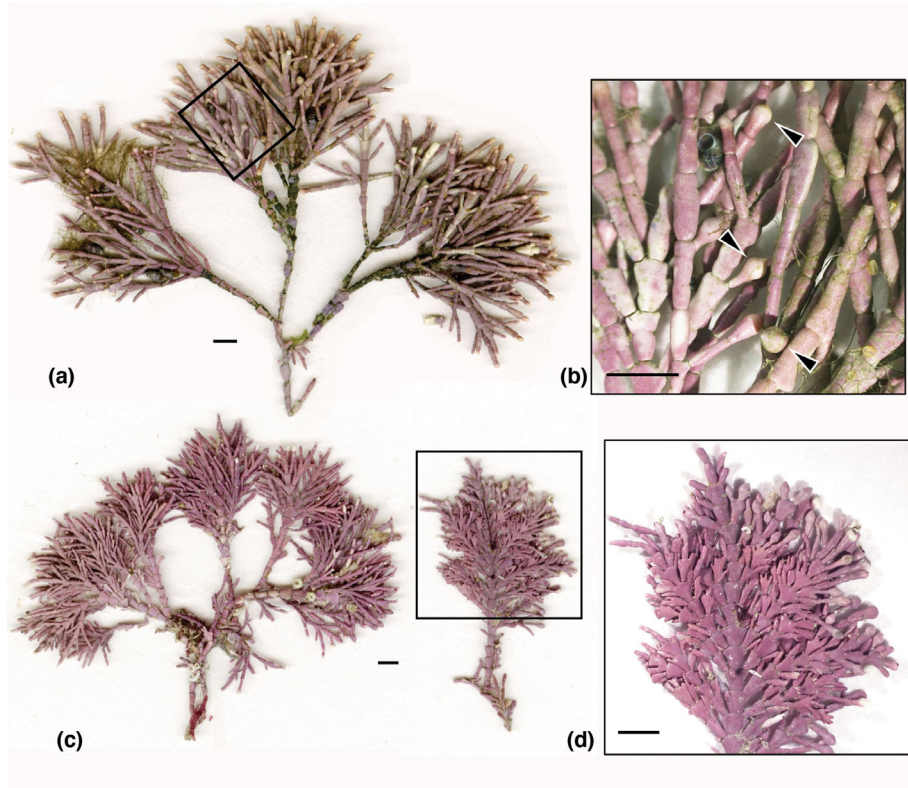
FIG. 5. Habit of *Corallina hakodatensis*. (a) Cape Tachimachi, Hakodate, Hokkaido, Japan, mid-intertidal pool, UBC A92977; (b) Inset magnification of intergenicula and conceptacles (arrowheads), UBC A92977; (c) Muroran, Hokkaido, Japan, collected as drift, UBC A92957 (d) Inset magnification of palmate intergenicula and wing-like appearance of secondary intergenicula, PTM 1419. All scale bars = 2 mm.

Morphology (amended from original description by Yendo 1902a in quotes): Erect articulated thalli most often 1–7 cm in length but "can reach lengths of 15 cm"; often grows in dense stands and forms mats, "stipitate", rarely corymbose, "regularly bi- or tri-pinnate", branching can appear dense and close together (Fig. 6B) or sparse (Fig. 6D) depending on length: width of intergenicula and angle of branching; intergenicula of main axes elongate, cuneate, or "subclavate"; mid- to terminal intergenicula may be long and "digitate", or compressed and obovate, composed of several fused intergenicula in both cases; mid- to distal intergenicula may be fused and palmate with 4–5 genicula and intergenicula developing at the distal end; conceptacles axial and globose or obovate and pedunculate, with 1–3 conceptacles per stalk, conceptacles often giving rise to two intergenicula (Fig. 6).

Comments: We were indeed fortunate to locate in UC the original material of both forms of *Corallina vancouveriensis* collected and identified by K. Yendo from the type locality because most of Yendo's geniculate coralline types are missing (Yoshida 1991). We were unable to locate the type specimen of *C. aculeata*, and therefore are unable to assess the taxonomic status of this form. For their new name for *C. vancouveriensis*, *C. officinalis* f.

multiramosa, Setchell and Gardner (1903) listed specimens from three syntype localities: Uyak Bay, Kodiak Island, Alaska, USA; Esquimalt, British Columbia, Canada; and Whidbey Island, Washington, USA. We sequenced the Uyak Bay specimen, designated here as the lectotype of *C. officinalis* f. *multiramosa*, which is a heterotypic synonym of *C. vancouveriensis*.

Corallina parva R.M.Wade, P.W.Gabrielson, K.R.Hind, & Martone sp. nov. Figure 7.

Holotype (designated herein): UBC A96978, May 25, 2017, Seppings Island, Barkley Sound, British Columbia, Canada, exposed boulder, low intertidal, collected by Hannah Avenant, collection no. HKA-18.

Paratype: UBC A96979, May 25, 2017, large boulder in surge channel, Seppings Island, Barkley Sound, British Columbia, Canada.

Habitat: Epilithic in the low- to mid-intertidal on exposed coasts, may be found growing under kelp.

Distribution: Canada: Haida Gwaii (UNB GWS012923); Calvert Island (UBC A96976); Vancouver Island (UNB GWS006659); USA: Oregon: Lone Ranch Beach (NCU 635525); California: Del Norte County (NCU 638008); Sonoma County (UC 677504); Monterey County (UNB GWS021429); San Luis Obispo County (NCU 677505).
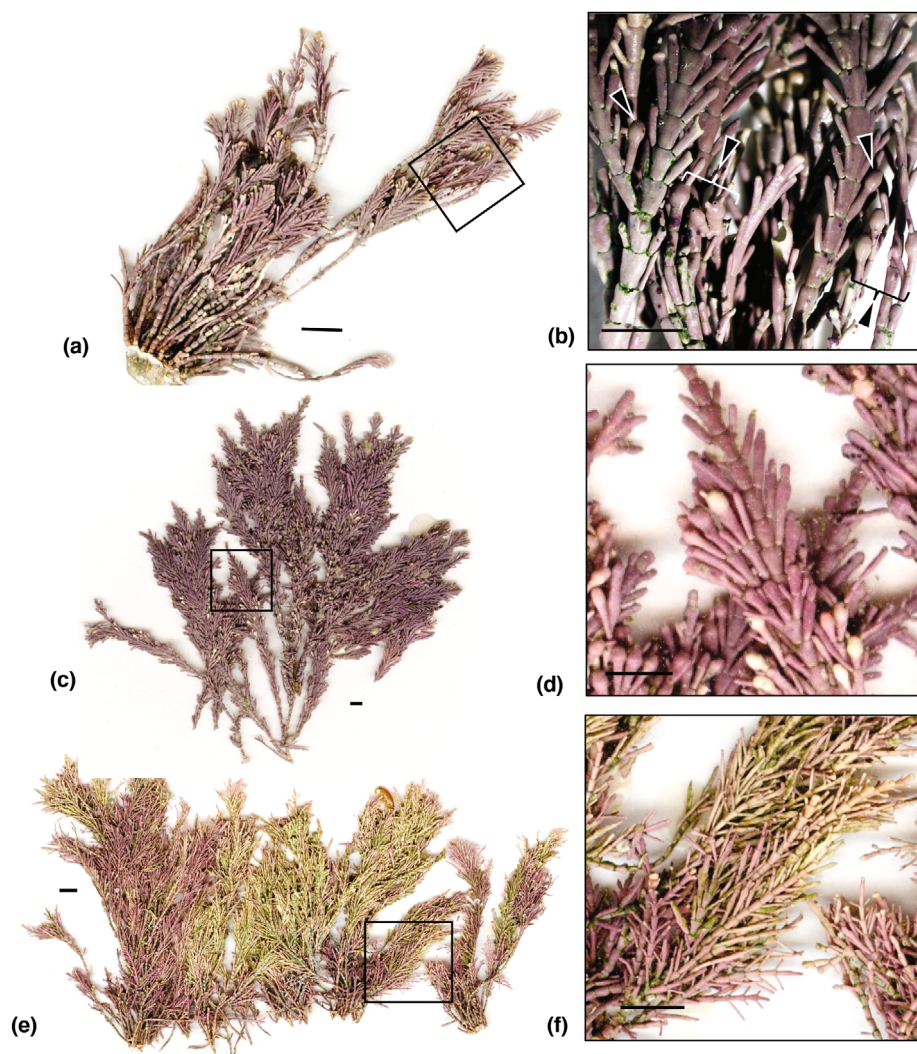
FIG. 6. Habit of *Corallina vancouveriensis*. All scale bars = 2 mm. (a) Calvert Island, British Columbia, Canada, mid-intertidal tidepool, UBC A91513; (b) Inset magnification showing the tight appearance of secondary intergenicula and conceptacles (arrowheads), UBC A91513; (c) Calvert Island, British Columbia, Canada, low intertidal, under kelp, UBC A89274; (d) Inset magnification showing a large, tight pattern of an understory individual, UBC A89274; (e) Calvert Island, British Columbia, Canada, high intertidal tidepool, UBC A89448; (f) Magnification showing the sparse branching and thin secondary intergenicula of an individual collected from the high intertidal zone, UBC A89448.

Diagnostic DNA sequences: *psb*A (OP703066–OP703075), *rbc*L (OP702999–OP703005), and COI (MN447965, MN448251) were used to identify this species.

Description: Erect fronds 1–3 cm in length; stipitate, regularly pinnate; intergenicula of main axes elongate and cuneate; elongate and digitate intergenicula common throughout thallus, subterete to compressed, appearing to be composed of multiple fused intergenicula; conceptacles axial and pedunculate, globose, or obovate, sometimes appearing bulbous (Fig. 7).

Comments: *Corallina parva* appears to be rare (18 DNA-confirmed collections to date) compared to *C. vancouveriensis* (over 100 DNA-confirmed specimens), from which it is nearly indistinguishable by morphology. *Corallina parva* occurs sympatrically in the same habitat as *C. vancouveriensis*, except in Alaska where *C. parva* has yet to be confirmed. *Corallina parva* is often smaller, with measurements in the lower range for the two species (range of maximum thallus length of *C. parva* = 12.5–30 mm; *C. vancouveriensis* = 9.2–72.6 mm; Fig. 4).

DISCUSSION

Historical records, biogeography, and current distributions of Corallina *spp.* Corallina pilulifera *and* C. arbuscula: After their description by Postels and Ruprecht (1840), the names *Corallina pilulifera* and
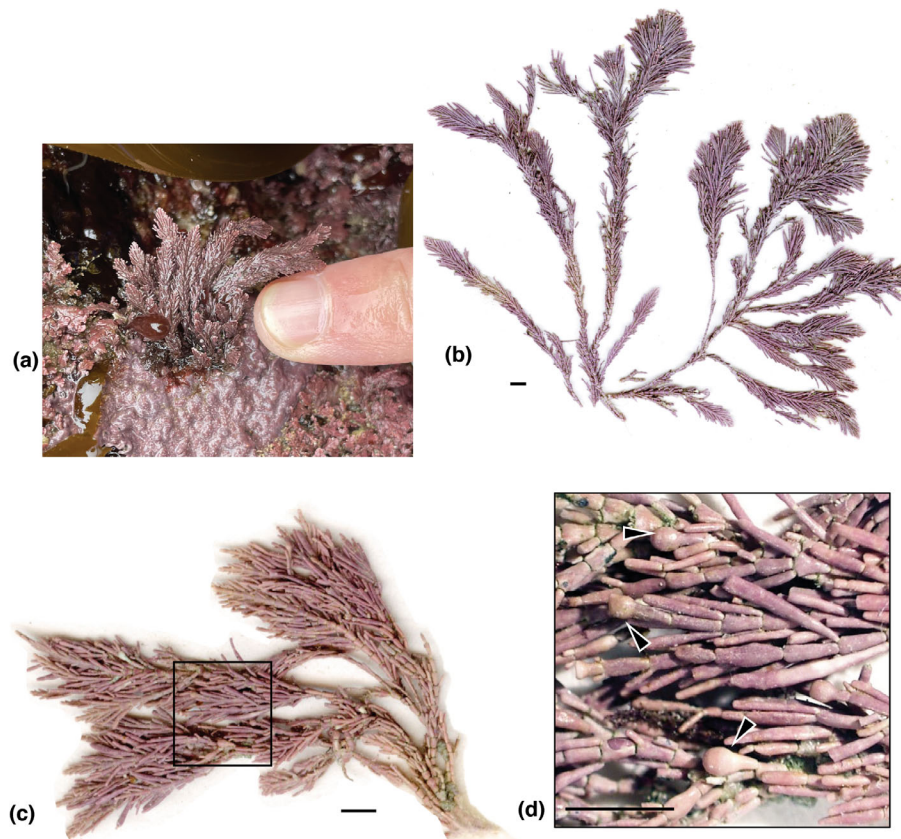
Fig. 7. Habit of *Corallina parva*. (a) North Beach Bench, Hakai Lúxvbálís Conservatory, Calvert Island, British Columbia, PTM 2038, low intertidal under *Hedophyllum* sp.; (b) Seppings Island, Barkley Sound, British Columbia, Canada, exposed boulder, low intertidal, dried and pressed specimen, UBC A96978; (c) North Beach, Calvert Island, British Columbia, Canada, low intertidal, under kelp, UBC A96976; (d) Inset magnification showing the digitate nature of some secondary intergenicula and conceptacles (arrowheads), UBC A96976. All scale bars = 2 mm.

C. arbuscula followed vastly different historical trajectories. Ruprecht (1850), based on collections from the Okhotsk Sea by Middendorf and Woesnessenski, recognized two new varieties of *C. pilulifera*: *C. pilulifera* var. *sororia* and *C. pilulifera* var. *filiformis*. We did not consider these varietal names in our taxonomic assessment because we have no knowledge of the specimens upon which these are based. Both forms were referenced by Kützing (1849: 706, *C. pilulifera*: 1849: 707, *C. arbuscula*) and by Areschoug (1852: 563). Kützing (1858: 29) described and illustrated *C. arbuscula* (pl. 60, fig. III) and *C. pilulifera* (pl. 64, fig. I) from the Cape of Good Hope, South Africa, but neither of these reports was carried forward in the literature. Yendo (1902b) first reported *C. pilulifera* from Japan and, like Ruprecht (1850), he noted the wide range of variation present in this species. Setchell and Gardner (1903: 366) reduced *C. pilulifera* to a form of *C. officinalis*, as *C. officinalis* f. *pilulifera*, and described it as "A dwarf form including the *Corallina arbuscula* and *C. pilulifera* of Postels and Ruprecht." In contrast, Yendo (1905) continued to recognize *C. pilulifera*, and, without comment, reduced *C. arbuscula* to

a form as *C. pilulifera* f. *arbuscula*. Perestenko (1994) placed *C. arbuscula* in synonymy under *C. pilulifera*. Cotton (1915: 192) reported *C. pilulifera* in an account of the cryptogamic flora of the Falkland Islands, where *Corallina* specimens were identified by Yendo. That commenced a long history of reports of *C. pilulifera* from the Falkland Islands (Lemoine in Skottsberg 1923, 1941, Levring 1945) and later from Chile (Levring 1945, Ramirez and Santelices 1991). Dawson (1945) expanded the distribution beyond the Pacific cold waters of North America, reporting the species from the Gulf of California. Scagel (1957) reported *C. pilulifera* from the cold temperate NE Pacific (Washington, USA), Pujals (1963) and Chapman and Parkinson (1974) from the temperate SW Pacific (New Zealand), Lawson and John (1982) from tropical West Africa, and Huang (2000) and Phang et al. (2016) from warm temperate to tropical SW Pacific localities.

On the basis of DNA sequences from field-collected and historical herbarium specimens, including those from Southeast Asia, Australia, Chile, Japan, New Zealand, and the coastal environments of western Canada and the United States, we

assert that *Corallina pilulifera* is restricted to cold temperate waters of the North Pacific (Fig. 3). Thus far, *C. pilulifera* has been DNA-confirmed from its western limit of Hokkaido, Japan, across the Commander and Aleutian Islands, and as far south in the eastern Pacific as Nanaimo, Vancouver Island, Canada. Other reports based on morphological similarities to *C. pilulifera* and outside the cold temperate North Pacific are extremely unlikely to be this species and need to be confirmed by DNA sequencing.

Corallina hakodatensis: The two collections of *Corallina hakodatensis* from Hokkaido, Japan suggest that this species is rare, but its collection alongside its sister species, *C. pilulifera*, indicates that these species are an excellent example of sympatry. If population-level genetic variability explained the divergence of *C. hakodatensis* from *C. pilulifera*, and therefore these clades represent one taxonomic entity, we would expect to see clade affinity based on population (e.g., *C. hakodatensis* and *C. pilulifera* sequences collected from the same location clustered together). Instead, we saw little within clade differentiation structured by geography, even from across the Pacific, in the case of *C. pilulifera*. Thus, in addition to the species delimitation analyses, the lack of intraspecific population-level differentiation supports *C. hakodatensis* and *C. pilulifera* as an example of sympatric and distinct species. Further collections are needed to confirm whether *C. hakodatensis* is restricted to Hokkaido, Japan.

Yendo (1902b) described two new species of *Corallina* from Hakodate, Hokkaido, Japan, *C. confusa* and *C. sessilis*, that we considered as potential names for *C. hakodatensis*. Baba et al. (1988) noted that Yendo (1902b) exclusively used the shape and position of conceptacle-bearing pinnae to distinguish these species (as well as *C. kaifuensis* Yendo, type locality: Kaifu, Honshu Island, Japan), but they showed that these characters varied seasonally, and thus were not taxonomically informative, although this conclusion was not based on sequenced specimens. We have found it impossible to know how to correctly apply these names due to missing type material (Yoshida 1991) and hope that Yendo's type specimens will be located in the future.

In addition to occurring sympatrically with *Corallina pilulifera*, *C. hakodatensis* was collected from the same locations where *C. yendoi* collections were made and described (Calderon et al. 2021). In addition to the phylogenetic evidence that supports *C. hakodatensis* and *C. pilulifera* as distinct from *C. yendoi* (Fig. 1), the appearances of the species are different: *C. yendoi* is compressed and appears flattened throughout, whereas *C. hakodatensis* and *C. pilulifera* maintain subterete to terete axes and pinnae throughout the thallus. However, the species have similar conceptacle shape and arrangement.

Corallina vancouveriensis: Yendo (1902a) described *Corallina vancouveriensis* on the basis of material collected in 1902 at the Minnesota Seaside Station (Botanical Beach) near Port Renfrew on Vancouver Island, British Columbia, Canada. Yendo (1902a) described two forms, *C. vancouveriensis* f. *typica*, now *C. vancouveriensis* f. *vancouveriensis* (Article 26.3 of the ICN; Turland et al. 2018) and *C. vancouveriensis* f. *densa*, although he noted, "Both forms approach one another and a sharp boundary is hard to draw." Although most of Yendo's geniculate coralline types are missing (Yoshida 1991), type specimens of both of these forms are in UC (*C. vancouveriensis* f. *vancouveriensis*, as *C.* f. *typica* UC 564666; *C.* f. *densa* UC 564667; Table S1). Partial *rbc*L sequences of these lectotype specimens were found to be identical; thus, we do not recognize different forms of *C. vancouveriensis*. Setchell and Gardner (1903: 364), in their treatment of the name *C. officinalis*, wrote, "After a careful and extensive consideration of the puzzling forms of *Corallina* of the western coast of North America, we have decided that the best arrangement for the present, at least is to place all the plants which have ecorniculate cystocarps under this species as forms." Thus, Setchell and Gardner (1903: 366) proposed the new name *Corallina officinalis* f. *multiramosa* (UC 1456186; Table S1) to include both forms of Yendo's *C. vancouveriensis*. The sequenced lectotype of *C. officinalis* f. *multiramosa* genetically groups with *C. vancouveriensis* and is, therefore, synonymous. *Corallina aculeata* Yendo also was described by Yendo (1902a), but from the NE Pacific, Botanical Beach, near Port Renfrew, British Columbia, Canada, the same type locality as *C. vancouveriensis* and described in the same publication. Yendo (1902b) wrote, "In other respects, it [*C. aculeata*] is closely allied to *Cor. vancouveriensis* f. *typica*, so that it might be taken as a local form caused by the mode of habit." On the basis of our own collections from Botanical Beach, including *Corallina* specimens from high intertidal pools that Yendo cited as the habitat of *C. aculeata*, as well as Yendo's observations, we consider *C. aculeata* a synonym of *C. vancouveriensis*. Setchell and Gardner (1903) expanded the distribution of *C. vancouveriensis* north to Uyak Bay, Kodiak Island, Alaska, and south to Whidbey Island, Washington, USA. Dawson (1953) expanded the distribution south to Baja California, Mexico; Norris et al. (2017) to the Gulf of California, Mexico; and O'Clair and Lindstrom (2000) to the Aleutian Islands. Dawson (1963) reported *C. vancouveriensis* from the Galápagos Archipelago (Ecuador) and Ramirez and Santelices (1991) from mainland Chile. Baba et al. (1988) noted that the species they called 'Corallina X' from Hokkaido, Japan, was morphologically similar to *C. vancouveriensis*, but, thus far, no specimen sequenced from Japan nor elsewhere in the northwest Pacific represents this species. Therefore, we affirm that *C. vancouveriensis* is a cold temperate species common in the NE Pacific from the Aleutians south-eastward to British

Columbia and it likely occurs continuously to its southern limit at Point Conception, California. Specimens collected south of this limit could be the highly cosmopolitan *C. berteroi* (Calderon et al. 2021), or a yet to be described species from the East Pacific (Hind and Saunders 2013). Additional UBC specimens from the central coast of Alaska (e.g., the most northern parts of the Gulf of Alaska) have been morphologically identified as *C. vancouveriensis* and are likely to be this species; however, these specimens have not yet been genetically assessed. All other records based on morphology and outside of this range need to be confirmed by DNA sequencing. It is unlikely that this species occurs anywhere in the South Pacific on the basis of our collections and sequences from Australia and Chile or published sequences from New Zealand (Twist et al. 2019).

Corallina parva: This species is sister to *Corallina vancouveriensis* and on average, differs in sequence identity among the three targeted loci by 1.84% (Table 1). For the *rbc*L locus, the sequence divergence is the same as that found for *Calliarthron cheilosporioides* and *C. tuberculosum* (~0.5%), also sister species in the NE Pacific (Gabrielson et al. 2011). *Corallina parva* is indistinguishable from *C. vancouveriensis* in the field, sharing the same habitat and similar morphology, although *C. parva* can be a more diminutive species. However, one cannot reliably differentiate juvenile *C. vancouveriensis* from *C. parva* without DNA sequencing. Like *C. vancouveriensis*, *C. parva* is a cold temperate species found only as far south as San Luis Obispo County, California, but with a more limited northern distribution in Haida Gwaii, Canada. We have no records from SE Alaska, but given its convergent morphology, rarity across its range, and small size, it may be present but overlooked at these northern latitudes. Like the relationship between *C. hakodatensis* and *C. pilulifera*, *C. parva* occurs sympatrically with its sister species *C. vancouveriensis*, and its status as a statistically supported species is based on genetic divergence due to speciation, not population differentiation.

Cryptic morphology of Corallina. Five *Corallina* species, *C. arbuscula*, *C. cretacea*, *C. frondescens*, *C. pilulifera*, and *C. tuberculosa*, were described by Postels and Ruprecht (1840) in their magnificently illustrated elephant folio. Alexander Postels, a naturalist and artist, illustrated the algal specimens, and Franz Josef Ruprecht, a botanist specializing in grasses, wrote the entire text for *Illustrationes Algarum* (Hughey et al. 2001). While the illustrations of the kelps and fleshy red algae were remarkably lifelike, those of the coralline species appeared more stylized, elegantly demonstrating the challenge of describing and distinguishing coralline algae. Our morphological assessment suggests that this is, in fact, the case for the taxa discussed here. The morphometrics of the two rarer species, *C. hakodatensis*

and *C. parva*, are largely within the range of their sister species, *C. pilulifera* and *C. vancouveriensis*, respectively, and therefore are seldom informative for species-level identification (Fig. 4). A specimen collected from Japan with more or less terete axes and at least narrowed to either *C. hakodatensis* or *C. pilulifera* may be preliminarily identified as *C. hakodatensis* if the specimen appears to have a large intergenicular length-to-width ratio (>1.5) and is over 3 cm in length. However, *C. yendoi* should also be carefully considered as a sympatric and morphologically cryptic species in the same geographic range as *C. hakodatensis* and *C. pilulifera*. Similarly, a specimen collected from the eastern Pacific that might be *C. parva* or *C. vancouveriensis* may be preliminarily identified as *C. vancouveriensis* if it is >3 cm long (Fig. 4). However, based on length alone, specimens from the eastern Pacific could also be *C. berteroi* (Calderon et al. 2021) or *C. chilensis* (Huber 2020), both with ranges overlapping that of *C. vancouveriensis*.

Phylogeny and molecular identification of Corallina *species.* The paucity of informative morphological characteristics emphasizes the importance of molecular markers for species identification for all coralline algae (Hind et al. 2014, 2015, 2018, Richards et al. 2017, Gabrielson et al. 2018, Pezzolesi et al. 2019, Twist et al. 2020, Calderon et al. 2021, Puckree-Padua et al. 2021). However, the phylogenetic signal documented here is somewhat opaque for *Corallina*. The lack of congruence among the three gene trees generated for this study reflects the disagreement in topology between their respective genomes and calls for additional work to be done to reconstruct a reliable phylogeny for *Corallina*. Fortunately, for species identifications, the affordable and accessible method of single-locus sequencing works well for the *Corallina* species presented here and elsewhere (i.e., Brodie et al. 2013, Hind et al. 2014, Williamson et al. 2015, Huber 2020, Calderon et al. 2021) and remains very useful for species delineation across crustose and geniculate coralline lineages.

CONCLUSIONS

Contrary to previously published distributions, our data indicate that *Corallina pilulifera* and *C. vancouveriensis* are restricted to the cold temperate North Pacific. Both species have sister taxa with overlapping distributions. Whether this distribution is due to sympatric speciation or overlapping distributions following separate speciation events is not clear and will require further work to clarify fully. Because these pairs of *Corallina* species are cryptic, DNA barcoding is the most reliable method for accurate identification. In-depth explorations of phylogeny and patterns of speciation using genomic data will increase our understanding of the ecology and evolution of *Corallina*.

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's web site:

Table S1. List of specimens for which data were generated for this study along with collection locality, habitat data, and GenBank accessions numbers.

Figure S1. Maximum likelihood phylogenetic reconstruction of the *rbc*L gene tree, including all historical and type specimens, and reference GenBank sequences that were identified as *Corallina arbuscula, C. pilulifera,* or *C. vancouveriensis.* Nodal values represent bootstrap support; only values >70 are shown. Tree scale represents the number of substitutions per site.

Figure S2. Maximum likelihood phylogenetic reconstruction of the COI gene tree, including all newly generated and reference GenBank sequences that were identified as *Corallina arbuscula, C. pilulifera,* or *C. vancouveriensis.* Nodal values represent bootstrap support; only values >70 are shown. Tree scale represents the number of substitutions per site.

Figure S3. Maximum likelihood phylogenetic reconstruction of the *psb*A gene tree, including newly generated and reference GenBank sequences that were identified as *Corallina arbuscula, C. pilulifera,* or *C. vancouveriensis.* Nodal values represent bootstrap support; only values >70 are shown. Tree scale represents the number of substitutions per site.

Figure S4. (A) *Corallina pilulifera* holotype specimen, LE (no accession number), Okhotsk Sea, Russia; (B) *C. arbuscula* lectotype specimen, S A2604, Unalaska Island, Alaska, USA; (C) Label and collection information for the lectotype specimen of *C. arbuscula*, S A2604, Unalaska Island, Alaska, USA.

Figure S5. (A) *Corallina vancouveriensis* f. *vancouveriensis* lectotype specimen, UC 564666, Botanical Beach, British Columbia, Canada; (B) *C. vancouveriensis* f. *densa* lectotype specimen, UC 564667, Port Renfrew, British Columbia, Canada, "a high tide form"; (C) *Corallina officinalis* f. *multiramosa* lectotype specimen, UC 1456186 Uyak Bay, Kodiak Island, Alaska, USA, epilithic, lowermost intertidal and on edges of tide pools higher in the intertidal.