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Morphometric and molecular analyses confirm two distinct species of *Calliarthron* (Corallinales, Rhodophyta), a genus endemic to the northeast Pacific

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Phylogenetic analyses of *rbc*L sequences demonstrate that *Calliarthron* as currently constituted is paraphyletic. *Calliarthron yessoense* and *C. latissimum* from the northwest Pacific belong in *Alatocladia* and are conspecific. After the transfer of *C. yessoense* and *C. latissimum*, *Calliarthron* is monophyletic, known only from the northeast Pacific and comprises two species, *C. cheilosporioides* and *C. tuberculosum*, which are distinct morphologically, biogeographically and by molecular sequence. Sequence data for the types of *C. regenerans* and *C. setchelliae* confirm that they are heterotypic synonyms of *C. tuberculosum*. Lectotypes are designated for *C. cheilosporioides*, *C. regenerans* and *C. setchelliae*. A morphometric analysis shows that three measured characters reliably distinguish *C. cheilosporioides* from *C. tuberculosum*. *Alatocladia* is monophyletic, known only from the northwest Pacific and comprises two species, *A. modesta* and *A. yessoensis*, which are distinct morphologically, biogeographically and by molecular sequence. *rbc*L sequence data of the type species of *Alatocladia*, *Bossiella*, *Calliarthron* and *Chiharaea* confidently differentiate these genera with strong bootstrap support.

KEY WORDS: *Alatocladia*, *Calliarthron*, Corallinales, northeast Pacific, *rbc*L, type material, discriminant analysis

INTRODUCTION

Recent studies have demonstrated that calcifying marine organisms likely will decline as anthropogenic carbon dioxide emissions accumulate in the atmosphere and cause increased temperatures, decreased ocean pH and significant changes to carbonate chemistry (e.g. Orr *et al.* 2005; Kuffner *et al.* 2008; Doney *et al.* 2009). In particular, the ecological implications of losing coralline algal biodiversity (Rhodophyta, Corallinales) may be widespread and significant (see Nelson 2009). To anticipate and detect species responses to climatic shifts, a re-evaluation of specific and generic concepts of Corallinales is both timely and essential.

Past molecular systematic investigations of Corallinales have focused on higher taxa, such as the monophyly of families (Broom *et al.* 2008), the number of subfamilies (Bailey & Chapman 1996; Harvey *et al.* 2003; Bailey *et al.* 2004) and intergeneric relationships (Bailey 1999; Kim *et al.* 2007). However, with the exception of Kim *et al.* (2007), these studies have not included generitype species for most genera in their analyses. In studies that have addressed questions at the species level, the generitype species either has not been included (Vidal *et al.* 2008) or has been studied only with morphological techniques (Walker *et al.* 2009). Thus, despite species-level resolution, generic concepts often remain uncertain.

For morphologically variable red algal species, including most coralline species, sequencing type material is the only reliable method to ensure the correct use of species names that are anchored to type specimens. This methodology was demonstrated by Hughey *et al.* (2001, 2002) who sequenced relatively short DNA segments (< 200 base pairs [bp]) of the nuclear encoded internal transcribed spacer 1 region (ITS 1) or the plastid-encoded RUBISCO spacer from numerous type specimens to clarify the use of species names in the Gigartinaceae (Gigartinales). Gabrielson (2008a, b) used short segments (< 200 bp) of the plastid-encoded, large subunit of the RUBISCO gene (*rbc*L) extracted from 18th, 19th and early 20th century type specimens to assure the correct application of their names and to clarify the distribution of species in the genus *Prionitis* (Halymeniales). Our approach to studying the taxonomy of coralline algae in the northeast Pacific is to sequence type specimens (or in some cases topotype specimens – see discussion for explanation of topotype specimens) of generitype species in order to clarify specific and generic concepts.

In this paper, we focus on the genus *Calliarthron* Manza, one of 12 currently recognized genera of subfamily Corallinoideae (Woelkerling *et al.* 2008), six of which are endemic to the north Pacific, *Alatocladia* (Yendo) H.W. Johansen, *Calliarthron*, *Chiharaea* H.W. Johansen, *Marginisporum* (Yendo) Ganesan, *Serraticardia* (Yendo) P.C. Silva and *Yamadaea* Segawa. *Calliarthron* shares with *Alatocladia*, uniquely among Corallinoideae, the character of having flexuous and interwoven medullary filaments but is differentiated from *Alatocladia* by conceptacle origin: marginal and lateral in the former and axial and marginal in the latter (Johansen 1969). We studied all of the species previously assigned to *Calliarthron*, including the currently recognized species *C. cheilosporioides* Manza, *C. tuberculo-*

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Table 1. List of specimens sequenced, including herbarium number, reason for their inclusion, collection data and GenBank accession number. Field-collected indicates a specimen placed in silica gel before being sequenced; herbarium indicates an air-dried specimen that was sequenced. Taxa are listed in alphabetical order; original name of specimen, if different from current name, is listed under reason for inclusion; specimens of *Calliarthron cheilosporioides* and *C. tuberculosum* are listed north to south.

Species	Herbarium specimen number	Reason for inclusion	Collection data	GenBank accession number
Alatocladia modesta	NCU 590276	field-collected phylogeny	Japan, Chiba Prefecture, Katsuura, Beach fronting Coastal Branch of Natural History Museum & Institute, 5 Aug 2009, *leg*. S.C. Lindstrom	HQ322274
Alatocladia modesta	UC 90826	topotype of *Cheilosporum anceps* var. *modesta* herbarium, Fig. 11	Japan, Hakodate, May 1903, ex-Herb. K. Yendo	HQ322275
Alatocladia yessoensis	UC 418147	topotype of *Cheilosporum latissimum*, Fig. 12 herbarium	Japan, Wada Province, Boshyu, 22. Aug 1928, sent by K. Yendo	HQ322276
Alatocladia yessoensis	NCU 588184	field-collected phylogeny	Japan, Miyako Prefecture, Todogasaki, 13 Jul 1994, *leg*. M.H. Hommersand (as *Calliarthron yessoense*)	HQ322277
Alatocladia yessoensis	UC 90783	topotype of *Cheilosporum yessoense*, Fig. 13 herbarium	Japan, Hakodate, May 1903, ex.-Herb. K. Yendo	HQ322278
Bossiella orbigniana	SGO 155070	herbarium phylogeny	Chile, Valpariso, Quintay, Playa Caleta, 16 Jun 2007, 5.5-m depth, *leg*. D. Letelier & R. García-Huidobro	HQ322279
Bossiella plumosa	UC1966627	field-collected topotype phylogeny	USA, California, San Mateo Co., Moss Beach, 16 Nov 2009, epilithic lower mid-intertidal, *leg*. K.A. Miller & P.T. Martone	HQ322280
Calliarthron cheilosporioides	UC 545724	lectotype, Fig. 3 morphometrics	USA, California, Monterey Co., Pacific Grove, 13 May 1933, *leg*. A.V. Manza	HQ322281
Calliarthron cheilosporioides	UBC A87283	topotype field-collected phylogeny/morphometrics	USA, California, Monterey Co., Pacific Grove, Hopkins Marine Station, 15 Mar 2007, epilithic, very low intertidal, *leg*. P.T. Martone	HQ322282
Calliarthron cheilosporioides	UBC A87303	topotype field-collected morphometrics	USA, California, Monterey Co., Pacific Grove, Hopkins Marine Station, 24 Feb 2004, epilithic, very low intertidal, *leg*. P.T. Martone	HQ322283
Calliarthron cheilosporioides	UBC A87286	topotype field-collected morphometrics	USA, California, Monterey Co., Pacific Grove, Hopkins Marine Station, 15 Mar 2007, epilithic, mid-intertidal tidepool, *leg*. P.T. Martone	HQ322284
Calliarthron cheilosporioides	UBC A87287	topotype field-collected morphometrics	USA, California, Monterey Co., Pacific Grove, Hopkins Marine Station, 8 Jan 2008, epilithic, low intertidal, *leg*. P.T. Martone	HQ322285
Calliarthron cheilosporioides	UBC A87289	topotype field-collected morphometrics	USA, California, Monterey Co., Pacific Grove, Hopkins Marine Station, 20 Jan 2008, epilithic, low intertidal, *leg*. P.T. Martone	HQ322286
Calliarthron cheilosporioides	UBC A87291	topotype field-collected morphometrics	USA, California, Monterey Co., Pacific Grove, Hopkins Marine Station, 20 Jan 2008, epilithic, low intertidal, *leg*. P.T. Martone	HQ322287
Calliarthron cheilosporioides	UBC A87297	topotype field-collected morphometrics	USA, California, Monterey Co., Pacific Grove, Hopkins Marine Station, 1 Jun 2008, epilithic, subtidal −7.62 m, *leg*. M. Boller	HQ322288
Calliarthron cheilosporioides	UBC A87298	topotype field-collected morphometrics	USA, California, Monterey Co., Pacific Grove, Hopkins Marine Station, 1 Jun 2008, epilithic, subtidal −7.62 m, *leg*. M. Boller	HQ322289
Calliarthron cheilosporioides	UBC A87299	topotype field-collected morphometrics	USA, California, Monterey Co., Pacific Grove, Hopkins Marine Station, 24 Feb 2004, epilithic, low intertidal, *leg*. P.T. Martone	HQ322290
Calliarthron cheilosporioides	UBC A87309	topotype field-collected morphometrics	USA, California, Monterey Co., Pacific Grove, Hopkins Marine Station, 20 Feb 2004, epilithic, very low intertidal, *leg*. P.T. Martone	HQ322291

Table 1. Continued

Species	Herbarium specimen number	Reason for inclusion	Collection data	GenBank accession number
Calliarthron cheilosporioides	UBC A87312	topotype field-collected morphometrics	USA, California, Monterey Co., Pacific Grove, Hopkins Marine Station, 25 Feb 2004, epilithic, very low intertidal, *leg.* P.T. Martone	HQ322292
Calliarthron cheilosporioides	UC 545721	syntype morphometrics	USA, California, Monterey Co., Pebble Beach, 12 May 1933, *leg.* A.V. Manza	HQ322293
Calliarthron cheilosporioides	NCU 585611	field-collected morphometrics	USA, California, Los Angeles Co., Catalina I., Parson's West, 3 Dec 2006, epilithic 19-m depth, *leg.* K. Benes	HQ322294
Calliarthron cheilosporioides	NCU 591312	field-collected morphometrics	USA, California, Los Angeles Co., Catalina I., Johnson's Pinnacles, 3 Dec 2006, epilithic 25-m depth, *leg.* K. Benes	HQ322295
Calliarthron cheilosporioides	UC 1838086	herbarium morphometrics	Mexico, Baja California Norte, Punta Baja, 2 Jan 1950, no habitat data, *leg.* E.Y. Dawson	HQ322296
Calliarthron cheilosporioides	UC 940186	herbarium morphometrics	Mexico, Isla Cedros, Punta Norte, 30 Oct 1951, no habitat data, *leg.* E.Y. Dawson	HQ322297
Calliarthron cheilosporioides	UC 1838097	herbarium morphometrics	Mexico, Isla Cedros, South Bay, 10 Mar 1934, dredged 18–27 m, *leg.* W. Schmitt	HQ322298
Calliarthron tuberculosum	NCU 588186	field-collected phylogeny	Canada, British Columbia, Vancouver Island, Port Renfrew, 'Botany Beach', 9 Aug 2007, epilithic low intertidal tidepool, *leg.* P.W. Gabrielson	HQ322299
Calliarthron tuberculosum	UC 545975	lectotype of *C. regenerans*, Fig. 5 morphometrics	USA, California, San Mateo Co., Moss Beach, 21 May 1932, *leg.* A.V. Manza	HQ322300
Calliarthron tuberculosum	UC 545737	isolectotype of *C. regenerans* morphometrics	USA, California, San Mateo Co., Moss Beach, 21 May 1932, *leg.* A.V. Manza	HQ322301
Calliarthron tuberculosum	UC 545738	isolectotype of *C. regenerans* morphometrics	USA, California, San Mateo Co., Moss Beach, 21 May 1932, *leg.* A.V. Manza	HQ322302
Calliarthron tuberculosum	UC 545733	lectotype of *C. setchelliae*, Fig. 4 morphometrics	USA, California, San Mateo Co., Moss Beach, 5 May 1931, *leg.* A.V. Manza	HQ322303
Calliarthron tuberculosum	UC 548904	syntype of *C. setchelliae* morphometrics	USA, California, San Mateo Co., Moss Beach, 2 Jan 1935, *leg.* A.V. Manza	HQ322304
Calliarthron tuberculosum	UC 696524	herbarium morphometrics	USA, California, San Mateo Co., Moss Beach, 27 Mar 1942, no habitat data, *leg.* M. Doty	HQ322305
Calliarthron tuberculosum	UBC A87304	field-collected morphometrics	USA, California, Monterey Co., Pacific Grove, Hopkins Marine Station, 24 Feb 2003, epilithic, low intertidal, *leg.* P.T. Martone	HQ322306
Calliarthron tuberculosum	UBC A87311	field-collected morphometrics	USA, California, Monterey Co., Pacific Grove, Hopkins Marine Station, 25 Nov 2003, epilithic, low intertidal, *leg.* P.T. Martone	HQ322307
Calliarthron tuberculosum	UBC A87307	field-collected morphometrics	USA, California, Monterey Co., Pacific Grove, Hopkins Marine Station, 26 Feb 2004, epilithic, low intertidal, *leg.* P.T. Martone	HQ322308
Calliarthron tuberculosum	UBC A87308	field-collected morphometrics	USA, California, Monterey Co., Pacific Grove, Hopkins Marine Station, 26 Feb 2004, epilithic, low intertidal, *leg.* P.T. Martone	HQ322309
Calliarthron tuberculosum	UBC A87306	field-collected morphometrics	USA, California, Monterey Co., Pacific Grove, Hopkins Marine Station, 26 Feb 2004, epilithic, low intertidal, *leg.* P.T. Martone	HQ322310
Calliarthron tuberculosum	UBC A87314	field-collected morphometrics	USA, California, Monterey Co., Pacific Grove, Hopkins Marine Station, 25 Jan 2005, epilithic, mid-intertidal, *leg.* P.T. Martone	HQ322311
Calliarthron tuberculosum	UBC A87305	field-collected morphometrics	USA, California, Monterey Co., Pacific Grove, Hopkins Marine Station, 25 Jan 2005, epilithic, mid-intertidal, *leg.* P.T. Martone	HQ322312

Table 1. Continued

Species	Herbarium specimen number	Reason for inclusion	Collection data	GenBank accession number
Calliarthron tuberculosum	UBC A87310	field-collected morphometrics	USA, California, Monterey Co., Pacific Grove, Hopkins Marine Station, 25 Jan 2005, epilithic, mid-intertidal, *leg.* P.T. Martone	HQ322313
Calliarthron tuberculosum	UBC A87302	field-collected morphometrics	USA, California, Monterey Co., Pacific Grove, Hopkins Marine Station, 26 Jan 2005, epilithic, mid-intertidal, *leg.* P.T. Martone	HQ322314
Calliarthron tuberculosum	UBC A87284	field-collected morphometrics	USA, California, Monterey Co., Pacific Grove, Hopkins Marine Station, 15 Mar 2007, epilithic, low intertidal, *leg.* P.T. Martone	HQ322315
Calliarthron tuberculosum	UBC A87285	field-collected morphometrics	USA, California, Monterey Co., Pacific Grove, Hopkins Marine Station, 15 Mar 2007, epilithic, mid-intertidal tidepool, *leg.* P.T. Martone	HQ322316
Calliarthron tuberculosum	UBC A87288	field-collected morphometrics	USA, California, Monterey Co., Pacific Grove, Hopkins Marine Station, 15 Mar 2007, epilithic, upper low intertidal, *leg.* P.T. Martone	HQ322317
Calliarthron tuberculosum	UBC A87290	field-collected morphometrics	USA, California, Monterey Co., Pacific Grove, Hopkins Marine Station, 20 Jan 2008, epilithic, low intertidal, *leg.* P.T. Martone	HQ322318
Calliarthron tuberculosum	UBC A87292	field-collected morphometrics	USA, California, Monterey Co., Pacific Grove, Hopkins Marine Station, 20 Jan 2008, epilithic, low intertidal, *leg.* P.T. Martone	HQ322319
Calliarthron tuberculosum	UBC A87293	field-collected morphometrics	USA, California, Monterey Co., Pacific Grove, Hopkins Marine Station, 20 Jan 2008, epilithic, low intertidal, *leg.* P.T. Martone	HQ322320
Calliarthron tuberculosum	UBC A87294	field-collected morphometrics	USA, California, Monterey Co., Pacific Grove, Hopkins Marine Station, 20 Jan 2008, epilithic, low intertidal, *leg.* P.T. Martone	HQ322321
Calliarthron tuberculosum	UBC A87295	field-collected morphometrics	USA, California, Monterey Co., Pacific Grove, Hopkins Marine Station, 20 Jan 2008, epilithic, low intertidal, *leg.* P.T. Martone	HQ322322
Calliarthron tuberculosum	UBC A87296	field-collected morphometrics	USA, California, Monterey Co., Pacific Grove, Hopkins Marine Station, 7 Feb 2008, epilithic, low intertidal, *leg.* P.T. Martone	HQ322323
Calliarthron tuberculosum	UC 491815	herbarium morphometrics	USA, California, San Luis Obispo Co., Cambria, 12 Oct 1929, no habitat data, *leg.* H.L. Mason	HQ322324
Calliarthron tuberculosum	NCU 590609	field-collected phylogeny	USA, Los Angeles Co., White's Point, 11 Apr 2005, tidepool, *leg.* P.W. Gabrielson	HQ322325
Calliarthron tuberculosum	UC 438841	herbarium morphometrics	USA, Los Angeles Co., White's Point, 1 Jan 1908, tidepool, *leg.* N.L. Gardner #1866	HQ322326
Calliarthron tuberculosum	UC 1838180	herbarium morphometrics	USA, Orange Co., Laguna, 8 Nov 1942, no habitat data, *leg.* N. Cooper (as *C. regenerans*)	HQ322327
Calliarthron tuberculosum	UC 392581	herbarium morphometrics	USA, Orange Co., 7 miles south of Laguna, Salt Creek Branch, 29 Nov 1927, no habitat data, *leg.* F.M. Reed #52	HQ322328
Calliarthron tuberculosum	UC 395465	herbarium morphometrics	USA, Orange Co., 2 miles south of Balboa, Mar.1912, upper intertidal tidepool, *leg.* N.L. Gardner #2492 (as *C. regenerans*)	HQ322329
Calliarthron tuberculosum	UC 1885083	herbarium morphometrics	USA, California, San Diego Co., New Hope Rock, 5 Sep 1969, no habitat data, *leg.* J. Stewart	HQ322330
Calliarthron tuberculosum	UC 1574414	herbarium morphometrics	Mexico, Islas Coronados, north end of South Island 5 Aug 1986, epilithic shallow subtidal with coarse sand, *leg.* K.A. Miller	HQ322331

Table 1. Continued

Species	Herbarium specimen number	Reason for inclusion	Collection data	GenBank accession number
Chiharaea bodegensis	UC 1944755	topotype field-collected phylogeny	USA, California, Marin Co., Bodega Head, Outlet Cove, 5 Jul 2008, low intertidal boulder, *leg.* K.A. Miller	HQ322332
Corallina pinnatifolia	UBC A88590	topotype field-collected phylogeny	USA, California, Laguna Beach, Corona del Mar, 10 Oct 2007, mid-intertidal tidepool, *leg.* S. Whitaker	HQ322333
Corallina vancouveriensis	NCU 588197	topotype field-collected phylogeny	Canda, British Columbia, Vancouver Island, Port Renfrew, 'Botany Beach', 10 Aug 2007, epilithic mid-intertidal, *leg.* P.W. Gabrielson	HQ322334
Lithophyllum impressum	NCU 585607	topotype field-collected phylogeny	Canda, British Columbia, Vancouver Island, Port Renfrew, 'Botany Beach', 9 Aug 2007, mid-intertidal tidepool, *leg.* P.W. Gabrielson	HQ322335
Lithothrix aspergillum	UBC A68043	herbarium phylogeny	Canada, British Columbia, Strait of Georgia, Bath Island, 19 Apr 1973, *leg.* S.C. Lindstrom	HQ322336
Mesophyllum vancouveriense	NCU 588185	topotype field-collected phylogeny	Canada, British Columbia, Vancouver Island, Port Renfrew, 'Botany Beach', 10 Aug 2007, epilithic low intertidal, *leg.* P.W. Gabrielson	HQ322337
Serraticardia macmillanii	NCU 588188	topotype field-collected phylogeny	Canada, British Columbia, Vancouver Island, Port Renfrew, 'Botany Beach', 9 Aug 2007, epilithic low intertidal, *leg.* P.W. Gabrielson	HQ322338

sum (Postels & Ruprecht) E.Y. Dawson, *C. latissimum* (Yendo) Manza and *C. yessoense* (Yendo) Manza. To explore morphological variability and biogeographic range limits of the two northeast Pacific species, *C. cheilosporioides* and *C. tuberculosum*, we sequenced *rbc*L from historic and recent collections. We generate a set of morphological characters useful for field identification by sequencing a wide range of morphologically variable specimens and statistically evaluating which morphological features gave results congruent with the molecular data.

MATERIAL AND METHODS

Specimens

Specimens were examined from the following herbaria: University of British Columbia (UBC), University of California at Berkeley (UC), Trinity College, University of Dublin (TCD), Museo National de Historía Natural, Santiago (SGO), Muséum National d'Histoire Naturelle (PC) and University of North Carolina at Chapel Hill (NCU). Voucher specimens were deposited in UBC, UC or NCU. Herbarium abbreviations follow Thiers (2010).

Molecular analysis

Specimens used in the molecular analysis are listed in Table 1. Prior to extraction, silica gel-dried or herbarium material was examined under high magnification with a dissecting microscope to check for red algal epiphytes. One to 20 intergenicula (depending on the size of the intergenicula) from each specimen of articulated coralline or fragments about 3 mm^3 total volume from crustose corallines were placed in heavy paper packets and crushed and ground to a fine powder before being extracted following the protocol in Hughey *et al.* (2001). The coding region of *rbc*L was amplified using primer combinations F-57 and R-753, F-753 and R-rbcS, and F-57 and R-rbcS (Freshwater & Rueness 1994). The primer pair F1152Cor/R1308Cor was designed from aligned rbcL sequences that we have deposited in GenBank. F1152Cor 5′-GTATACATTGTGGACAAATGC-3′ and R1308Cor 5′-TCCAGCACTAAAACATCGTC-3′ covered conserved regions of the *rbc*L gene and amplified a 135-bp variable region (Table 2). Amplification and sequencing protocols were those of Hughey *et al.* (2001). Sequences were obtained from an ABI 3100 Genetic Analyzer (DNA Analysis Core Facility, Center for Marine Sciences, University of North Carolina, Wilmington) and were manually aligned and compiled using Sequencher (Gene Codes Corp., Ann Arbor, MI, USA), and Sequence Alignment Editor available at http://tree.bio.ed.ac.uk/software/seal/.

Thirteen *rbc*L sequences from the family Corallinaceae were analysed with *Mesophyllum vancouveriense* (Foslie) Steneck & R.T. Paine from the sister family Hapalidaceae (Broom *et al.* 2008) serving as the outgroup (Table 1, Fig. 1). The included taxa were selected to give phylogenetic context for this first published *rbc*L analysis of Corallinales, and each species with a northeast Pacific type locality, except those in *Calliarthron*, will be the subject of a subsequent study. Models of sequence evolution and characteristics of the data set were obtained using Modeltest v. 3.6 (Posada & Crandall 1998) and PAUP* v. 4.0β10 (Swofford 2002), and the phylogenetic analysis was performed using PAUP*.

A maximum likelihood (ML) analysis was done using a GTR + I + G model of evolution and the following

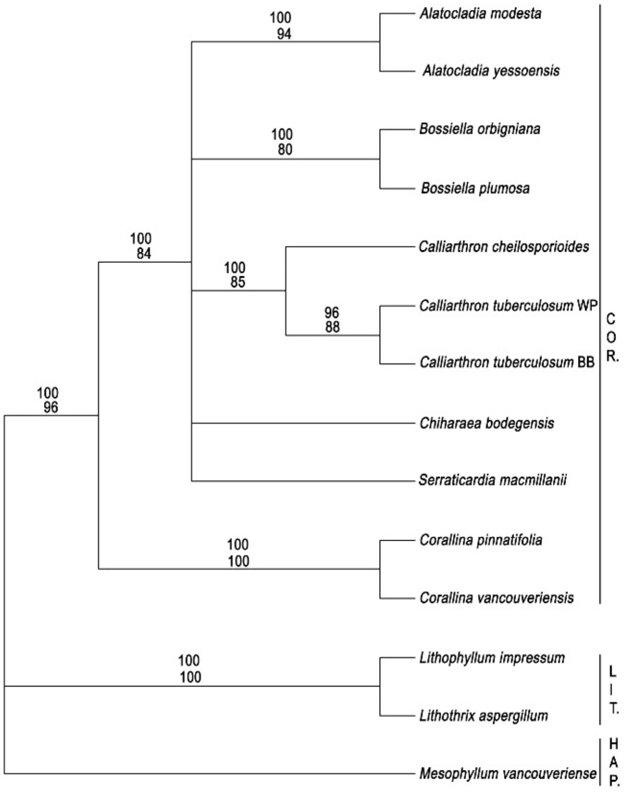


Fig. 1. Consensus maximum likelihood tree inferred from *rbc*L sequences. Upper numbers at each node are bootstrap values for parsimony analysis; lower numbers are for maximum likelihood analysis. Cor = subfamily Corallinoideae; Lit = subfamily Lithophylloideae; Hap = family Hapalidaceae; BB = Botany Beach, Vancouver Island, British Columbia, Canada; WP = White's Point, Los Angeles County, California, USA.

parameters obtained from the Modeltest program: base frequencies (A = 0.3342, C = 0.1453, G = 0.2074, T = 0.3231), Nst = 6, rate matrix = (1.8575, 5.9039, 2.9369, 0. 2675, 19.2425, 1.0000), gamma distribution shape (0.5531) and proportion of invariable sites (0.4375). Five separate searches with random sequence additions using the tree bisection–reconnection (TBR) branch swapping algorithm were completed. The ML analysis had 1000 replications of bootstrap resampling. Parsimony analysis (MP) was a heuristic search of 1000 random sequence additions with TBR, MULTREES and STEEPEST DESCENT branch swapping options used. Parsimony bootstrap analyses had 1000 replications of simple sequence additions.

Morphometric analysis

To explore the range of morphological variation in *Calliarthron* species and to facilitate species identification, 49 *Calliarthron* fronds were collected from southern to northern California, representing a broad range of morphologies and habitats. Most specimens (61%) were collected from the Monterey Peninsula, where the geographic distributions of *C. cheilosporioides* and *C. tuberculosum* were thought to overlap.

Two intergenicula were measured from each frond: the fifth intergeniculum counting up from the base (the 'basal intergeniculum') and the fifth intergeniculum counting back from the apex of a randomly selected branch ('apical intergeniculum'). Given that intergenicular shape can vary widely and unpredictably within a single frond, we did not measure extremes (e.g. the widest, thickest or narrowest intergeniculum). Segments were severed at genicula and held upright under a dissecting microscope for cross-sectional measurements (± 0.01 mm). Major and minor diameters were measured for basal and apical genicula and intergenicula (Fig. 2). In addition to diameter measurements, two composite variables were also calculated: 'intergenicular wing expansion' was calculated by dividing the major diameter of apical intergenicula by the major diameter of basal intergenicula, quantifying the broadening of intergenicular wings from frond base to tip, and 'apical intergeniculum out-of-round' was calculated by dividing the major diameter of apical intergenicula by the minor diameter of apical intergenicula, quantifying the cross-sectional shape of apical intergenicula (see Fig. 2).

Molecular analysis classified the 49 *Calliarthron* fronds into two species, *C. cheilosporioides* ($N = 18$) and *C. tuberculosum* ($N = 31$). Average diameter measurements and composite variables were calculated for each species and compared using a t-test. Morphometric data (i.e. diameters and composite variables) were then entered stepwise into a discriminant analysis (DA) to assign specimens to species groups based on morphological similarity. Morphometric data were log-transformed when necessary to ensure normal distributions. All statistics were computed using JMP 7 (SAS Institute, Cary, NC, USA).

RESULTS

Molecular results

The analysed alignment of 1401 bp showed that 412 bp were variable (29.4%), and 283 bp were parsimony informative. The overall relationships of the taxa were similar in both the ML and MP analyses, and only the maximum-likelihood topology with bootstrap results from both methods is presented (Fig. 1).

The *rbc*L sequence results show that *Calliarthron*, as currently constituted, is paraphyletic, with the northwest Pacific species belonging in *Alatocladia*. *Calliarthron* and *Alatocladia* are distinct genera, each with strong bootstrap support and each differentiated by morphological characters and biogeography. Two species of *Calliarthron*, the generitype *C. cheilosporioides* and *C. tuberculosum*, are differentiated based on molecular sequencing, morphometrics and biogeography. Two species of *Alatocladia* are recognized based on *rbc*L sequence differences, morphology and biogeography.

Generic and subfamilial relationships

Our *rbc*L sequence data resolved subfamily Lithophylloideae as distinct from Corallinoideae and because generitype species were included, the genera *Alatocladia*, *Bossiella* P.C. Silva, *Calliarthron* and *Chiharaea* were confidently differentiated with strong bootstrap support (Fig. 1). The two

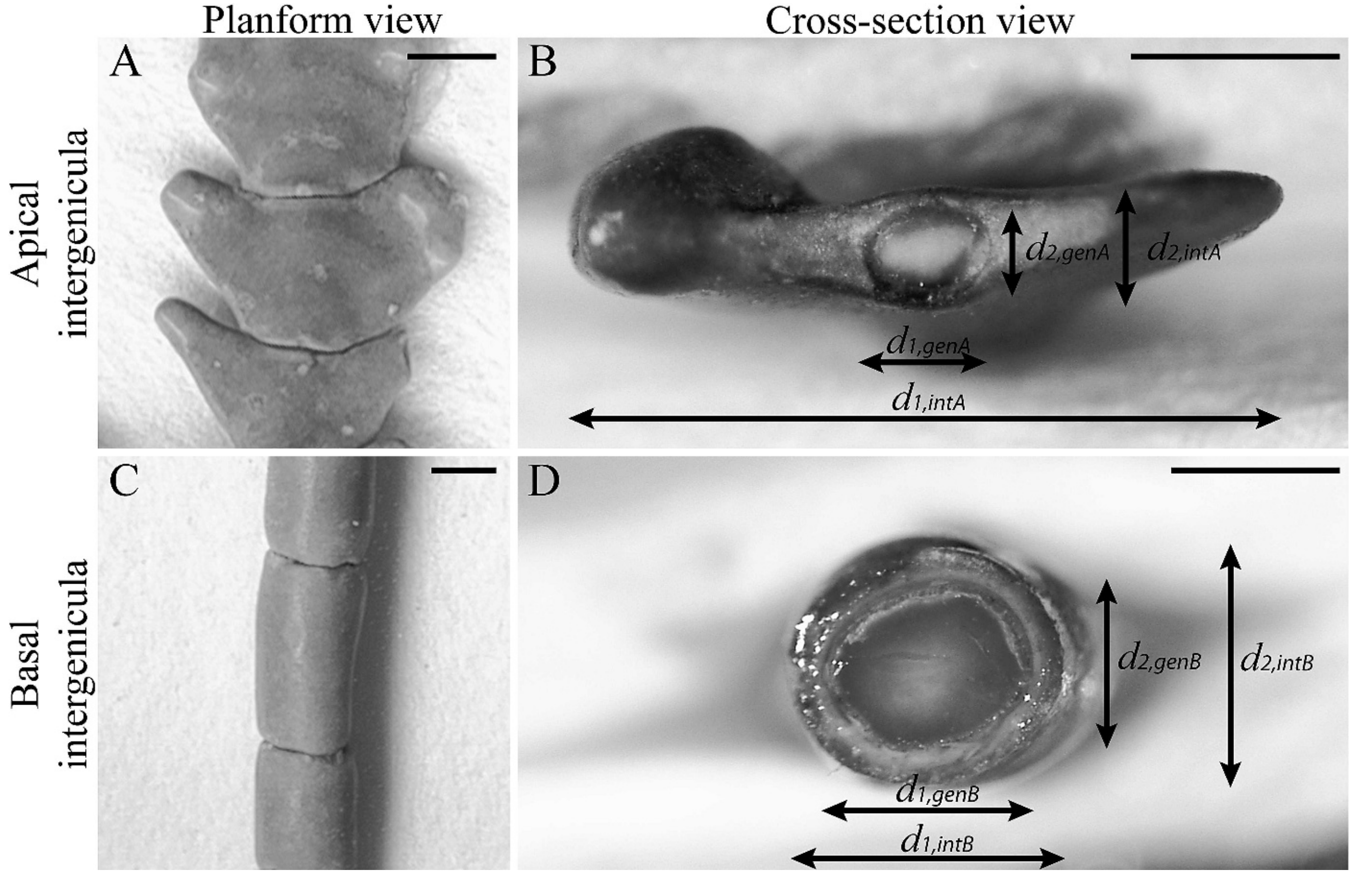


Fig. 2. Planform and cross-sectional views of *Calliarthron* segments. Arrows represent diameters of genicula and intergenicula measured for morphometric analysis. Diameter (*d*) subscripts indicate major (1) or minor (2) axis of apical (A) or basal (B) genicula (gen) or intergenicula (int). A–D = UBC A87306. Scale bars = 1 mm.

geographically separated *Bossiella* species, *B. plumosa* and *B. orbigniana*, had an *rbc*L sequence divergence of only 1.2% (17 bp); whereas, the intergeneric sequence divergence between these two *Bossiella* species and the two northeast Pacific species of *Calliarthron* was over 4% (minimum 58 bp). The northwest Pacific species *Calliarthron yessoense* was more closely related to *Alatocladia modesta* (Yendo) Johansen than to either *Calliarthron* species. *Serraticardia macmillanii* (Yendo) P.C. Silva was distinct from the other genera, but its relationship to the generitype species *S. maxima* (Yendo) P.C. Silva is unknown.

Calliarthron cheilosporioides

The 1401 bp *rbc*L sequence obtained from topotype material of the generitype species (UBC A87283, Table 1) distinguished *Calliarthron* from other coralline genera (Fig. 1). An identical sequence was seen from a specimen from Catalina Island, California (NCU 585611, Table 1). The variable 1173–1307 bp region of *rbc*L from topotype material was identical to that of type material (Table 2). Manza (1937a) collected type material of *C. cheilosporioides* in two different localities: Pebble Beach (12 May 1933) and Pacific Grove (Monterey County), California (13 May 1933). Abbott & Hollenberg (1976: 416) cited Pacific Grove as the type locality. We sequenced the variable 1173–1307 bp region of *rbc*L from both the Pacific Grove material (UC 545724; tetrasporic) and the Pebble Beach material (UC 545721; male), and they are identical (Table 2). In accordance with Art. 9.21 of the International Code of Botanical Nomenclature (ICBN), we herein designate UC 545724 (Fig. 3) as the lectotype of *C. cheilosporioides*.

Calliarthron tuberculosum

We obtained three 1401-bp *rbc*L sequences of *C. tuberculosum* from field-collected material: one from the northern part of its range (Vancouver Island, British Columbia, Canada, NCU 588186), one from Pacific Grove, Monterey County, California (UBC A87284), and one from White's Point, Los Angeles County, California (NCU 590609, Table 1). The ML and MP analyses indicated that this species belongs in *Calliarthron* and is sister to *C. cheilosporioides* (Fig. 1). The sequences were identical except for the occurrence of a single nucleotide polymorphism at position 1233. We also obtained numerous short sequences from the variable region (1173–1307) of *rbc*L (Table 1) showing this same polymorphism, which was also present among type specimens of *C. regenerans* collected at the same time from a single locality (Table 2). This polymorphism does not correlate with geographic distribution or with reproductive

Table 2. Comparison of rbcL sites 1173 to 1307 for topotype material of *Alatocladia modesta* [as *Cheilosporum anceps var. modesta* (Fig. 11), *A. yessoensis* [as *Cheilosporum yessoense* (Fig. 13) and *Cheilosporum latissimum* (Fig. 12)] type material of *Calliarthron cheilosporioides* (Fig. 3) and synonyms of *C. tuberculosum*, *C. regenerans* (Fig. 5) , and *C. setchelliae* (Fig. 4). All specimens cited in Table 1. Only those sites where base pair variation occurs are shown.

	1176	1188	1189	1191	1197	1203	1221	1233	1245	1257	1263	1272
Cheilosporum anceps var. *modesta*	G	C	C	A	C	A	C	A	T	A	T	C
Cheilosporum yessoense	G	T	T	A	C	A	C	A	T	A	G	C
Cheilosporum latissimum	G	T	T	A	C	A	C	A	T	A	G	C
Calliarthron cheilosporioides	A	C	T	G	T	T	T	A	C	C	A	T
Calliarthron regenerans	A	C	T	G	T	T	C	A/G	T	C	A	T
Calliarthron setchelliae	A	C	T	G	T	T	C	A	T	C	A	T

phase. *Calliarthron tuberculosum* consistently differed from *C. cheilosporioides* by 7 bp (0.57% sequence divergence) at the same positions in *rbc*L. Two of these positions were in the short, variable region (1173–1307 bp) (Table 2).

We obtained short sequences from the variable region (1173–1307 bp) of *rbc*L from type material of two synonyms of *Calliarthron tuberculosum*, *C. setchelliae* Manza and *C. regenerans* Manza, both collected by A.V. Manza from Moss Beach, San Mateo County, California. Type material of *C. setchelliae*, named for Clara Setchell, wife of W.A. Setchell, was collected on two different dates, tetrasporic material (UC 545733) on 5 May 1931 and male material (UC 548904) on 2 January 1935. These sequences were identical to each other and to other field-collected and herbarium material identified as *C. tuberculosum* (Tables 1, 2). Because these specimens were collected on different dates, they cannot together be considered the holotype of *C. setchelliae* (Art. 8.2 of the ICBN, McNeill *et al.* 2006), and therefore we herein designate the earlier collected tetrasporic specimen (UC 545733, Fig. 4) as the lectotype of *C. setchelliae*. Original material of *C. regenerans* consists of tetrasporic (UC 545737), female (UC 545738) and male (UC 545975, Fig. 4, incorrectly cited in Manza 1937b as UC 545775) specimens all collected on the same date, 21 May 1932. Their sequences were identical to each other except for the single nucleotide polymorphism at position 1233, identical to sequences obtained from field-collected material identified as *C. tuberculosum* and distinct from sequences obtained from *C. cheilosporioides* type material (Tables 1, 2). Because Manza did not label these three preparations as being part of a single specimen, they are regarded as duplicates (Art. 8.3 of the ICBN, McNeill *et al.* 2006) and must be treated as syntypes. Herein, we designate the male specimen (UC 545975, Fig. 5) as the lectotype of *C. regenerans*.

We were unable to obtain a sequence from an intergeniculum of the type specimen of *Amphiroa vertebralis* Decaisne (Fig. 6), and we were unable to obtain type material of *Corallina tuberculosa* Postels & Ruprecht and *Amphiroa epiphlegnoides* J. Agardh ex Harvey (Figs 7–10).

Alatocladia modesta

Alatocladia was resolved as a distinct genus based on the 1401 bp *rbc*L sequence of the generitype species (Fig. 1). The identity of this specimen from Katsuura, Chiba Prefecture, Japan, was confirmed by comparing its sequence to a partial *rbc*L sequence in the variable 1173–1307 bp region of a topotype specimen collected, identified and sent by Yendo to UC (Tables 1, 2, Fig. 11).

Calliarthron yessoense

The 1401-bp *rbc*L sequence obtained from recently collected material identified as *Calliarthron yessoense* from Todogasaki, Miyako Prefecture, Japan, was sister to *Alatocladia modesta* and not *Calliarthron cheilosporioides* (Fig. 1). The identity of this specimen was confirmed by comparing its sequence and morphology to that of a topotype specimen from Hakodate, Japan, collected, identified and sent by Yendo to UC (Table 2, Fig. 13). The partial *rbc*L sequence (178 bp) covering the variable 1173–1307 bp region was identical in the recent collection and in the historic topotype specimen. On this basis, we are transferring *Calliarthron yessoense* to *Alatocladia*. Also identical was the 135-bp variable region of *rbc*L from a specimen of *Cheilosporum latissimum* collected, identified and sent by Yendo to UC (Table 1, Fig. 12). Thus, *Cheilosporum latissimum* and *C. yessoense* are the same species.

Morphometric analysis

Calliarthron cheilosporioides and *C. tuberculosum* differed significantly in several intergenicular and genicular measured characters (See Fig. 2 and Table 3). Apical intergenicula of *C. cheilosporioides* were significantly broader and thinner than those *of C. tuberculosum* ($d_{1,\mathrm{int\ A}}$, $P < 0.05$; $d_{2,\mathrm{int\ A}}$, $P < 0.001$). Basal intergenicula of *C. cheilosporioides* were significantly narrower than those of *C. tuberculosum* ($d_{1,\mathrm{int\ B}}$, $P < 0.001$). Thus, there was a significantly greater wing expansion in *C. cheilosporioides* ($d_{1,\mathrm{int\ A}}/d_{1,\mathrm{int\ B}}$, $P < 0.001$); from base to tip, intergenicula of *C. cheilosporioides* more than doubled in width; whereas, those of *C. tuberculosum* widened only slightly. On average, apical intergenicula of *C. cheilosporioides* were nearly six times wider than they were thick; whereas, those of *C. tuberculosum* were only three times wider than they were thick ($d_{1,\mathrm{int\ A}}/d_{2,\mathrm{int\ A}}$, $P < 0.001$).

Intergenicular wing expansion was the single most informative factor in the DA, correctly classifying 72% of the *C. cheilosporioides* specimens and 81% of the *C. tuberculosum* specimens (Wilks' lambda = 0.462; Table 4). Adding a second factor, 'minor diameter of apical intergeniculum', to the DA improved species classifications. Combined, these two factors were sufficient to correctly

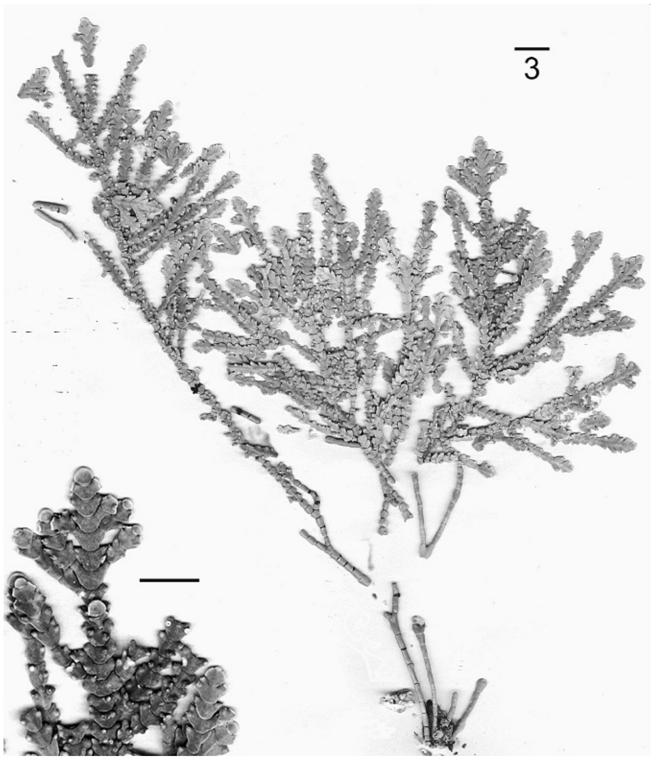
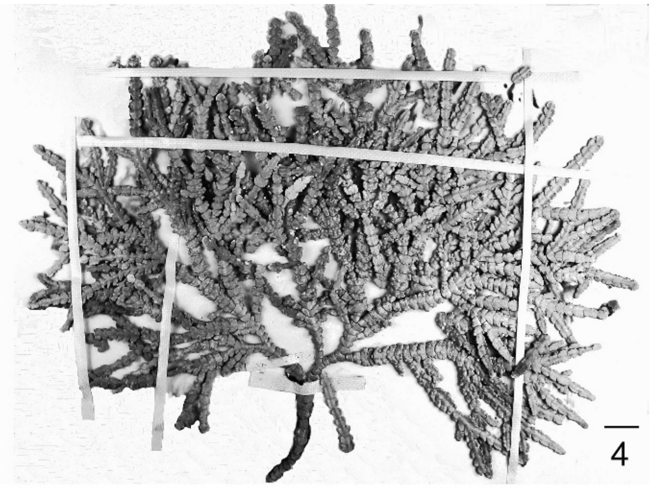
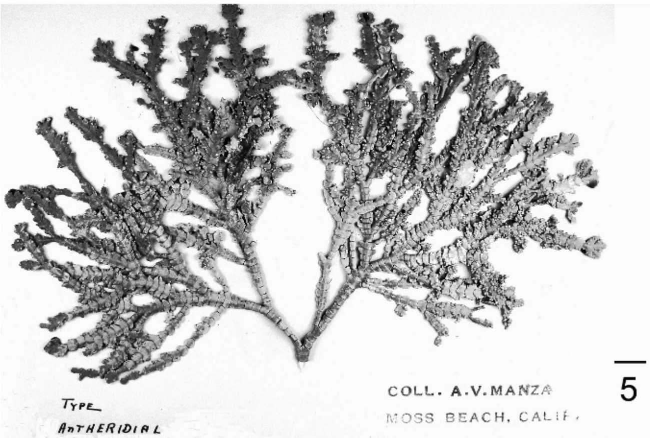


Fig. 3. Lectotype of *Calliarthron cheilosporioides* (UC 545724), USA, California, Monterey County, Pacific Grove, 13 May 1933, *leg.* A.V. Manza. Scale bar = 1 cm. Inset is enlargement of branch of this specimen.





Figs 4, 5. Type material of synonyms of *Calliarthron tuberculosum*. Scale bar = 1 cm.

Fig. 4. Lectotype of *Calliarthron setchelliae* (UC 545733), USA, California, San Mateo County, Moss Beach, 5 May 1931, *leg.* A.V. Manza.

Fig. 5. Lectotype of *Calliarthron regenerans* (UC 545975), USA, California, San Mateo County, Moss Beach, 21 May 1932, *leg.* A.V. Manza.

categorize 100% of the *C. cheilosporioides* specimens and 97% of the *C. tuberculosum* specimens (Wilks' lambda = 0.342; Table 4). These two factors were not highly correlated (Pearson's correlation = 0.52). In general, fronds produced by *C. cheilosporioides* have thin apical intergenicula with broad wings; whereas, fronds produced by *C. tuberculosum* have thick apical intergenicula with narrow wings or no wings at all (Fig. 14).

Canonical coefficients used by the DA were 1.45 and −7.06 for intergenicular wing expansion and minor diameter of apical intergeniculum, respectively, and the following equation was used to determine canonical scores:

$$\text{Canonical score} = 1.45\left(\frac{d_{1,\text{intA}}}{d_{1,\text{intB}}}\right) - 7.06 \times \log_{10}(d_{2,\text{intA}})$$

Fronds of *C. tuberculosum* scored between −0.08 and 3.96 in the DA; whereas, those of *C. cheilosporioides* scored between 3.82 and 6.84 (Fig. 15A). Despite the wide range of morphological variability exhibited by the two *Calliarthron* species (Fig. 15B–K), the DA successfully classified nearly all specimens in this study.

DISCUSSION

*rbc*L sequencing of Corallinales

The plastid-encoded *rbc*L gene has been a preferred molecule for assessing phylogenetic relationships among species, genera, families and orders of red algae for the past 16 years (Freshwater *et al.* 1994, 1995; Sherwood & Sheath 2000; Lin *et al.* 2001; Gurgel & Fredericq 2004; De Clerck *et al.* 2005; Hughey & Hommersand 2008). Broom *et al.* (2008) noted that *rbc*L was an obvious candidate for a more rapid evolving marker than the nuclear small-subunit ribosomal gene (nSSU), which had been used previously to evaluate relationships among Corallinales (Bailey & Chapman 1996; Bailey 1999; Harvey *et al.* 2003; Bailey *et al.* 2004; Broom *et al.* 2008; Kim *et al.* 2007; Vidal *et al.* 2008; Walker *et al.* 2009). However, Broom *et al.* (2008) were unable to obtain consistent amplifications of the *rbc*L locus with their primer combinations and material. We did not have this difficulty. With few exceptions, DNA extracted from field-collected corallines and herbarium specimens, including type specimens, from the northeast, northwest and southeast Pacific has amplified readily using previously designed primer combinations F-57/R-753 and F-753/RrbcS (Freshwater & Rueness 1994) or newly designed primers (see Material and Methods).

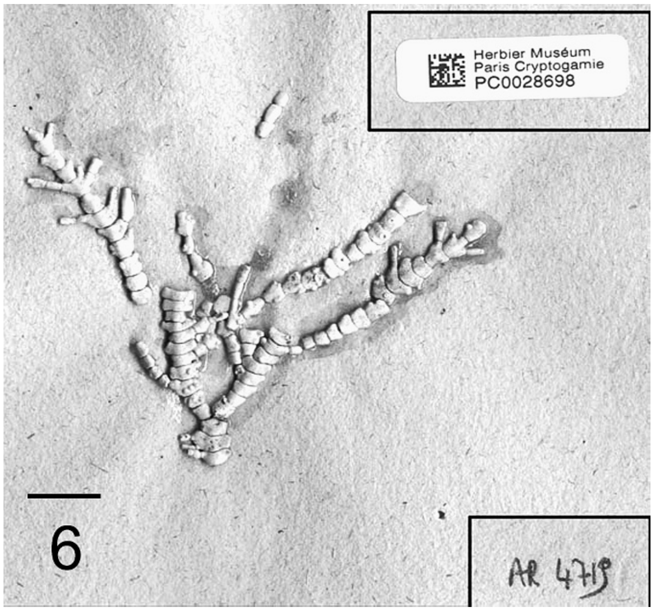


Fig. 6. Holotype of *Amphiroa* (*Arthrocardia*) *vertebralis* (AR 4719 in PC) collected at (USA, California) Monterey. Scale bar = 1 cm.

Our approach to applying molecular methods to systematic problems in the Corallinales focuses on sequences obtained from type specimens of generitype species and of other species included in a particular genus. This approach, at present, does not allow for broad comparisons with the phylogenies presented by other authors, namely those using nSSU (Bailey & Chapman 1996; Bailey 1999; Harvey *et al.* 2003; Bailey *et al.* 2004; Broom *et al.* 2008) or *psb*A (Broom *et al.* 2008). However, our approach clearly demonstrates which name is correctly applied to recent collections based on sequences obtained from type or topotype material.

Our molecular results, which include sequences from the generitype species, *Bossiella plumosa* and *Calliarthron cheilosporioides*, support the morphological evidence that *Bossiella* and *Calliarthron* are distinct genera. Previous analyses of nSSU sequence data, regardless of the method employed (Bailey & Chapman 1998, fig. 1; Bailey *et al.* 2004, figs 1, 2; Broom *et al.* 2008, fig. 5), failed to separate the genera *Bossiella*, *Calliarthron* and *Serraticardia* (represented by *S. macmillanii*). One possible reason that nSSU sequences do not distinguish these genera is that the gene is too conserved; Bailey & Chapman (1996) reported a sequence divergence value of only 0.8% for the genera *Bossiella*, *Calliarthron* and *Serraticardia*. Another distinct possibility is that some of their specimens may not have been correctly identified. Our ML and MP analyses clearly distinguished the genera *Bossiella* and *Calliarthron* with robust bootstrap support. We note that the generitype species of *Serraticardia* is *S. maxima* from the northwest Pacific (Japan), but we are not certain that the northeast Pacific *S. macmillanii* belongs in that genus.

Chiharaea, an endemic, monotypic and morphologically very distinct northeast Pacific genus, characterized by an expansive crustose base and 1- to 5-mm-long erect, irregularly branched axes (Johansen 1966), is included here in a coralline phylogeny for the first time and appears to be a distinct genus.

Topotype specimens

Topotype material or topotype specimen(s) are specimens collected at the type locality of a species after the original collection. It is important to note that topotype material is not type material and is not governed by the ICBN (McNeill *et al.* 2006), as is the case with, for example, a holotype, lectotype or syntype(s). For some type material or specimens, a specific locality is provided in the protologue of the species so that one can return to the type locality and collect topotype material; for other species, the type locality designated is broad, for example, Vancouver Island, or too broad to be useful, for example, 'mar australe'. Thus, topotype material is meaningful only if the locality is clearly specified in the protologue of a species. Anyone at anytime can collect topotype material, but specimens collected by the original collector, particularly when that person also is the author of the species, are the most useful.

The genera *Calliarthron* and *Alatocladia*

Calliarthron was established by Manza (1937a) to accommodate articulated corallines in which conceptacles were laterally positioned and intergenicular medullary filaments were flexuous and interlacing. Previously, only Weber-van Bosse (1904) had used both conceptacle position and vegetative anatomy to characterize *Amphiroa*, with lateral conceptacles and intergenicular medullary filaments arranged in long and short transverse bands. Manza (1937a) saw his work as a logical extension of the application of Weber-van Bosse's observations to other articulated coralline algae, and his key to genera includes both vegetative anatomical characters and characters related to conceptacle position. Earlier workers (Decaisne 1842a, b; Areschoug 1852; Yendo 1902a, b) used conceptacle position in combination with vegetative characters, such as intergenicular shape and/or overall branching pattern, to characterize genera of articulated corallines. Yendo (1905a) contributed the importance of the origin, rather than the position, of conceptacles, whether from the medullary region resulting in axial or marginal conceptacles or from the cortical region resulting in laterally positioned conceptacles. Indeed, Manza's (1937a) generic key characterized *Calliarthron* as having solely lateral conceptacles. But in his generic diagnosis, Manza stated that both marginal and lateral conceptacles are present, and he continued to use this characterization for additional species that he transferred to the genus (Manza 1937b). Manza (1937b) included *Calliarthron* species from the northeast Pacific that earlier had been segregated from *Amphiroa* to *Arthrocardia* by Weber van Bosse (1904), namely *Arthrocardia epiphlegnoides*, *A. tuberculosa* and *A. vertebralis*, and from the northwest Pacific that had been placed in the genus *Cheilosporum* section *Alatocladia* by Yendo (1905b), namely *C. anceps* var. *modestum*, *C. latissimum* and *C. yessoense*. Yendo (1905a) wrote, 'It is a matter of question, however, if for systematic purpose the vegetative character can with propriety be made to supersede the reproductive character in importance.

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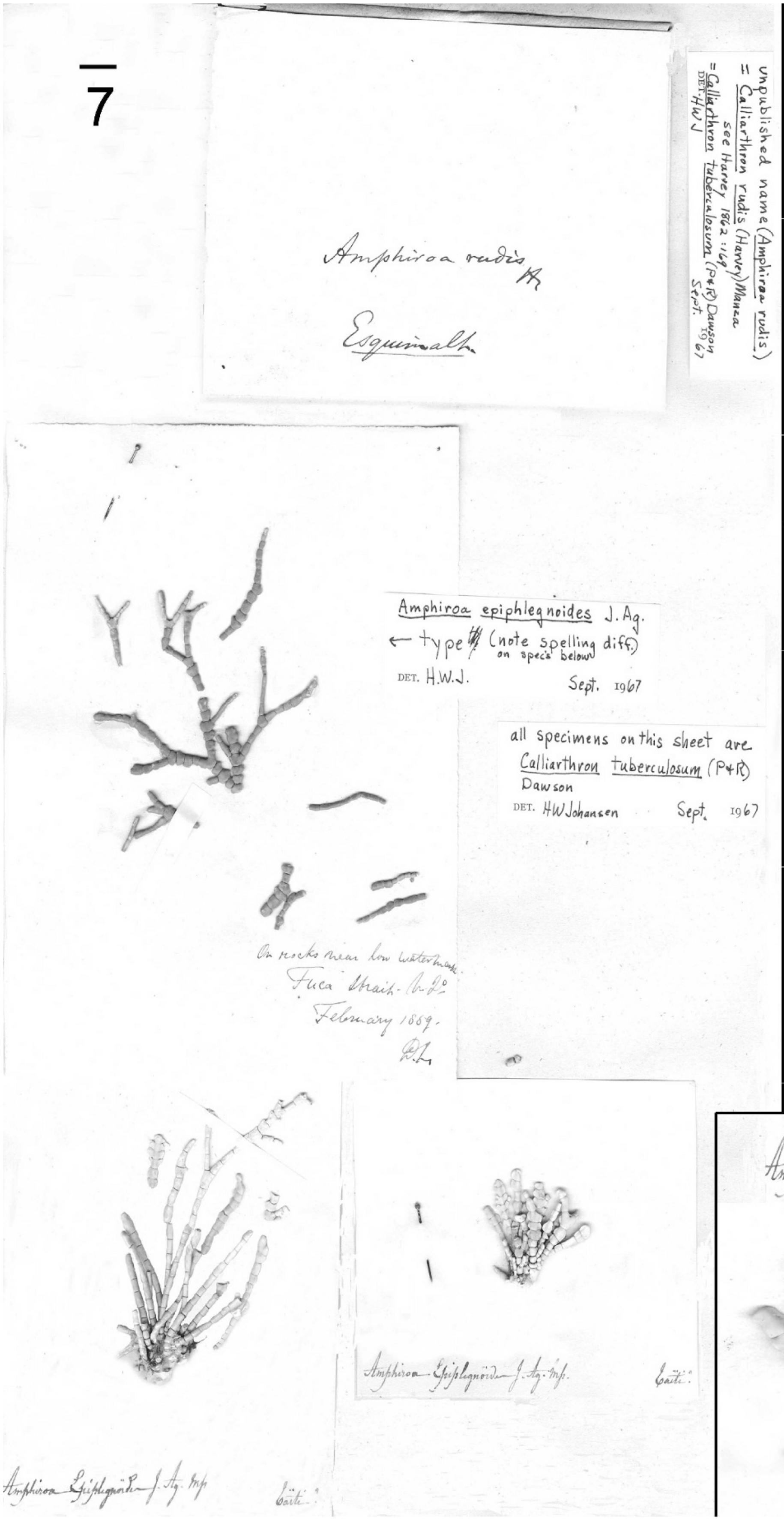
Amphiroa rudis H.
Esquimalt.
unpublished name (Amphiroa rudis)
= Calliarthron rudis (Harv.) Manza
see Harvey 1862: 169
= Calliarthron tuberculosum (P&R) Dawson
DET: H.W.J
Sept. 1967
Amphiroa epiphlegnoides J. Ag.
← type (note spelling diff.) on spec's below
DET. H.W.J.
Sept. 1967
all specimens on this sheet are Calliarthron tuberculosum (P&R) Dawson
DET. HWJohansen
Sept. 1967
On rocks near low watermark
Fuca Strait. V. I.
February 1869.
Amphiroa Epiphlegnoides J. Ag. Msc.
Cäiti
Amphiroa Epiphlegnoides J. Ag. Msc.
Cäiti

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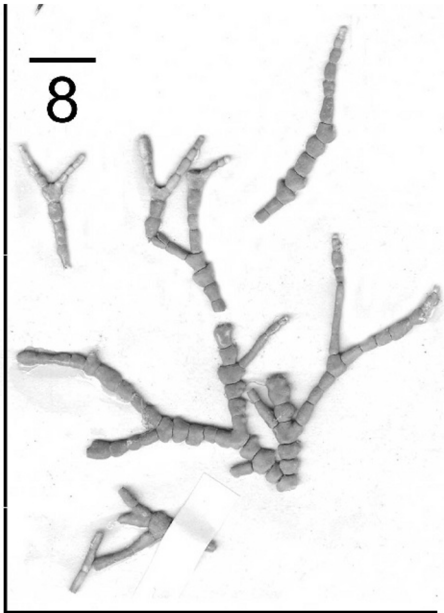

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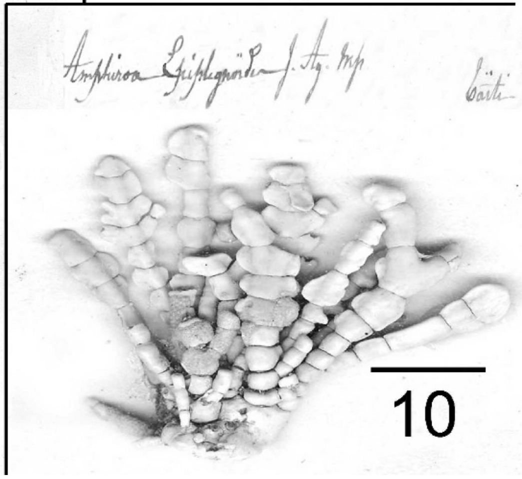
10


Amphiroa Epiphlegnoides J. Ag. Msc
Cäiti

From this standpoint of view, I cannot wholly agree in the principle of arrangement done by Madam Weber van Bosse.' And although Yendo did not follow Weber-van Bosse's generic characterization, he did recognize the utility of her approach, stating, 'Still it can not be denied that her work opened a way towards smoothing away the confusion that had existed in the system of the Corallinae.'

Johansen (1969, pp. 51–53, fig. 27) adopted Yendo's (1905a, p. 119) emphasis on conceptacle origin and illustrated the origins of the three types of conceptacle positions: axial, marginal and lateral. Johansen (1969) regarded conceptacle origin as the most important feature in classifying and characterizing articulated coralline genera in the subfamily Corallinoideae. Thus, Johansen (1969) elevated Yendo's section *Alatocladia* of *Cheilosporum* and his section *Marginisporum* of *Amphiroa* to generic rank based primarily on conceptacle position, axial and marginal in the former and marginal and lateral in the latter. But he also recognized the importance of vegetative anatomical features, designating *Marginisporum* as a distinct genus because it lacked both the intergenicular medullary filaments arranged in long and short transverse bands diagnostic of *Amphiroa* and the interlacing medullary filaments diagnostic of *Calliarthron*.

The molecular results reported here support the recognition of *Alatocladia* as distinct from *Calliarthron* but not the diagnostic utility of conceptacle position or origin. Manza (1937a) and Johansen (1969) characterized *Calliarthron* as having marginal and lateral conceptacles, the former originating from the medullary region and the latter from the cortical region; whereas, *Alatocladia*, according to Johansen (1969), has axial and marginal conceptacles, both originating in the medullary region. On the basis of *rbc*L sequences, however, *C. yessoense* and *C. latissimum*, with axial and marginal conceptacles, belong in *Alatocladia* and not in *Calliarthron*. Akioka *et al.* (1981) noted the difficulty of assessing conceptacle origin and recommended that only tetrasporangial plants be used because conceptacles may be crowded and their origin unclear in gametangial plants. In the type species of *Alatocladia*, *A. modesta*, a rare lateral conceptacle was reported (Akioka *et al.* 1981, fig. 23).

Within the subfamily Corallinoideae, only *Alatocladia* and *Calliarthron* share the character of interlacing medullary filaments, so it was reasonable that Johansen (1969) and Akioka *et al.* (1981) hypothesized a close relationship between these genera. Relationships among the northeast and northwest Pacific genera currently are unresolved in our phylogram (Fig. 1) but thus far *Alatocladia* and *Calliarthron* do not exhibit a sister taxon relationship.

One reproductive character that distinguishes these morphologically highly variable genera is the presence of sterile paraphyses among the tetrasporangia of *Alatocladia* and their absence in *Calliarthron*. Segawa (1941) was the first to report paraphyses in the tetrasporangial conceptacles of *Alatocladia yessoensis* (as *Cheilosporum yessoense*), and their presence was confirmed by Murata & Masaki (1978, as *Calliarthron yessoense*). Murata & Masaki (1978) also first reported their presence in *Alatocladia modesta*, a finding later confirmed by Akioka *et al.* (1981). Johansen (1969, p. 30) noted the absence of paraphyses in both *C. cheilosporioides* and *C. tuberculosum* in the northeast Pacific. Although the presence or absence of paraphyses in tetrasporangial conceptacles appears diagnostic for distinguishing *Calliarthron* and *Alatocladia*, its value as a character for other genera in the Corallinoideae requires further assessment. Moreover, as now constituted, *Alatocladia* and *Calliarthron* are geographically separate with the former endemic to the northwest Pacific and the latter to the northeast Pacific.

In summary, the basic nomenclatural/taxonomic data for each genus is as follows:

GENUS: *Calliarthron* Manza (1937a: 46)

TYPE SPECIES: *C. cheilosporioides* Manza (1937a: 46)

FAMILY AND SUBFAMILY PLACEMENT: Corallinaceae, subf. Corallinoideae

DIAGNOSTIC FEATURES: medullary (core) region filaments flexuous; tetrasporangial conceptacles lacking paraphyses. The first separates *Calliarthron* from other genera of Corallinoideae except for *Alatocladia*; the second distinguishes *Calliarthron* from *Alatocladia*. *rbc*L sequence differences between these two genera are summarized in Table 2.

GENUS: *Alatocladia* (Yendo) H.W. Johansen (1969: 55)

BASIONYM: *Cheilosporum* sect. *Alatocladia* Yendo (1905b: 2)

TYPE SPECIES: *A. modesta* (Yendo) H.W. Johansen (1969: 55)

FAMILY AND SUBFAMILY PLACEMENT: Corallinaceae, subf. Corallinoideae

DIAGNOSTIC FEATURES: medullary (core) region filaments flexuous; tetrasporangial conceptacles with paraphyses. The first separates *Alatocladia* from other genera of Corallinoideae except for *Calliarthron*; the second distinguishes *Alatocladia* from *Calliarthron*. *rbc*L sequence differences between these two genera are summarized in Table 2.

Calliarthron species taxonomy

The molecular, morphological and biogeographic evidence convincingly demonstrates that two species of *Calliarthron* are present in the northeast Pacific, confirming Johansen's

←

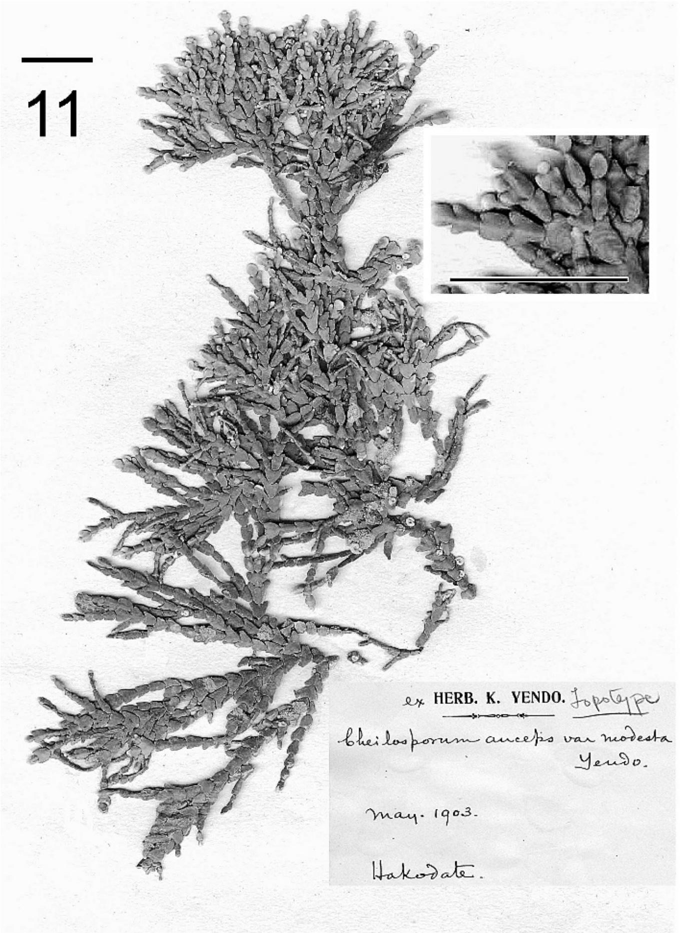
Figs 7–10. Type sheet of *Amphiroa epiphlegnoides* (TCD). Scale bar = 1 cm.

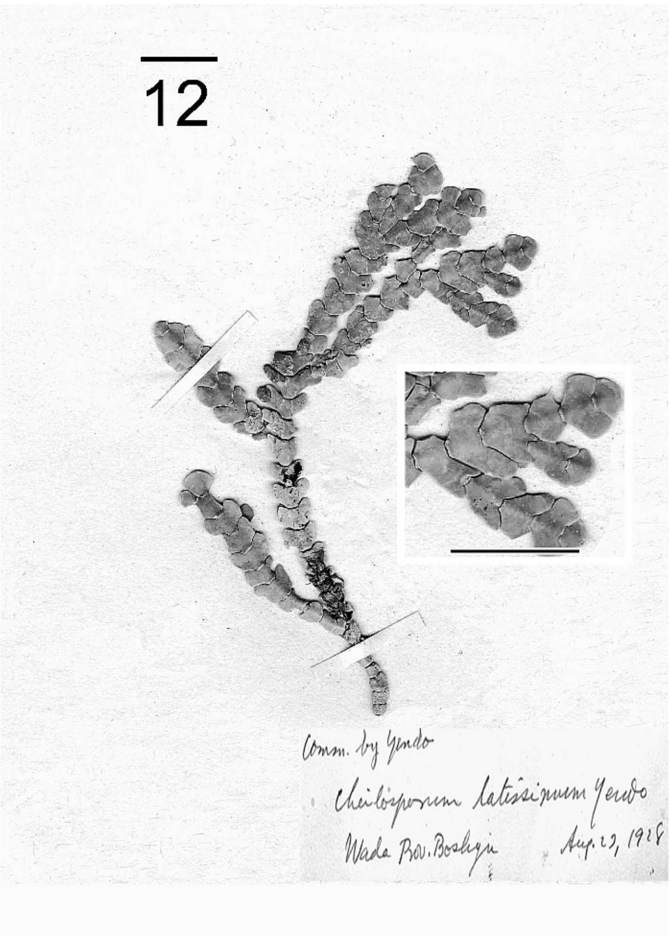
Fig. 7. Entire type sheet in TCD with packet at top containing fragments of Harvey's unpublished name, '*A. rudis*' from (Canada, British Columbia, Vancouver Island) Esquimalt, middle fragments, likely from a single specimen, from 'Fuca Strait' (Strait of Juan de Fuca), that was designated as lectotype of *Amphiroa epiphlegnoides* by H.W. Johansen and two bottom specimens labelled '*A. epiplegnoides* J. Ag. ms. Tahiti?' in J. Agardh's hand. Scale bar = 1 cm.

Fig. 8. Major portion of lectotype specimen of *A. epiphlegnoides*. Scale bar = 1 cm.

Fig. 9. Left specimen of J. Agardh's '*A. epiplegnoides*' with labels. Scale bar = 1 cm.

Fig. 10. Right specimen of J. Agardh's '*A. epiplegnoides*'. Scale bar = 1 cm.


11
ex HERB. K. YENDO. Topotype
Cheilosporum anceps var modesta Yendo.
may. 1903.
Hakodate.


12
Comm. by Yendo
Cheilosporum latissimum Yendo
Wada Prov. Boshyu Aug. 27, 1928

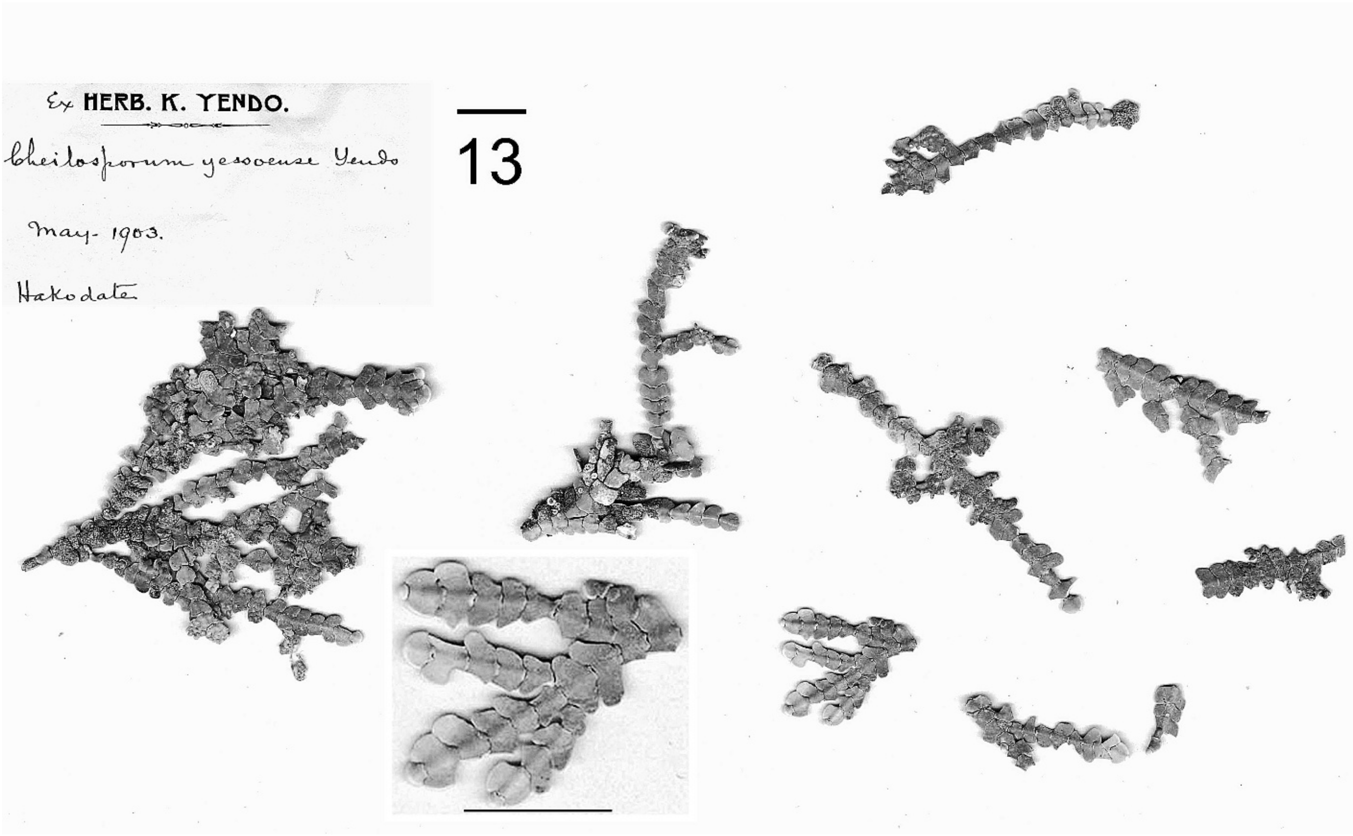

Ex HERB. K. YENDO.
Cheilosporum yessoense Yendo
may. 1903.
Hakodate
13

Table 3. Morphometric comparison of *Calliarthron* species (mean ± SD).

Factor		*C. cheilosporioides*	*C. tuberculosum*	
Intergenicular wing expansion[1]	$d_{1,\text{int A}} / d_{1,\text{int B}}$	2.4 ± 0.4	1.3 ± 0.6	$P < 0.001$
Apical intergeniculum out-of-round	$d_{1,\text{int A}} / d_{2,\text{int A}}$	5.8 ± 1.3	3.3 ± 1.1	$P < 0.001$
Basal intergeniculum				
Major diameter (mm)	$d_{1,\text{int B}}$	1.41 ± 0.55	2.15 ± 0.56	$P < 0.001$
Minor diameter (mm)	$d_{2,\text{int B}}$	1.24 ± 0.34	1.41 ± 0.33	NS
Apical intergeniculum				
Major diameter (mm)	$d_{1,\text{int A}}$	3.37 ± 0.93	2.70 ± 0.95	$P < 0.05$
Minor diameter (mm)[1]	$d_{2,\text{int A}}$	0.59 ± 0.17	0.88 ± 0.17	$P < 0.001$
Basal geniculum				
Major diameter (mm)	$d_{1,\text{gen B}}$	0.95 ± 0.25	1.06 ± 0.28	NS
Minor diameter (mm)	$d_{2,\text{gen B}}$	0.82 ± 0.25	0.79 ± 0.28	NS
Apical geniculum				
Major diameter (mm)	$d_{1,\text{gen A}}$	0.67 ± 0.17	0.73 ± 0.17	NS
Minor diameter (mm)	$d_{2,\text{gen A}}$	0.40 ± 0.08	0.49 ± 0.11	$P < 0.01$

[1] Factors used in the discriminant analysis.

treatment (Johansen 1969). The two long *rbc*L sequences (1401 bp) of *C. cheilosporioides*, one a topotype specimen from Pacific Grove, Monterey County, California (UBC A87283) and the other from San Diego County, California (NCU 585611) were identical as were all of the short, 135-bp sequences in the variable region (1172–1307 bp) of *rbc*L, including that from the lectotype (Table 2). The three long *rbc*L sequences (1401 bp) of *C. tuberculosum*, one from the northern part of this species' range (Vancouver Island, British Columbia, Canada, NCU 588186), one from Pacific Grove, Monterey County, California (UBC A87284) and one from White's Point, Los Angeles County, California (NCU 590609) consistently differ from *C. cheilosporioides* by 7 bp (0.57% sequence divergence) at the same positions in *rbc*L. Two of these positions are in the short, 135-bp variable region (1173–1307 bp) (Table 2).

South of Monterey Bay, California, the ranges of *C. cheilosporioides* and *C. tuberculosum* overlap (Fig. 16), and where the two co-occur, differentiating the species in the field can be difficult. The morphometric analysis presented here indicates that measures of intergenicular thickness and wingspan are sufficient to distinguish *Calliarthron* species in the field and can be used as a proxy for sequence data to differentiate these species. These characters can be easily calculated from three caliper measurements of *Calliarthron* fronds: major diameter of basal intergenicula ($d_{1,\text{int B}}$), and major and minor diameters of apical intergenicula ($d_{1,\text{int A}}$ and $d_{2,\text{int A}}$).

Calliarthron species key

1. Minor diameter of apical intergeniculum often > 0.7 mm; intergenicular wing expansion generally < 2; morphometric canonical score < 4; common in low intertidal tidepools in moderate to exposed habitats; from Isla San Geronimo, Baja California Norte, Mexico to southeast Alaska (*C. tuberculosum*).
2. Minor diameter of apical intergeniculum ≤ 0.7 mm; intergenicular wing expansion often > 2; with few exceptions, morphometric canonical score > 4; subtidal, rarely found in the low intertidal; from Isla Cedros, Baja California Norte to Monterey County, California (*C. cheilosporioides*).

Calliarthron cheilosporioides Manza (1937a: 46)

LECTOTYPE: UC 545724, USA, California, Monterey County, Pacific Grove, 13 May 1933, tetrasporic, *leg.* A.V. Manza.

SPECIMENS EXAMINED: See Table 1.

Calliarthron cheilosporioides shows no variation in *rbc*L sequences throughout its range (Tables 1, 2). The use of the name is confirmed by sequences from field-collected material matching the partial *rbc*L sequence of the lectotype specimen. Specimens of *C. cheilosporioides* may be variable in morphology but tend to have thinner apical intergenicula and broader wings than *C. tuberculosum* (Fig. 14). The

←

Figs 11–13. Topotype material of *Alatocladia* spp. collected by Yendo and sent to UC. Scale bars = 1 cm.

Fig. 11. *Alatocladia modesta* (as *Cheilosporum anceps* var. *modesta*), UC 90826, Japan, Hakodate, May 1903. Inset is enlargement of branch of this specimen showing the absence of scutiform intergenicula.

Fig. 12. *Alatocladia yessoensis* (as *Cheilosporum latissimum*), UC 418147, Japan, Wada Province, Boshyu, 22 August 1928. Note the wider intergenicula that Manza considered characteristic of this species as compared to *Cheilosporum yessoense*. Inset is enlargement of branch of this specimen and shows some scutiform intergenicula characteristic of this species.

Fig. 13. *Alatocladia yessoensis* (as *Cheilosporum yessoense*), UC 90783, Japan, Hakodate, May 1903. Inset is enlargement of branch of this specimen and shows some scutiform intergenicula characteristic of this species.

Table 4. Utility of morphological factors entered step-wise in the discriminant analysis.

Factors	Correctly classified (%)			
	C. cheilosporioides	*C. tuberculosum*	Wilks' lambda	
Intergenicular wing expansion	72	81	0.462	$P < 0.001$
Intergenicular wing expansion and log (minor diameter of apical intergeniculum)	100	97	0.342	$P < 0.001$

distribution of *C. cheilosporioides* is more limited than that of *C. tuberculosum*; it does not occur north of Monterey Bay, California, but it occurs farther south, to Isla Cedros, Baja California, Mexico (Fig. 16). Several specimens in UC, collected from as far north as Fort Bragg, Mendocino County, California (UC 1944761) and purported to be *C. cheilosporioides*, are identified as *C. tuberculosum* by sequence.

Calliarthron tuberculosum (Postels & Ruprecht) E.Y. Dawson (1964: 540)

BASIONYM: *Corallina tuberculosa* Postels & Ruprecht (1840, 20, pl. 40, fig. 100)

HOMOTYPIC SYNONYMS:

Amphiroa tuberculosa (Postels & Ruprecht) Yendo (1902a: 714)

Arthrocardia tuberculosa (Postels & Ruprecht) Weber-van Bosse (1904: 105)

Cheilosporum tuberculosum (Postels & Ruprecht) Yendo (1905b: 20)

HETEROTYPIC SYNONYMS:

Amphiroa vertebralis Decaisne (1842b: 124)

Arthrocardia vertebralis (Decaisne) Weber-van Bosse (1904: 106)

Calliarthron vertebralis (Decaisne) Manza (1940: 267)

Amphiroa epiphlegnoides J. Agardh *ex* Harvey (1862: 169)

Arthrocardia epiphlegnoides (J. Agardh *ex* Harvey) Weber-van Bosse (1904: 105)

Calliarthron regenerans Manza (1937b: 565)

Calliarthron setchelliae Manza (1937b: 566)

All of the *rbc*L sequences that we obtained for *C. tuberculosum* (including those from holotype material of *C. regenerans* and *C. setchelliae*) were identical, except for the single nucleotide polymorphism at position 1233 (Table 2). This polymorphism does not correlate with geographic distribution, with reproductive phase or with any morphological feature that we were able to discern. The application of the name *C. tuberculosum* remains somewhat problematic because we were unable to obtain type material to sequence, and the species is absent at its purported type locality, Sitka, Alaska (Dawson 1964). Recent collecting efforts at Sitka, Alaska, have failed to find this species (Sandra C. Lindstrom, personal communication). However, the identity of the type material as *C. tuberculosum* is supported by the digital image of the disarticulated intergenicula of the lectotype specimen in LE designated by Johansen (1969) (see image at http://herbarium.botany.ubc.ca/index.html) and the illustration of interwoven medullary filaments, characteristic of *Calliarthron*, by Postels & Ruprecht (1840, fig. 107). The Postels & Ruprecht (1840, fig. 100) material looks like *C. tuberculosum*. The type specimen of *Amphiroa vertebralis* kindly sent by Dr. Bruno de Reviers (PC) failed to yield amplifiable DNA, but its morphology (Fig. 3) appears to be that of *C. tuberculosum* and not *C. cheilosporioides*, which can be found at the same locality.

The identity of *Amphiroa epiphlegnoides* with *C. tuberculosum* also appears to be correct. Three fragmentary specimens and a packet containing one or more specimens (Fig. 7) are included on a single sheet in Harvey's herbarium. The two lower specimens are similar in pigmentation, appear to be from the same collection and both are labelled in J. Agardh's hand '*A. epiplegnoides* ms. Tahiti' (Figs 9, 10); this accounts for Harvey's (1862:169) last statement under his description *A. epiphlegnoides*, 'A native also of Tahiti'. The middle specimen (Fig. 8) has no name, but it is labelled 'on rocks near low water mark Fuca Strait Nr. 20 February 1859 D. L.' The packet labelled 'A. rudis Esquimalt' was mentioned by Harvey (1862: 169) under *A. epiphlegnoides*, clearly indicating that he thought these specimens were the same species. Johansen lectotypified *A. epiphlegnoides* with the Strait of Juan de Fuca specimen collected by David Lyall. The morphology and the provenance of this specimen support the identification of this and the Esquimalt material as *C. tuberculosum*. The J. Agardh–labelled specimens also appear to be *C. tuberculosum*, but the provenance cited (Tahiti) is certainly an error.

According to Johansen (1969, p. 9), 'The shapes of the non-basal intergenicula of *C. tuberculosum* are extremely variable from plant to plant or even within the same plant.' Intergenicula of *C. tuberculosum* reportedly lack upswept wings (Johansen 1969, Abbott and Hollenberg 1976), but we found this trait to be unreliable and subjective. Fronds of *C. tuberculosum* may exhibit dichotomous, pinnate or irregular branching patterns (Johansen 1969; Abbott and Hollenberg 1976); thus, branching pattern also is uninformative for species determinations. We agree with Johansen (1969) that fronds of *C. tuberculosum* sometimes develop cylindrical apices and that this growth pattern rarely occurs in *C. cheilosporioides*; however, many specimens of *C. tuberculosum* lack this feature. *Calliarthron tuberculosum* commonly occurs in tidepools, where *C. cheilosporioides* is rarely found. In general, *C. tuberculosum* can be distinguished from *C. cheilosporioides* by thick apical intergenicula with narrow wings or no wings at all (Fig. 14). *Calliarthron tuberculosum* ranges from Cape Chacon, Prince of Wales Island, Alaska (UBC 21844) to Isla San Geronimo, Baja California, Mexico (Dawson 1961) (Fig. 16). We were unable to obtain a sequence from this southern record (M 201087 in UC), but the morphology of the mostly disarticulated intergenicula clearly suggests *C. tuberculosum* and not *C. cheilosporioides*. The southern record (Isla Cedros, Baja California, Mexico) reported in

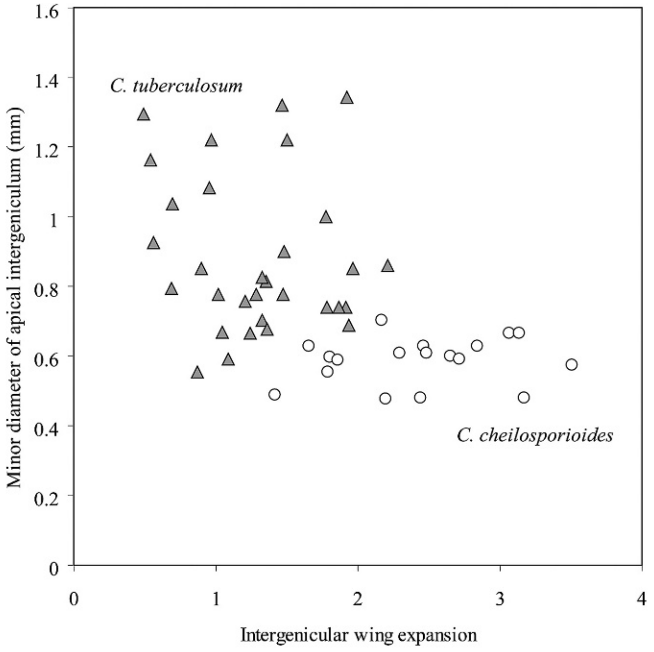


Fig. 14. Morphometric comparison of fronds produced by *C. tuberculosum* (closed triangles) and *C. cheilosporioides* (open circles), depicting factors used in discriminant analysis.

Abbott & Hollenberg (1976) may be an error and is not supported by a voucher.

Alatocladia species taxonomy

Alatocladia modesta and *A. yessoensis* are distinct species on the basis of their morphology, *rbc*L sequences and biogeography. *Alatocladia yessoensis*, in the upper parts of the thallus, has distinctive flange-like intergenicula that are expanded basally on their ventral and dorsal surfaces just above subtending genicula so that each intergeniculum overhangs and obscures the subtending geniculum (Figs 12, 13 insets). In the original description of *A. yessoensis* (as *Cheilosporum yessoense*), Yendo (1902b) described this characteristic as '…articulis inferioribus scutiformibus…' ('lower intergenicula shield-shaped'); this feature can be seen in his illustrations of both *Cheilosporum yessoense* (pl. II, fig. 12 and pl. VI, fig. 5) and *C. yessoense* f. *angustum* (pl. II, fig. 14, pl. VI, fig. 6). More recently, these distinctive intergenicula have been sectioned and illustrated in the sagittal plane, clearly showing the distinct lower dorsal and ventral flanges that overhang the subtending geniculum (Yoshida & Baba 1998, p. 543, pls 3–16, fig. C). These scutiform intergenicula are not present in *A. modesta* (Fig. 11 inset and Yoshida & Baba 1998, p. 529, pls 3–12, fig. C). The *rbc*L sequence divergence between the two species is 1.18% (16 bp), which is twice the sequence divergence observed between the two species of *Calliarthron* (0.57%, 7 bp) but similar to the sequence divergence (1.2%, 17 bp) of the *Bossiella* species included in this analysis. Further, *A. yessoensis* is endemic to Japan (Yoshida & Baba 1998); whereas, *A. modesta* is reported from Japan (Yoshida & Baba 1998), Korea (Lee 2008) and western Russia (Perestenko 1994).

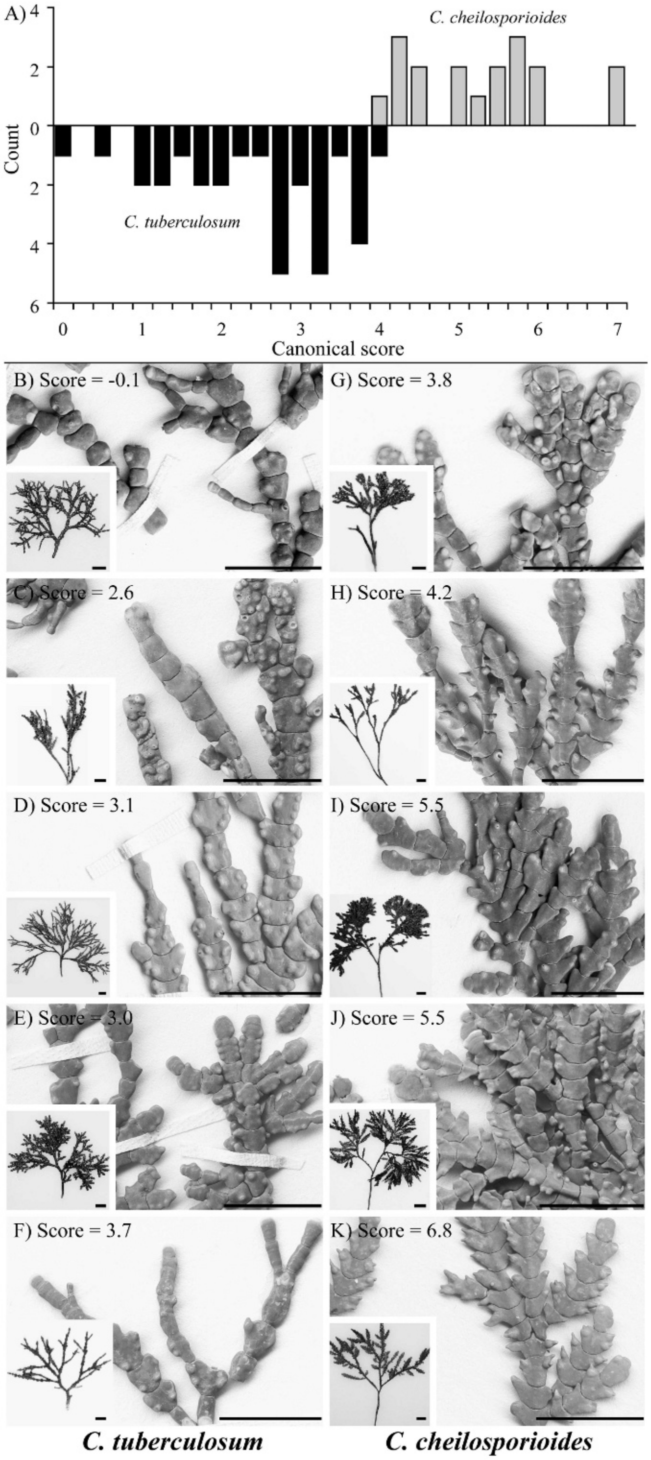


Fig. 15. Canonical scores assigned to *Calliarthron* fronds by discriminant analysis. Images represent morphological variability expressed by *C. tuberculosum* (B = UBC A87305; C = UBC A87288; D = UBC A87306; E = UBC A87311; F = UBC A87290) and *C. cheilosporioides* (G = UBC A87289; H = UBC A87283; I = UBC A87287; J = UBC A87309; K = UBC A87299). Scale bars = 1 cm.

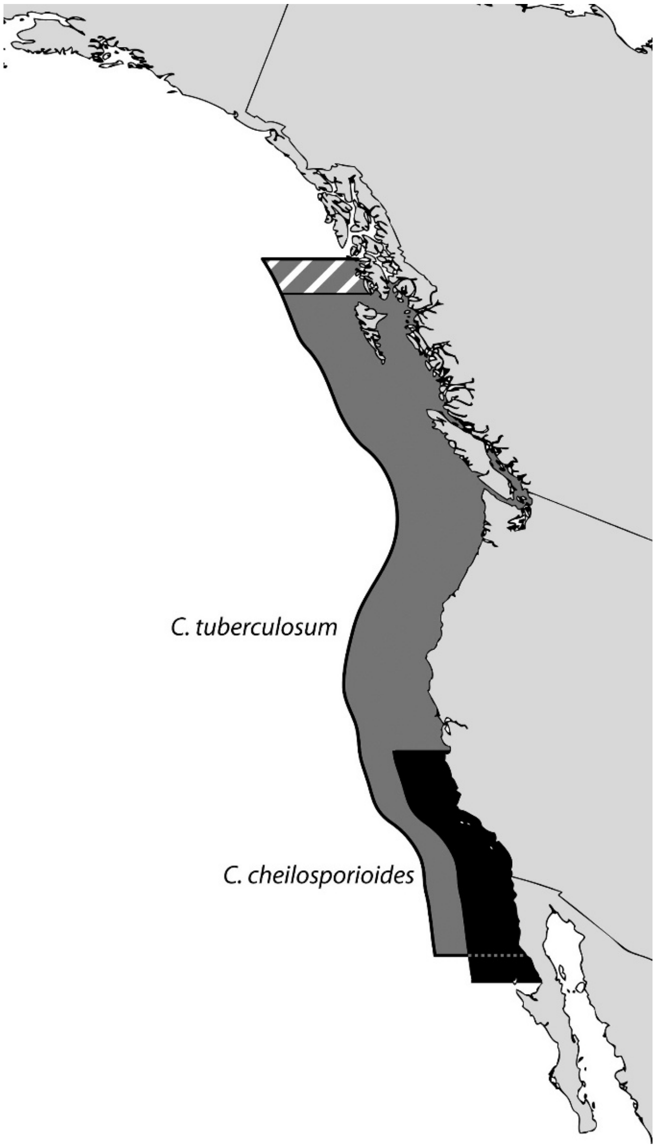


Fig. 16. Biogeographic ranges of *C. tuberculosum* (grey) and *C. cheilosporioides* (black). Striped area represents unconfirmed northern limit of *C. tuberculosum*, mysteriously absent from its purported type locality (see text for details).

Alatocladia species key

1. Intergenicula of upper parts of thallus with distinct dorsal and ventral flange that overhangs and obscures the subtending geniculum; endemic to Japan (*A. yessoensis*).
2. Intergenicula of upper parts of thallus lacking flanges, subtending genicula clearly seen; reported from Japan, Korea and northwest Russia (*A. modesta*).

Alatocladia modesta (Yendo) H.W. Johansen (1969: 55)

BASIONYM: *Cheilosporum anceps* (Kützing) var. *modestum* ('*modesta*') Yendo (1902b: 19, pl. 2, fig. 9, pl. 6, fig. 3)

HOMOTYPIC SYNONYM: *Calliarthron modestum* (Yendo) Manza (1937b: 564)

Alatocladia yessoensis (Yendo) *comb. nov.*

BASIONYM: *Cheilosporum yessoense* Yendo: (1902b: 19–20, pl. II, figs 12, 13, pl. VI, fig. 5)

HOMOTYPIC SYNONYM: *Calliarthron yessoense* (Yendo) Manza (1937b: 566)

HETEROTYPIC SYNONYMS:
Cheilosporum yessoense Yendo f. *angustum* ('*angusta*') Yendo (1902b: 19–20, pl. II, figs 14, 15, pl. VI, fig. 6)
Cheilosporum latissimum Yendo (1902b: 21, pl. II, figs 16, 17, pl. VI, fig. 7)
Calliarthron latissimum (Yendo) Manza (1937b: 564)

Calliarthron latissimum (as *Cheilosporum latissimum*) was described and illustrated by Yendo (1902b) in the same paper as *Alatocladia modesta* (as *Cheilosporum anceps* var. *modestum*), and *A. yessoensis* (as *Cheilosporum yessoense*). Yendo (1902b) did not compare *Cheilosporum latissimum* with *Cheilosporum yessoense*, but when Manza transferred these species to *Calliarthron*, he noted that *Calliarthron latissimum* had broader and thicker intergenicula than *Calliarthron yessoense*. These differences can be seen in Yendo's original figures (compare pl. II, figs 12, 13, *Cheilosporum yessoense* and pl. II, figs 14, 15, *C. yessoense* f. *angustum* with pl. II, figs 16, 17, *Cheilosporum latissimum*). Scutiform intergenicula were also illustrated (Yendo 1902b, pl. II, fig. 16, pl. VI, fig. 7).

The short variable segment of *rbc*L sequenced using the primers F-1152/R-1308 is identical for topotype material of both *A. yessoensis* and *Cheilosporum latissimum*. These specimens appear to differ only in the width and thickness of their intergenicula; otherwise, their morphology, sequence identity and geographic distribution (both are endemic to Japan [Yoshida & Baba 1998]) suggest that they represent a single species. We also note that *Calliarthron latissimum*, while included in Yoshida & Baba (1998, pp. 541–542), is not illustrated, nor is this species included in Baba (2000). Both species are described in the same publication (Yendo 1902b), so neither has nomenclatural priority, but given the long and current usage of the name *Calliarthron yessoense*, we propose that *C. latissimum* be placed into synonymy under *A. yessoensis*.

Conclusions

In this study, we demonstrated that (1) it is essential to include generitype species in phylogenetic analyses to correctly identify the clades to which generic names have been applied (in this case, genera of Corallinales), (2) *rbc*L sequence data are useful in distinguishing species and genera of Corallinales and (3) molecular sequencing provides an independent test of morphological features used to distinguish genera and species of Corallinales and verifies the characters of phylogenetic significance. We show that the two northeast Pacific *Calliarthron* species, *C. cheilosporioides* and *C. tuberculosum*, and the two northwest Pacific *Alatocladia* species, *A. modesta* and *A. yessoensis*, are distinct morphologically, geographically and by molecular sequence.

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