

Notes on the marine algae of the Bermudas. 7. Additions to the flora including *Chondracanthus saundersii* sp. nov. (Rhodophyta, Gigartinales) based on *rbcL* sequence analysis

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Ten species are added to the benthic marine algal flora of the Bermuda islands: *Caulerpella ambigua*, *Champia salicornioides*, *Chondracanthus saundersii* sp. nov., *Dictyota pinnatifida*, *Gelidiella lubrica*, *Gelidiopsis planicaulis*, *Peyssonnelia simulans*, *Pterocladia caerulea*, *Laurencia decumbens* and *Ulva chaetomorpha*. The new species, *C. saundersii*, is distinguished from congeners by its morphology and molecular identity and was previously known in Bermuda and much of the western Atlantic as *C. acicularis*.

INTRODUCTION

Collections in the Bermuda islands continue to add species to the recently published list of taxa (Schneider 2003, 2004). In this report, 10 new records, including the description of a new species of *Chondracanthus* Kützinger, *C. saundersii* C.W. Schneider & C.E. Lane, are added to the benthic marine flora of Bermuda. Morphological characters and its *rbcL* sequence differentiate it from the slightly similar *C. acicularis* (Roth) Fredericq and *C. teedei* (Mertens ex Roth) Kützinger, the two species to which specimens from Bermuda had been assigned in the past (Kemp 1857; Collins & Hervey 1917; Howe 1918). One of the new collections, *Pterocladia caerulea* (Kützinger) Santelices & Hommersand, is confirmed by an A.F. Kemp specimen (FH) mounted in 1855 that he identified as *Gelidium corneum* (Hudson) J.V. Lamouroux ('i, abnorme').

MATERIAL AND METHODS

Standard methods

Specimens were pressed fresh onto herbarium paper with fragments preserved in 5% formalin–seawater. Site locations on shore were taken using a GPS III Plus (Garmin, Olathe, KS, USA). Habit photographs were taken with a PowerShot G2 with macro settings (Canon, Tokyo, Japan) using Kodachrome 64 slide film, and the images were digitized with a Sprint Scan 4000 at 1200 dpi (Polaroid, Waltham, MA, USA). Photomicrographs were taken using an Eclipse E600 microscope (Nikon, Tokyo, Japan) equipped with a model 4.2 Spot InSight QE digital camera (Diagnostic Instruments, Sterling Heights, MI, USA). The digital images were composed in Photoshop 6.0.1 (Adobe Systems, San Jose, CA, USA). Pen and ink drawings were made with the aid of a camera lucida (Zeiss,

Oberkochen, Germany). Voucher specimens are deposited in the first author's personal herbarium (CWS), with duplicates of most sent to MICH, NY, and the Bermuda Natural History Museum (BAMZ), and some to C, DUKE, GALW, MSM and US. The holotype was deposited in MICH. The *Phycotheca Borealis-Americana* (P.B.-A.) exsiccata referred to represents the set originally purchased by Wellesley College (MA, USA), now belonging to the first author. When listed, herbarium abbreviations follow Holmgren *et al.* (1990), and initials for authorities' given names are from Brummitt & Powell (1992).

Molecular methods

Specimens of the new taxon were dried on silica gel in the field. In the lab, the dried sample was ground under liquid nitrogen and stored at –20°C. DNA was extracted using a modification of the protocol in Saunders (1993). Rather than an alcohol precipitation after the final phenol–chloroform extraction step, the aqueous phase from the mixture was transferred to a 1.5 ml microcentrifuge tube containing 1 ml of Wizard DNA Clean-Up System resin (Promega, Madison, WI, USA), and the manufacturer's protocol was followed. Purified DNA was amplified in a 2400 GeneAmp PCR System (PerkinElmer, Wellesley, MA, USA) or IcyCycler (Bio-Rad Laboratories, Hercules, CA, USA), using the Takara Ex-Taq DNA polymerase kit (PanVera, Madison, WI, USA). Oligonucleotide primers were constructed for polymerase chain reaction (PCR) (forward – RR1 5'ATGTCTAACTCTGTAGAAG3' and reverse – Rrr 5'ATCTCACTATTCTATACTCC3'), and internal primers were designed for sequencing (forward – RrIf 5'TCTCAGCCTTTTATGCGTTG3' and reverse – RrIr 5'GGTTAACACCTTCCATTGAAT3'). The thermal profile for PCR reactions included an initial denaturation cycle of 94°C for four minutes, followed by 38 cycles of 94°C for one minute, 50°C for one minute and 72°C for two minutes. The final extension step occurred at 72°C for seven minutes, fol-

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lowed by storage at 4°C until the samples were removed from the machine.

Amplification products were visualized on a 0.8% electrophoresis grade agarose gel (MP Biomedicals, Irvine, CA, USA). Bands were excised and centrifuged, at $8500 \times g$, through glass wool columns (Saunders 1993) to separate the DNA from the agarose. The resulting DNA solution was alcohol-precipitated, and linear amplification was performed with the Big Dye [v. 3.0, PE Applied Biosystems (ABI), Foster City, CA, USA] sequencing kit according to the manufacturer's protocol. Samples were analysed using an ABI 3100 automated sequencer. Complimentary, overlapping sequences were edited and aligned using SeqEd (ABI). The *rbcL* sequences of *Chondracanthus* and *Gigartina* Stackhouse species were downloaded from GenBank, and an alignment was constructed with the computer program SeqPup (Gilbert 1995). Fifty heuristic search replicates were used in unweighted parsimony analyses. Model parameters used in neighbour joining (NJ) and maximum likelihood (ML) analyses were estimated with ModelTest (Posada & Crandall 1998). Bootstrap values (Felsenstein 1985) were calculated with 1000 replicates using 10 random additions under the heuristic search method for parsimony and the NJ search method for distance trees.

Bayesian analyses were used to estimate posterior probabilities for ML topologies and were completed with MrBayes v 2.01 (Huelsenbeck & Ronquist 2001) using the GTR + I + G model with parameters estimated during the analyses. One million generations, with trees sampled every 100, were run with four chains. The first 4000 trees were discarded as the 'burn-in' phase, and the remaining trees were used to compute the consensus tree.

OBSERVATIONS

Ulvoephyceae: Ulvales, Ulvaceae

Ulva chaetomorphoides (Børgesen) H.S. Hayden,
Blomster, Maggs, P.C. Silva, Stanhope & Waaland
(2003, p. 288)

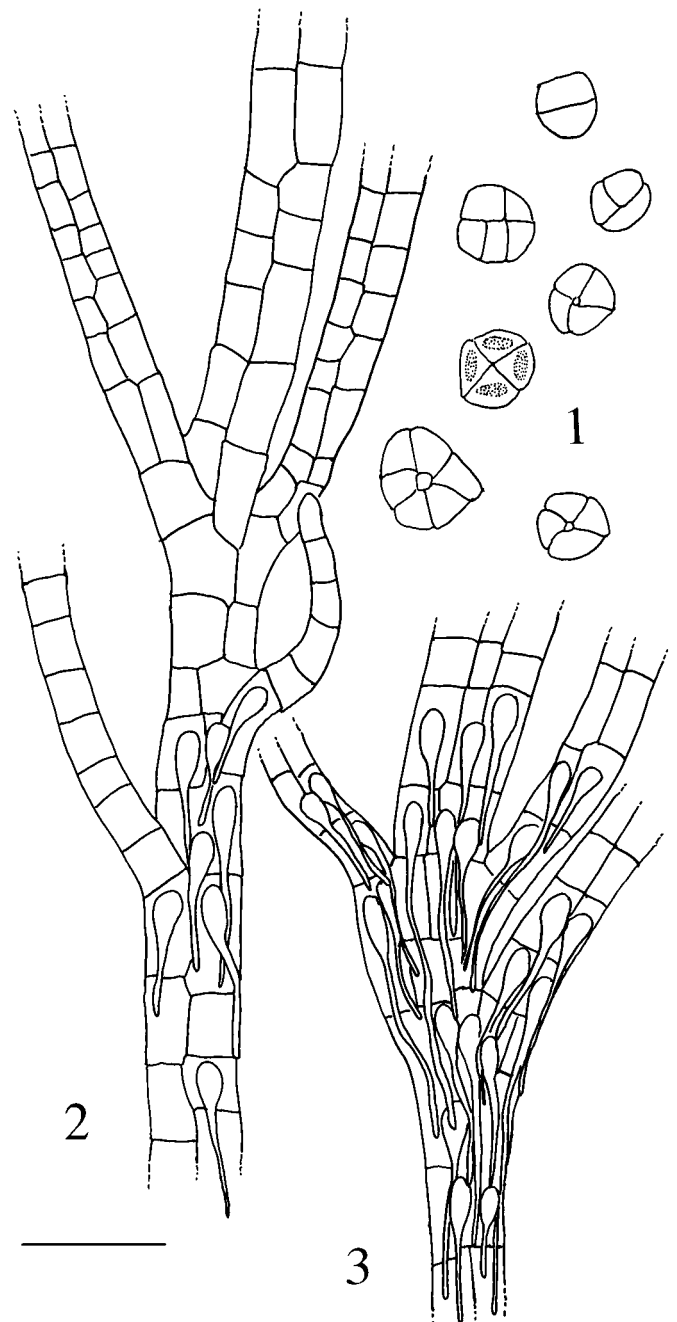
Figs 1–3

BASIONYM: *Enteromorpha chaetomorphoides* Børgesen (1911, p. 149, fig. 12).

TYPE LOCALITY: Bavoni Lagoon, St Thomas, Virgin Islands, Caribbean Sea.

COLLECTION: **Bermuda**. C.W. Schneider (CWS)/C.E. Lane (CEL) 02-6-26, 14 April 2002, West Whale Bay, Southampton, Bermuda Island, 32°15.3'N, 64°52.5'W, on intertidal rock.

Because this species was only recently transferred to *Ulva* Linnaeus (Hayden *et al.* 2003), all earlier literature reports were as *E. chaetomorphoides*. The Bermuda collection perfectly fits the specifications found in the protologue (Børgesen 1911) and more recent descriptions (Taylor 1960; Littler & Littler 2000). By far, most of the specimens collected on the West Whale surf-impacted rocks were *Lyngbya majuscula* (Dillwyn) Harvey, many fewer being *U. chaetomorphoides*, as is obvious on the prepared herbarium cards. Børgesen (1913) reported this species growing along with the same cyanobacterium in sheltered environments in the Virgin Islands. Our plants are only slightly hollow in basal portions, in most



Figs 1–3. *Ulva chaetomorphoides* (CWS/CEL 02-6-26). Scale bar = 50 μ m.

Fig. 1. Cross-sections of lower axes.

Fig. 2. Lower axis branching and rhizoid production.

Fig. 3. Rhizoid production from proximal cells of axis at base.

places solid with (2–)4 cells forming a cross-section of the blade (Fig. 1). Branching takes place only in basal portions, and rhizoids are issued from several rows of proximal cells (Figs 2, 3), firmly attaching the individuals to rock in the high energy environment.

In the western Atlantic, this species is widely distributed in the Caribbean and Gulf of Mexico (Littler & Littler 2000) as well as being known from Brazil (Joly 1957; Yoneshigue 1985). In the eastern Atlantic, collections from Sierra Leone have been questioned (Lawson & John 1987), and Feldmann's

(1954) record of this species from northwest France was not included in South & Tittley's (1986) North Atlantic checklist.

Caulerpales, Caulerpaceae

Caulerpella ambigua (Okamura) Prud'homme van Reine & Lokhorst (1992, p. 114, figs 1–4, 6, 7, 9–13)

BASIONYM: *Caulerpa ambigua* Okamura (1897, p. 4, pl. 1, figs 3–12)

TYPE LOCALITY: Ogasawara-jima (Bonin Islands), Japan, western Pacific Ocean.

COLLECTIONS: **Bermuda.** CWS/CEL 99-16-18, 22 July 1999, Coot Pond, Achilles Bay, St George's Island, 32°23.2'N, 64°40.7'W, depth 1 m; CWS/CEL 03-37-18, 3 October 2003, Horseshoe Bay, Bermuda Island, 32°15.1'N, 64°49.4'W, depth 1–4 m; CWS/CEL 03-52-25, 8 October 2003, Tobacco Bay, St George's Island, 32°23.3'N, 64°40.7'W, depth 2 m.

Although known as *Caulerpa vickersiae* Børgesen in Taylor's (1960) comprehensive flora for the Caribbean and adjacent areas, a binomial maintained by some (Littler & Littler 2000), this species was merged with *C. ambigua* from the Pacific and moved to the monotypic genus *Caulerpella* Prud'homme van Reine & Lokhorst (1992) on the basis of its eucarpic reproduction. *Caulerpa* J.V. Lamouroux is holocarpic. Bermudian collections of 5–7 mm tall specimens were discovered growing along decumbent bases of *Pterocladia caerulescens* (Kützinger) Santelices & Hommersand and other larger macroalgae. They represent a new northern limit of distribution for this species in the western Atlantic.

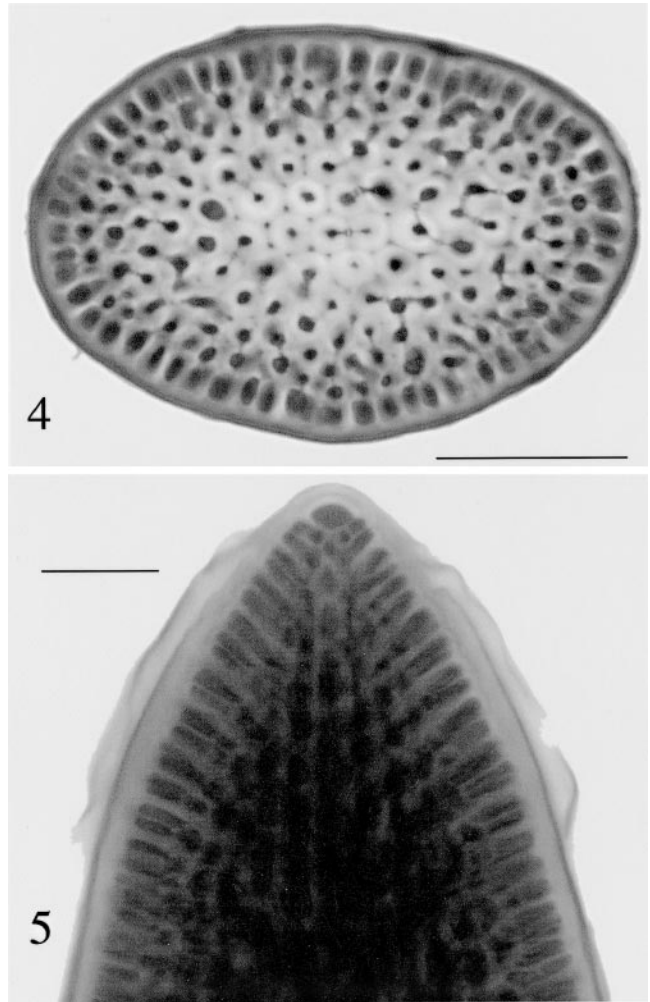
Phaeophyceae: Dictyotales, Dictyotaceae

Dictyota pinnatifida Kützinger (1859, p. 16, pl. 39, fig. 1)

TYPE LOCALITY: Antigua, Lesser Antilles, Caribbean Sea.

SELECTED COLLECTIONS: **Bermuda.** CWS/CEL 01-16-24, 14 November 2001, Canton Point, John Smith's Bay, Bermuda Island, 32°19.0'N, 64°42.8'W, depth 4–9 m; CWS/CEL 01-17-8, male, 14 November 2001, Warwick Long Bay, Bermuda Island, 32°15.3'N, 64°48.6'W, depth 1–3 m on boilers; CWS/CEL 02-3-14, 12 April 2002, Canton Point, *ibid.*; CWS/CEL 02-7-4, 14 April 2002, Warwick Long Bay, *ibid.*; CWS/CEL 03-29-3, 3 April 2003, Horseshoe Bay, Bermuda Island, 32°15.0'N, 64°49.2'W, depth 2 m; CWS/CEL 03-37-14, 3 October 2003, Horseshoe Bay, *ibid.* depth 1–4 m; CWS/CEL 03-52-2, 8 October 2003, Tobacco Bay, St George's Island, 32°23.3'N, 64°40.7'W, depth 1–3 m.

This species is commonly collected on the boiler reefs of the south shore and on outcroppings of the north shore, yet interestingly has not been reported until now from Bermuda. In the past, *Dictyota pinnatifida* was known as *Dilophus alternans* J. Agardh in the Caribbean (Taylor 1960, p. 216), and was transferred to *Dictyota* J.V. Lamouroux by Hörnig *et al.* (1992, 1993). After looking at type material, De Clerck & Coppejans (1997) found the earlier name, *D. pinnatifida*, which superseded *D. alternans* (J. Agardh) Hörnig, Schnetter & Prud'homme van Reine, the name in current usage. Bermudian specimens are highly variable in blade width (1–5 mm), but all have the distinctive alternate branching pattern and, as typical for the species, upper blade portions are monostromatic in the centre flanked by distromatic margins.



Figs 4, 5. *Gelidiella lubrica* (CWS 03-54-2). Scale bars = 25 μ m (Fig. 4) or 50 μ m (Fig. 5).

Fig. 4. Cross-section, erect axis.

Fig. 5. Vegetative axis tip with dome-shaped apical cell.

Rhodophyceae: Gelidiales, Gelidiaceae

Gelidiella lubrica (Kützinger) Feldmann & Hamel (1934, p. 535, figs 3–5)

Figs 4, 5

BASIONYM: *Acrocarpus lubricus* Kützinger (1843, p. 405, pl. 60-II).

TYPE LOCALITY: Naples, Italy, Mediterranean Sea.

COLLECTIONS: **Bermuda.** CWS 03-54-2, 8 October 2003, Harrington Sound, Bermuda Aquarium, Flatts, concrete dock, 32°19.4'N, 64°44.2'W, at MLT mark; CWS 04-2-4, 28 April 2004, Bermuda Aquarium dock, *ibid.*

A sizable population of a small spreading *Gelidiella* Feldmann & Hamel was found on the lowermost step of the BAMZ dock in October growing intermixed with *Herposiphonia tenella* (C. Agardh) Ambronn and *Cladophora conferta* P. Crouan & H. Crouan, a step that is periodically scraped and cleansed of algae for safety purposes. Despite cleansing, *G. lubrica* was still present, albeit in smaller numbers, when the site was revisited six months later. These specimens were not reproductive, but have the classic vegetative morphology

of the genus, including a lack of rhizines in the medulla (Fig. 4), a dome-shaped apical cell (Fig. 5) and an outer cortex with rows in straight or irregularly straight longitudinal rows in surface view (Feldmann & Hamel 1934). Although without tetrasporic plants it is difficult to distinguish between diminutive *Gelidiella* species, many authors have managed to put epithets on their vegetative specimens (e.g. Yoneshigue 1985; Price & Scott 1992; Wynne 1995, 2001b; Shimada & Masuda 1999, 2000), whereas others simply used the designation *Gelidiella* sp. (Cribb 1983). These earlier reports use height of erect branches, diameter of spreading axes and the uprights they bear, level and type of branching present, as well as geographical distributions in discriminating between species.

Our vegetative specimens are less than 1 cm tall, with mostly simple upright axes that are terete near their bases and flatten out somewhat above to a maximum of 100 μm in diameter. The thalli are purplish-red in the field and dry a darker shade, approaching black. Evidence of grazing is present with many of the tips regenerating from wounds. Based on habit, size and morphological characters, the Bermuda collections could be *G. lubrica* (Kützting) Feldmann & Hamel, *G. pannosa* (Feldmann) Feldmann & Hamel, or possibly *G. sanctarum* Feldmann & Hamel among the species of *Gelidiella* known from the Caribbean basin (Wynne 1998). All three species were described and differentiated in Feldmann & Hamel (1934), *G. lubrica* from the Caribbean coast of Colombia (Schnetter 1980), *G. pannosa* from Puerto Rico [Blomquist & Almodovar (1961), as *G. tenuissima* Feldmann & Hamel] and Brazil [Joly *et al.* (1963), as *G. tenuissima*] and *G. sanctarum* from Guadeloupe (Feldmann & Hamel 1934), Caribbean Mexico (Huerta *et al.* 1987), Bonaire (Vroman & Stegenga 1988) and Belize (Littler & Littler 1997). Feldmann & Hamel (1934) describe *G. sanctarum* as having a 'fronde très ramifiée', seemingly ruling out that name for our plants, which have mostly simple uprights, despite the use of the name in instances where the illustrated plants are mostly simple and not highly branched (Littler & Littler 1997, 2000). Feldmann & Hamel (1934) describe *G. lubrica* with terete axes and cortical cells irregularly disposed below the region of the apex, but Hatta & Prud'homme van Reine (1991) found variation in their Indonesian specimens. After evaluating the lectotype of *Gelidium bornetii* Weber-van Bosse (Weber-van Bosse 1926) [= *Gelidiella bornetii* (Weber-van Bosse) Feldmann & Hamel], a somewhat smaller species with compressed to flattened uprights, Hatta & Prud'homme van Reine (1991) found it to be conspecific with *G. lubrica*. They differentiated *G. lubrica* from *G. pannosa* vegetatively on the only character that they found reliable, *G. pannosa* possessing a medulla composed of a single tier of cells. The medulla of our Bermuda plants (Fig. 4) has multiple rows of isomorphic (in cross section) cells larger than the cortex, composed of a few cell layers, in conformity with the concept of Hatta & Prud'homme van Reine (1991) for *G. lubrica*. Cortical cells of the Bermudian plants are 3–6 μm in diameter and up to 7.5 μm long, and are arranged in irregular longitudinal rows in surface view. Based upon their mostly simple and short upright branches, cortical cell patterns and more than a single medullary tier, the Bermudian specimens are best placed under *G. lubrica* until tetrasporangia can be located.

Along with the Caribbean report from Colombia, *G. lubrica* is known from the Mediterranean, South Africa, Indian Ocean,

tropical Australia, Indonesia and Vietnam (Guiry & Nic Dhonncha 2003). The record for Bermuda is only the second in the western Atlantic.

***Pterocladia caerulea* (Kützting) Santelices & Hommersand (1997, p. 118)**

Figs 6–10

BASIONYM: *Gelidium caeruleum* Kützting (1868, pp. 19–20, pl. 56c, d).

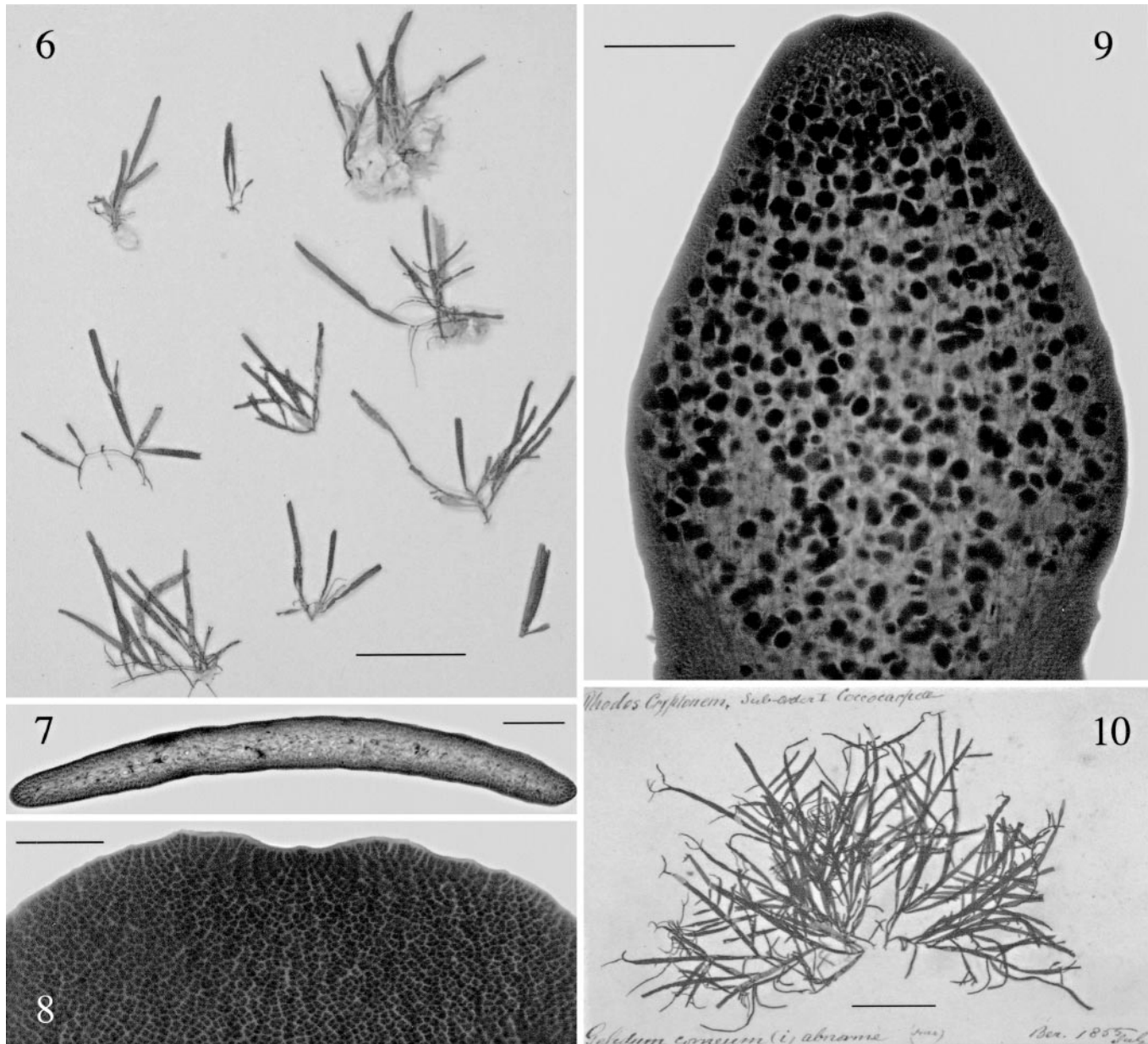
TYPE LOCALITY: Wagap, New Caledonia, south Pacific.

COLLECTIONS: **Bermuda.** A.F. Kemp, July 1855, as *Gelidium corneum* ('i, abnorme') [FH]; CWS/CEL 03-52-7, ⊕, 8 October 2003, Tobacco Bay, St George's Island, 32°23.3'N, 64°40.7'W, on horizontal rock at 2 m.

We have collected specimens in Bermuda that clearly resemble the vegetative and tetrasporic morphology of *P. caerulea*, yet to date we have not found cystocarpic material. This species is highly variable (Santelices 1976, 1978) and less abundantly rebranched and smaller than the more commonly reported species in the western Atlantic, *P. capillacea* (S.G. Gmelin) Santelices & Hommersand (Wynne 1998). The Bermudian specimens have branches that gradually taper to constricted bases, and lack the marked constriction of its sibling species, *P. beachii* Freshwater (Thomas & Freshwater 2001). All of the upright branches of *P. beachii* are rebranched (Thomas & Freshwater 2001), whereas most in the Bermuda population remain simple (Fig. 6). Tetrasporangia have not been found in *P. beachii* to date, so cystocarps are necessary to truly separate it from *P. caerulea*, and these we have yet to find in Bermuda specimens.

Our specimens of *P. caerulea* were collected from thinly populated flat rocks and are 1–2 cm tall from decumbent axes, the uprights either simple or once pinnately to irregularly branched. The strap-shaped blades (Fig. 7) up to 1.2 mm wide and 100 μm thick have abundant rhizines in the medulla, obvious apical cells in truncated axial tips (Fig. 8), peg-like attachments issued from spreading axes, and slightly broadened terminal sporangial sori (Fig. 9) with cruciately divided tetrasporangia that are 27–33 μm in diameter and 30–38 μm long. Specimens from Bermuda have tetrasporangia that are somewhat larger than those cited for Venezuela by Rodríguez de Ríos (1992) (17–20 μm in diameter \times 20–52 μm long), and smaller than those reported from Japan (24–36 \times 44–64 μm) by Shimada & Masuda (2000), but well within the range reported from Australia by Price & Scott (1992) (15–35 μm in maximum diameter). Many reports of this species do not include the dimensions of tetrasporangia. Our plants look remarkably similar to those illustrated as *P. capillacea* by Littler & Littler (2000); both the Caribbean plants (which we have not examined) therein depicted and our specimens have the dark purple to black pigmentation, smaller stature, and branching typical of *P. caerulea* (Kützting 1868; Santelices 1976; Cribb 1983; Hatta & Prud'homme van Reine 1991). This species is widely distributed in the south Pacific, Hawaii and Asia (Shimada & Masuda 2002), the Arabian Sea (Wynne 2001a) and Brazil, Venezuela and Caribbean Mexico (Wynne 1993, 1998).

Pterocladia caerulea was reported for Bermuda by Howe (1918), as *Gelidium caeruleum*, with a question mark, and Taylor (1960, p. 358) listed this species as uncertain



Figs 6–10. *Pterocladia caerulescens*. Scale bars = 50 μ m (Fig. 8), 100 μ m (Fig. 7), 200 μ m (Fig. 9), 1 cm (Fig. 6) or 2 cm (Fig. 10).

Fig. 6. Habit (CWS/CEL 03-52-7).

Fig. 7. Cross section, mid-axis (CWS/CEL 03-52-7).

Fig. 8. Vegetative axis tip with dome-shaped apical cell (CWS/CEL 03-52-7).

Fig. 9. Tip segment with tetrasporangial sorus (CWS/CEL 03-52-7).

Fig. 10. Kemp specimen (FH) from 1855 as *Gelidium corneum* ('i, abnorme').

for the subtropical to tropical western Atlantic, stating 'All American records are probably referable to *Pterocladia americana* W.R. Taylor [= *G. americanum* (W.R. Taylor) Santelices], or less plausibly *G. corneum* (Hudson) J.V. Lamouroux'. Reports subsequent to Taylor (1960) highlighted above proved this speculation wrong. Howe (1918) wrote that axes of his plants of *G. caerulescens* were broader than *G. crinale* (Turner) Gaillon, '1/4–1/2 line' (= c. 0.5–1.0 mm), the branches regularly disposed and coloured red-purple and often iridescent. A 4.5 cm specimen collected and deposited in FH by A.F. Kemp as *G. corneum* (i, abnorme) (Har[vey]), Ber[muda] July 1855 [locality not specified] (Fig. 10), is probably rep-

resentative of what he later published as *G. abnorme* nom. nud. (Kemp 1857), a report repeated and questioned in the literature by Rein (1873) (see Schneider 2003, p. 284). Collins & Hervey (1917) mentioned two specimens in the Kemp herbarium labelled *G. corneum*, one marked 'var. k, abnorme Harv.' and thus presumably from the same Bermuda collection as that in FH, and they found them to 'resemble ordinary European forms' of *G. corneum*, which today could be any number of gelidioids, including *Pterocladia* Santelices & Hommersand, as shown in the on-line AlgaeBase (Guiry & Nic Dhonncha 2003). Examination of the FH 'abnorme' specimen (Fig. 10) allowed us to reasonably identify it as *P. ca-*

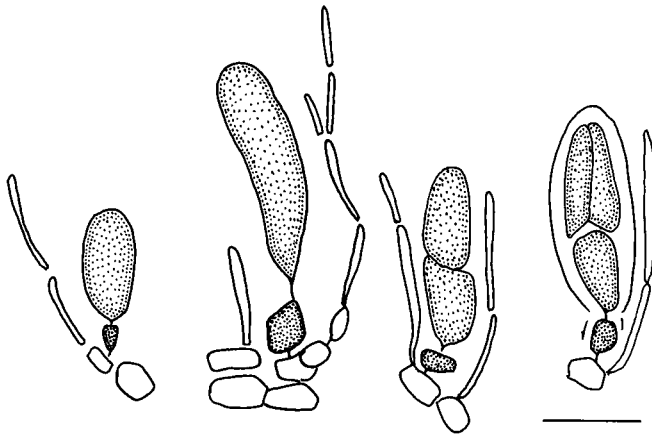


Fig. 11. *Peyssonnelia simulans*. Developmental sequence of sporangia (left to right) (CWS/CEL 03-29-10). Scale bar = 25 μ m.

erulescens despite its vegetative condition and 150 years in a desiccated state. This specimen is considerably larger than the recent Tobacco Bay specimens, and its grazed tips have produced narrower new growth than portions lower on the strap-shaped axes (Fig. 6). A second, narrower *G. corneum* specimen of Kemp's from Bermuda (no date or location given) in FH is highly branched and placed in *G. spinosum* (S.G. Gmelin) P.C. Silva, a species we have yet to collect in the islands.

Gigartinales, Peyssonneliaceae

Peyssonnelia simulans Weber-van Bosse in Børgesen (1916, p. 142, figs 138, 140, 148)

Fig. 11

SYNTYPE LOCALITIES: West of Walter Island, St Thomas, and off St Cruz Bay and Ram's Head, St Jan, Virgin Islands, Greater Antilles, Caribbean Sea.

COLLECTION: **Bermuda**. CWS/CEL 03-29-10, ⊕, 3 April 2003, Horseshoe Bay, Bermuda Island, 32°15.0'N, 64°49.2'W, on intertidal rock.

Abundant individuals of *Peyssonnelia simulans* were found among intertidal algae at the upper edge of a pink band dominated by *Spermothamnion macromeres* Collins & Hervey (CWS/CEL 03-29-11, ⊕) in Horseshoe Bay on the south shore in March 2003. In October 2003, we attempted to recollect this species, but the habitat where it was found was completely inundated by massive rock slides and sand from beach re-configuration due to Hurricane Fabian, which struck the islands on 6 September 2003. At low tide, the *Peyssonnelia* Decaisne thalli were dark purplish-red *in situ*, and upon drying became a dull crimson. The 4–5 cm diameter thalli were loosely attached for more than 1 cm from the margins, but centrally they were somewhat more difficult to remove as there they were firmly fixed to rock by unicellular rhizoids and hypobasal calcification.

Our specimens have morphological features and dimensions matching those reported for *P. simulans* from Cape Lookout jetty, near Beaufort, North Carolina (Schneider & Reading 1987; Schneider & Searles 1991), including smaller tetrasporangia than those described in the protologue (Børgesen 1916). Tetrasporangia from Bermuda thalli are up to 25 μ m

in diameter and 55 μ m in height, and are immersed in raised nemathecium on the upper surfaces. They develop in a pattern typified by *P. squarmaria* (S.G. Gmelin) Decaisne with pseudosympodial paraphyses (Marcot *et al.* 1977) (Fig. 11). Although their vegetative morphology is virtually indistinguishable from that of *P. valentinii* Yoneshigue & Boudouresque (Yoneshigue 1985), recently reported from deeper waters off Bermuda (15–34 m, Schneider & Searles 1998), that species has tetrasporangia developing terminally on perithallial cells without subtending paraphyses as in the *P. rara-avis*-type (Marcot *et al.* 1977; Schneider & Searles 1998). *Peyssonnelia simulans* represents the third verified species in the genus from Bermuda (Schneider 2003).

Gigartinaceae

Chondracanthus saundersii C.W. Schneider & C.E. Lane, *sp. nov.*

Figs 12–18

Plants saxicolous, lubricous, purplish-red, up to 4.5 cm tall, attached by small, discoid holdfasts, giving rise to one or more erect, branched, curved axes, soon becoming secondarily attached by adventitious rhizoidal pads issued from decumbent axes and branches, spreading and becoming entangled (Fig. 12); axes distinctly flattened, up to 1 mm wide and 300 μ m thick in lower portions, irregularly to alternately branched, often secund on recurved branches, tapering to acute apices \pm 200 μ m in diameter (Fig. 13) and less markedly to bases; medulla of loosely entangled elongate filaments, 5–10 μ m in diameter (Fig. 14), giving rise to the radially organized inner cortex with anastomosing, elongate stellate cells, and an outer cortex of one to two globose to ovoid cells bearing ultimate paired narrowly elongate to obclaviform cells, 2–3 μ m in diameter, 4–10 μ m long (Fig. 15), round in surface view; spermatangia developing from outer cortical cells (Fig. 16), formed in slightly raised patches, spherical spermatia 1–2 μ m in diameter; tetrasporangia and carpophytes unknown.

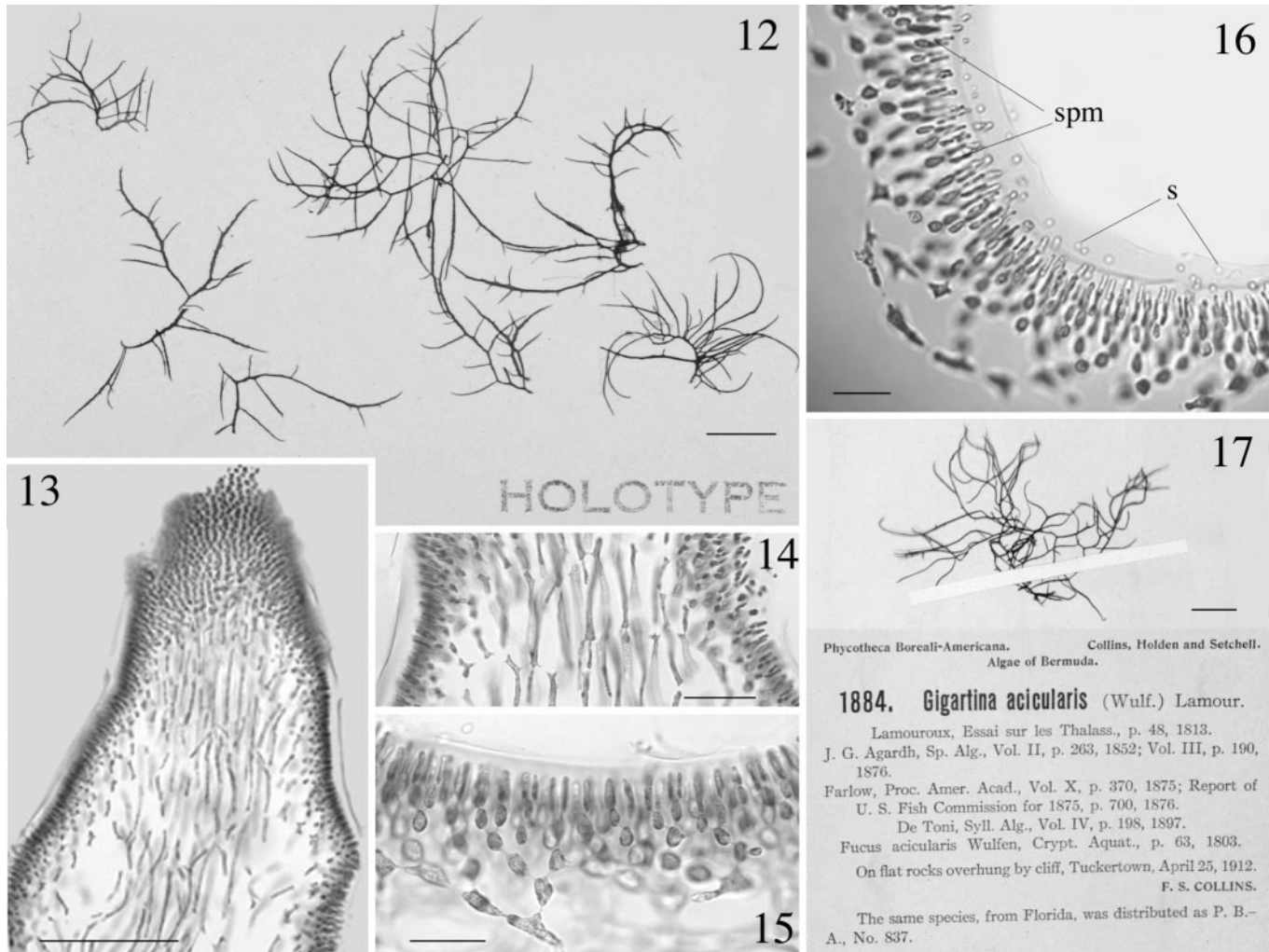
DIAGNOSIS: *Chondracantho aciculari* respectu ordinationem ramorum similis sed axibus angustioribus complanatis lubricis et medulla laxa differt; *Chondracantho teedei* axibus complanatis angustis similis, autem differt parvitate et ramificatione minus copiosa *Chondracanthi saundersii*.

Similar to *Chondracanthus acicularis* in its overall branching pattern but differing in its narrower, flattened, lubricous axes and less dense medulla; similar to *C. teedei* by its flattened narrow axes, but smaller in size and less copiously branched.

TYPE COLLECTION: CWS/CEL 03-16-6, male, 31 March 2003, Walsingham Pond, Hamilton Parish, Bermuda Island, western Atlantic, 32°20.7'N, 64°42.8'W, depth 3–6 m on shaded rock underhangs on north ledge (GenBank accession no. AY698062).

HOLOTYPE (designated here): MICH (Fig. 12); Isotypes: Herb. CWS, MSM, NY, US.

ADDITIONAL COLLECTIONS: **Bermuda**. F.S. Collins, 25 April 1912, Tucker's Town Bay, Castle Harbor, Bermuda Island [P.B.-A. XXXVIII:1884, as *Gigartina acicularis* (Wulfen) J.V. Lamouroux: MICH, Herb. CWS] (Fig. 17); W.R. Taylor (WRT)/A.J. Bernatowicz (AJB) 49-363, 23 March 1949, fish pond, southside of Great Bay, St David's Island, depth 0.5 m [as *G. acicularis*: MICH]; AJB 49-604, 6 April 1949, Walsingham Park, Calabash pool, depth 2 m [as *G. acicularis*: MICH]; CWS/CEL 01-22-23, 16 November 2001, Walsingham Pond, *ibid.*: CWS/CEL 02-9-15, male, 15 April 2002, Walsingham Pond, *ibid.*: CWS/CEL 03-27-3, 3 April 2003, Green Bay, Harrington Sound, on wall at mouth of cave, 32°19.9'N, 64°44.2'W, depth 1–2 m. **Brazil**. W.L. Schmitt 24, male, 24 July 1925, Pedra de Itapuca, Nichtheroy, vic. Rio de Janeiro [as *Gelidium corneum*: MICH]. **Cuba**. E. Baardseth 102, 26 December 1966, Playa Viriato, Havana [as *Gigartina acicularis*: MICH]. **Hai-**



Figs 12–17. *Chondracanthus saundersii* sp. nov. Scale bars = 30 μ m (Fig. 15), 50 μ m (Figs 14, 16), 200 μ m (Fig. 13) or 1 cm (Figs 12, 17).

Fig. 12. Habit, holotype (MICH).

Fig. 13. Axis tip, isotype.

Fig. 14. Central medullary filaments, isotype.

Fig. 15. Cortical rows, isotype.

Fig. 16. Spermatangia (spm) and spermatia (s) in outer cortex; holotype.

Fig. 17. P.B.-A. no. 1884, as *Gigartina acicularis* from Tucker's Town Bay, April 1912 (Herb. CWS).

ti. E. Bartlett 17900, 6 May 1941, Jérémie, La Pointe [as *G. acicularis*: MICH].

ETYMOLOGY: Named in honour of Dr Gary W. Saunders (University of New Brunswick, Fredericton, Canada) for his many significant contributions to the molecular phylogenetics of red and brown algae.

Several collections of this species have recently been made in Walsingham Pond and Harrington Sound from different seasons. The vegetative morphology of these specimens had similarities to *Chondracanthus*, and a comparison of its *rbcL* sequence (CWS/CEL 03-16-6) with *Chondracanthus* and *Gigartina* species in GenBank (Table 1) showed Walsingham Pond specimens firmly embedded in the *Chondracanthus* clade with robust support from all analyses (Fig. 18). The generated phylogenetic tree also differentiated it from *C. acicularis* and *C. teedei*, the two species to which Bermuda specimens had been assigned in the past [Kemp (1857), as *G. teedei*; Collins *et al.* (1912); Collins & Hervey (1917); Taylor

(1960), all as *G. acicularis*], as well as from other species with some morphological similarities. The *rbcL* sequence alignment contained 1364 base pairs from 16 taxa, 13 of which were members of *Chondracanthus*. Unfortunately, the only reproductive cells that have been found in *C. saundersii* are spermatangia and spermatia (Fig. 16), despite several collections of the new species from all seasons and over several years. Male characteristics are not valuable in separating species of *Chondracanthus*.

Chondracanthus (Kützting 1843) was resurrected by Hommersand *et al.* (1993) in their revision of the Gigartiniaceae. A number of species, at that time mostly considered as *Gigartina* (Stackhouse 1809), were transferred to *Chondracanthus*, including *C. acicularis* (lectotype locality: Adriatic Sea) and *C. teedei* (type locality: Portugal). Morphologically, these two species have the most similarities to *C. saundersii*, and both have distributional ranges overlapping it in the western Atlantic. Kemp (1857) was the first to collect *Chondracanthus*

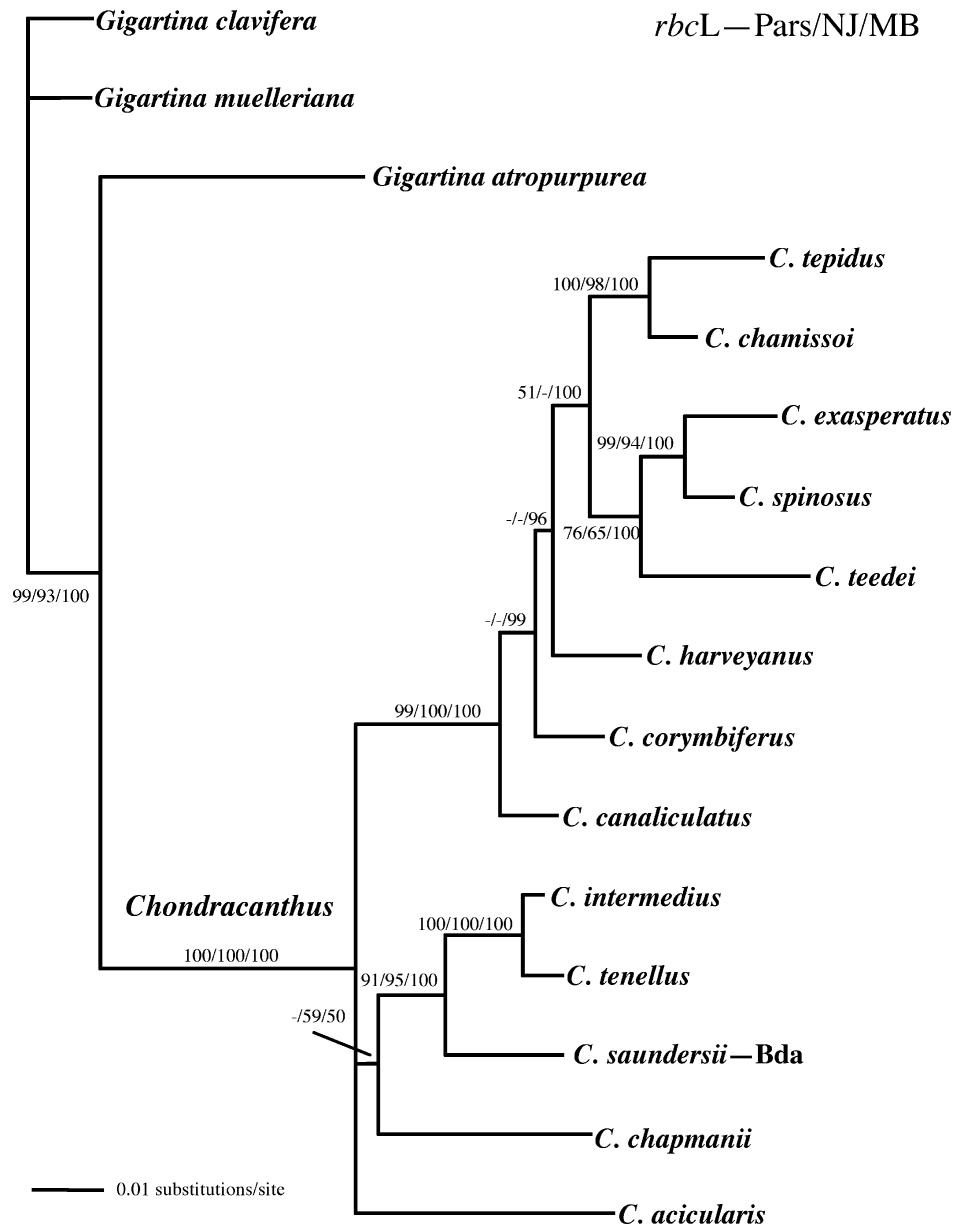


Fig. 18. Bayesian consensus tree for an *rbcL* sequence alignment from 16 species of *Chondracanthus* and *Gigartina* showing the relationship of *C. saundersii* sp. nov. to other species in the genus. *Chondracanthus saundersii* from Bermuda (Bda) is genetically distinct from the morphologically similar *C. acicularis*. Support values are parsimony bootstrap (Pars), neighbour joining bootstrap (NJ) and Bayesian posterior probabilities (MB), respectively. Branch lengths are proportional to the number of base pair substitutions per site.

in Bermuda and, like many other names he applied to the local flora, he chose a European type, *G. teedei*, with which to associate his subtropical specimens. Collins & Hervey (1917) [based upon *P.B.-A.* 1884 (Collins *et al.* 1912)], followed by Howe (1918), looked at the same specimens and determined they were better associated with *G. acicularis*. An examination of *P.B.-A.* 1884 (Fig. 17) and all other previous collections of that species from Bermuda in W.R. Taylor's herbarium (assimilated into MICH) showed that they all belong to the new species, effectively removing *C. acicularis* from the island flora (Schneider 2003). Ironically, although the new *Chondracanthus* is neither of two taxa previously thought by early workers to occur in Bermuda, it is clearly intermediate in habit to both. The distinctly flattened axes and smaller over-

all dimensions and cells sizes of *C. saundersii* easily distinguish it from the robust, cartilaginous *C. acicularis*. *P.B.-A.*, 837 [Atlantic Florida, Collins *et al.* (1901), as *G. acicularis*] is in morphological agreement with *C. acicularis* from Europe and Cape Lookout jetty, North Carolina (Schneider & Searles 1991, as *G. acicularis*), although Florida and North Carolina material should be sequenced to see if *C. acicularis* is truly an amphi-Atlantic species. *Chondracanthus acicularis* specimens are terete, twice the height (up to 10 cm) of *C. saundersii* and have dense filamentous medullas and compact cortices, giving them a wiry texture that maintains its axial form when removed from water. The new flattened species, with its loose medulla and thin cortex, is limp and lubricous out of water. In the *rbcL* tree (Fig. 18), *C. acicularis* from Europe

Table 1. List of taxa used in *rbcL* analysis, their sources and GenBank accession numbers.

Taxon	Location (citation)	GenBank accession number
<i>Chondracanthus acicularis</i> (Roth) Fredericq	Île Verte, Roscoff, Brittany, France (Hommsand <i>et al.</i> 1994)	U02938
<i>Chondracanthus canaliculatus</i> (Harvey) Guiry	Pigeon Point, San Mateo County, CA, USA (Hommsand <i>et al.</i> 1994)	U02939
<i>Chondracanthus chamissoi</i> (C. Agardh) Guiry	Lechagua, Chiloe, Chile (Hommsand <i>et al.</i> 1999)	AF146193
<i>Chondracanthus chapmanii</i> (J.D. Hooker & Harvey) Fredericq	Island Bay, Wellington, New Zealand (Hommsand <i>et al.</i> 1994)	U02940
<i>Chondracanthus corymbiferus</i> (Kützinger) Guiry	Pigeon Point, San Mateo County, CA, USA (Hommsand <i>et al.</i> 1994)	U02941
<i>Chondracanthus exasperatus</i> (Harvey & Bailey) Hughey	Tacoma Narrows, WA, USA (Hommsand <i>et al.</i> 1999)	AF146194
<i>Chondracanthus harveyanus</i> (Kützinger) Guiry	Pacific Grove, CA, USA (Hommsand <i>et al.</i> 1999)	AF146195
<i>Chondracanthus intermedius</i> (Suringar) Hommsand	Tokawa, Choshi, Chiba Prefecture, Japan (Hommsand <i>et al.</i> 1994)	U02942
<i>Chondracanthus saundersii</i> C.W. Schneider & C.E. Lane, <i>sp. nov.</i>	Walsingham Pond, Hamilton Parish, Bermuda (present study, type collection)	AY698062
<i>Chondracanthus spinosus</i> (Kützinger) Guiry	Pacific Grove, CA, USA (Hommsand <i>et al.</i> 1999)	AF148519
<i>Chondracanthus teedei</i> (Mertens <i>ex</i> Roth) Kützinger	Praia de Peruibe, Itanhaém, São Paulo, Brazil (Hommsand <i>et al.</i> 1994)	U02945
<i>Chondracanthus tenellus</i> (Harvey) Hommsand	Wang Hai Xiang, Taiwan (Hommsand <i>et al.</i> 1999)	AF146196
<i>Chondracanthus tepidus</i> (Hollenberg) Guiry	Mission Bay, CA, USA (Hommsand <i>et al.</i> 1999)	AF146198
<i>Gigartina atropurpurea</i> (J. Agardh) J. Agardh	Island Bay, Wellington, New Zealand (Hommsand <i>et al.</i> 1994)	U03423
<i>Gigartina clavifera</i> J. Agardh	Princess Bay, Wellington, New Zealand (Hommsand <i>et al.</i> 1994)	U03424
<i>Gigartina muelleriana</i> Setchell & N.L. Gardner	Flinders jetty, Victoria, Australia (Hommsand <i>et al.</i> 1994)	U03427

occurs in a clade with *C. saundersii*, but it is not as closely related as two western Pacific species, *C. tenellus* and *C. intermedius*. *Chondracanthus teedei*, similar in axial dimensions and overall size to *C. saundersii*, is more robustly branched (Dixon & Irvine 1977; Guiry & Maggs 1985, both as *G. teedei*), and only distantly related to the new species (Fig. 18). One additional species in the western Atlantic, *C. elegans* (Greville) Guiry from Brazil (Cordeiro-Marino 1978, as *G. elegans* Greville), is narrowly strap-shaped and copiously branched (Taylor 1960, as *G. elegans*), like several of the Pacific species and unlike the new species. Braga (1986, as *G. elegans*) considered *C. elegans* a morphological extreme of *C. teedei*, but others maintain them as separate entities (Wynne 1998).

A majority of *Chondracanthus* species are restricted to the Pacific basin (Hommsand *et al.* 1993) and have strap-shaped to foliose blades. Three Pacific species warrant comparison because their branching patterns and narrow axes are somewhat reminiscent of *C. saundersii*. *Chondracanthus chapmanii* is nearly twice the size, has mostly terete axes, and tends towards pinnate branching (Adams 1994, as *G. chapmanii* J.D. Hooker & Harvey). Two species from the Asian Pacific with flattened axes, *C. tenellus* and *C. intermedius*, although somewhat similar in appearance and texture to *C. saundersii*, have more frequent alternately pinnate branches and more layers of cortical cells (Harvey 1860, as *G. tenella* Harvey; Suringar 1870, as *G. tenella* and *G. intermedia* Suringar; Okamura 1908, as *G. tenella*; Segawa 1935, as *Chondrus filiformis* Okamura & Segawa [= *C. tenellus*]; Mikami 1965, as *G. tenella* and *G. intermedia*). *Chondracanthus saundersii* is shown as distinct from these Pacific species in the *rbcL* tree (Fig. 18).

A few specimens in MICH identified as *G. acicularis* can

clearly be assigned to *C. saundersii*, thus extending its range to Haiti and Cuba in the Caribbean, and as far south as Rio de Janeiro, Brazil. Other more robust, terete specimens from these and other western Atlantic sites in MICH are in good agreement with *C. acicularis* from Florida and the Carolinas as mentioned above.

Rhodymeniales, Rhodymeniaceae

Gelidiopsis planicaulis (W.R. Taylor) W.R. Taylor (1960, p. 353)

BASIONYM: *Wurdemannia miniata* var. *planicaulis* W.R. Taylor (1943, p. 158).

TYPE LOCALITY: Jérémie, Haiti, Caribbean Sea.

SELECTED COLLECTIONS: **Bermuda.** CWS/CEL 01-22-19, 16 November 2001, Walsingham Pond, Bermuda Island, 32°20.7'N, 64°42.8'W, depth 2–5 m; CWS/CEL 02-9-25, 15 April 2002, Walsingham Pond, *ibid.*; CWS/CEL 02-10-13, 16 April 2002, Tucker's Town Bay, Castle Harbour, Bermuda Island, 32°19.9'N, 64°41.6'W, depth 2–3 m; CWS/CEL 03-13-2, 30 March 2003, The Dumplings, west of Hall's Island, Harrington Sound, 32°20.3'N, 64°42.8'W, depth 3–5 m; CWS/CEL 03-16-18, 31 March 2003, Walsingham Pond, *ibid.*; CWS/CEL 03-28-10, 3 April 2003, Tucker's Town Bay, *ibid.*; CWS/CEL 03-44-5, 5 October 2003, Cliff Pool, Walsingham Park, Bermuda Island, 32°20.8'N, 64°42.7'W, depth 1–3 m; CWS/CEL 03-52-10, 8 October 2003, Tobacco Bay, St George's Island, 32°23.3'N, 64°40.7'W, in grotto cave from 1 to 2 m.

This wiry species is common in autumn to spring collections in Walsingham Pond and associated pools, Tobacco Bay and Tucker's Town Bay on vertical rock walls to a depth of 5 m. The plants, up to 8 cm tall, are distinctly compressed in upper portions and fit all of the dimensions of the protologue (Taylor 1943, as *Wurdemannia miniata* var. *planicaulis*). This character, as well as its height, separates the species from the

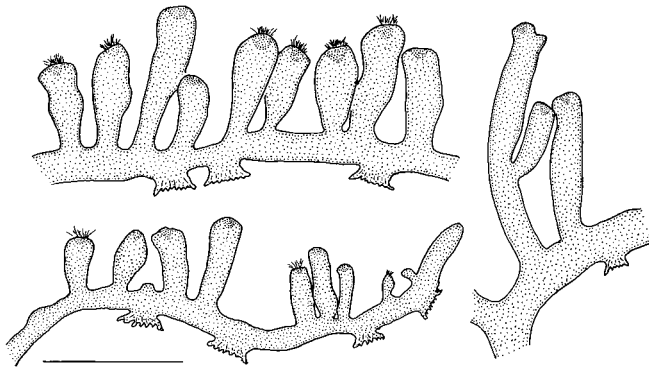


Fig. 19. *Laurencia decumbens*, habit (CWS/CEL 01-15-16). Scale bar = 1 mm.

other known *Gelidiopsis* F. Schmitz in Bermuda, *G. intricata* (C. Agardh) Vickers [P.B.-A. XXXVIII: 1887a, b (1912), as *W. setacea* Harvey; Taylor (1960)].

Littler & Littler (1997, 2000) found evidence in their plants from Belize to maintain the separation of *G. planicaulis* from *G. variabilis* (J. Agardh) F. Schmitz, a synonymy proposed by Norris (1987). Bermuda represents a new northern distributional limit for the species.

Champiaceae

Champia salicornioides Harvey (1853, pp. 76–77, pl. 19 B)

TYPE LOCALITY: Key West, Florida, western Atlantic.

COLLECTIONS. **Bermuda.** WRT/AJB 49-486, 28 March 1949, south side of Castle Rock, depth 0–1 m [MICH]; CWS/CEL 03-29-16, 3 April 2003, Horseshoe Bay, Bermuda Island, 32°15.0'N, 64°49.2'W, depth 1 m.

A single robust specimen was found recently in a crevice on the boilers (undercarved inshore coral reefs) at Horseshoe Bay on the south shore of Bermuda Island. The second collection subsequently discovered in MICH was made more than half a century ago, and was not reported by the collectors (Taylor 1960), who noted on the single specimen card that it was rare in the islands.

Ceramiales, Rhodomelaceae

Laurencia decumbens Kützinger (1863, p. 18)

Fig. 19

TYPE LOCALITY: New Caledonia, southwestern Pacific Ocean.

COLLECTIONS. **Bermuda.** CWS/CEL 01-15-16, 13 November 2001, West Whale Bay, Southampton, Bermuda Island, 32°15.3'N, 64°52.5'W, on intertidal rock; CWS/CEL 02-6-24, 14 April 2002, West Whale Bay, *ibid.*; CWS/CEL 03-36-28, 3 October 2004, West Whale Bay, *ibid.*

Originally known from the Pacific and Indian Oceans (Silva *et al.* 1996), *Laurencia decumbens* has subsequently been reported from the western Atlantic as *L. pygmaea* Weber-van Bosse from Brazil (Oliveira & Ugadim 1974) and Venezuela (Rodríguez de Ríos & Lobo 1984). Jaasund (1970) suggested that *L. pygmaea* was the same as the entity known as *L. decumbens*; this was first effected by Furnari & Cormaci (1990),

then followed by others (Wynne 1995, 1998; Silva *et al.* 1996).

This species is found in a cryptic habitat at the base of *L. microcladia* Kützinger on sand-swept rocks in the intertidal of West Whale Bay along the southwestern coast of Bermuda Island. It is characteristically a spreading species with numerous attachment pads affixing it to rock (Fig. 19). The close-packed uprights are commonly simple although occasional ones are rebranched. In November, conspicuous tufts of trichoblasts were found at the summits of branches (Fig. 19). Prostrate axes range from 170 to 500 µm in diameter and upright branches 180 to 380 µm in diameter, somewhat smaller than those reported from other oceans and those found in Venezuela (uprights 260–460 µm in diameter; Rodríguez de Ríos & Lobo 1984), but larger than those reported from Brazil (149–226 µm in diameter; Oliveira & Ugadim 1974). Until fertile plants are discovered, we choose to maintain these specimens as *L. decumbens*. The report of *L. decumbens* from Bermuda is a new northern distributional limit for the species.

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