

Notes on the marine algae of the Bermudas. 11. More additions to the benthic flora and a phylogenetic assessment of *Halymenia pseudofloresii* (Halymeniales, Rhodophyta) from its type locality

CRAIG W. SCHNEIDER^{1*}, CHRISTOPHER E. LANE² AND GARY W. SAUNDERS³

¹Department of Biology, Trinity College, Hartford, CT 06106-3100, USA

²Department of Biological Sciences, University of Rhode Island, Kingston, RI 02881, USA

³Centre for Environmental & Molecular Algal Research, Department of Biology, University of New Brunswick, Fredericton, NB E3B 5A3, Canada

SCHNEIDER C.W., LANE C.E. AND SAUNDERS G.W. 2010. Notes on the marine algae of the Bermudas. 11. More additions to the benthic flora and a phylogenetic assessment of *Halymenia pseudofloresii* (Halymeniales, Rhodophyta) from its type locality. *Phycologia* 49: 154–168. DOI: 10.2216/09-46.1

This paper contains the first reports of *Veleroa magneana* in the Atlantic Ocean, *Chylocladia schneideri* outside of its type locality in Puerto Rico, and *Verdigellas peltata* and *Cladocephalus luteofuscus* from shallow water. Also reported are new northern limits of distribution for *Chondria leptacremom*, *Dasya antillarum*, *Laurencia caraibica*, *Lomentaria corallicola*, *Myriogramme prostrata* and *Udotea caribaea* as well as the first four mentioned. Fertile gametophytes are documented for *Ptilothamnion speluncarum* for the first time from the type locality. Molecular evidence shows that *Halymenia pseudofloresii*, a species with its type locality in Bermuda, is sister to *Halymenia floresii*, the generitype, in the present analysis. More critically, molecular data establish that *H. pseudofloresii* has a broad range of morphological variation encompassing that displayed by true *H. floresii* and bringing into question reports of the latter from Bermudian waters.

KEY WORDS: Bermuda, *Chondria*, *Chylocladia*, *Cladocephalus*, *Dasya*, *Halymenia*, *H. pseudofloresii*, *Laurencia*, *Lomentaria*, *Myriogramme*, *Ptilothamnion*, *Udotea*, *Veleroa*, *Verdigellas*

INTRODUCTION

After a quarter century of work in the Bermudas, new collections and study of historical vouchers continue to bring new additions to the known flora (Schneider 2003, 2004; Schneider & Lane 2005, 2007, 2008; Schneider *et al.* 2006; Saunders *et al.* 2006; Schneider & Wynne 2009). We report herein several interesting new records of marine algae for the islands, including one, *Veleroa magneana* A. Millar, known previously only from the tropical South Pacific (Millar 1990), and a second, *Verdigellas peltata* D.L. Ballantine & J.N. Norris, for the first time in shallow water.

Because many species have their type localities in Bermuda (Schneider 2003), molecular studies of specimens from the islands are valuable in determining phylogenetic relationships with sequences obtained from Caribbean collections and those from other locations reported for the same or closely related species. Such studies have helped clarify phylogenetic ambiguities and problems (Schneider & Lane 2005, 2008; Saunders *et al.* 2006). In the present paper, *Halymenia pseudofloresii* Collins & Hervey, with a type locality in Walsingham Park, Bermuda, is investigated morphologically and by comparing molecular sequences. Nuclear large subunit (LSU) ribosomal DNA and the protein-coding elongation factor 2 (EF2) of *H. pseudofloresii* from its type locality were compared with other members of the Halymeniales. The species groups with *Halymenia floresii* (Clemente) C. Agardh, the type of the

genus. To assess intraspecific divergence, two variable markers, the mitochondrial cytochrome oxidase subunit I (COI)-5P and universal plastid amplicon (UPA), were utilized and indicate that all collections form a single genetic species despite significant morphological variation.

MATERIAL AND METHODS

Standard methods

Underwater collections were made by snorkeling, scuba or surface-supplied air, and specimens were pressed fresh onto herbarium paper with fragments preserved in 4–5% formalin–seawater and in some cases desiccated in silica gel. Site locations were recorded using a Garmin™ global positioning system (GPS) III Plus (Olathe, Kansas, USA). Herbarium specimens were scanned on an HP 2175 scanner (Hewlett-Packard Company, Palo Alto, California, USA), and photomicrographs were taken using Zeiss Axioskop 40 microscope (Oberkochen, Germany) equipped with a model 11.2 Spot InSight 2 digital camera (Diagnostic Instruments, Sterling Heights, Michigan, USA). The digital images were assembled using Adobe Photoshop™ 10.0.1 (Adobe Systems, San Jose, California, USA). Voucher specimens are deposited in CWS's personal herbarium with duplicates of most sent to MICH, MSM, NY and the Bermuda Natural History Museum (BAMZ), and some to C, DUKE, GALW, UNB and US. The *Phycotheca Boreali-Americana* (P.B.-A.) exsiccata referred to represents the set

* Corresponding author (cschneid@trincoll.edu).

Table 1. Collection details for specimens included in molecular analyses. Sequence data newly determined here indicated in bold type. Collection details only provided where new data were generated for a collection. ND indicates sequences not determined.

Taxon	Collection details	Genbank
<i>Cryptonemia undulata</i> Sonder	G0081 - Portsea, Port Phillip Bay, Vic., Australia. G.T. Kraft & GWS 24 March 1992.	LSU/EF2 COI-5P/UPA AF419133/ GQ471902 ND/ND
<i>Epiphloea bullosa</i> (Harvey) De Toni		DQ343693/EF033562 ND/ND
<i>Gelinararia ulvoidea</i> Sonder	GWS000932 - Queenscliff Jetty, Port Phillip Heads, Vic., Australia. GWS 4 December 2000.	GQ471910/GQ471903 ND/ND
<i>Grateloupia ovata</i> Womersley & J.A. Lewis	GWS000439 - Cape Jaffa, SA, Australia. GTK & GWS 29 October 1998.	GQ471911/ND ND/ND
<i>Grateloupia turuturu</i> Yamada		DQ364071/ND ND/ND
<i>Halymenia floresii</i> (Clemente) C. Agardh	GWS011961 - Armacao de Pere, Portugal. E. Bercibar. 21 August 2005.	GQ471912/GQ471904 GQ862071/ND
<i>Halymenia maculata</i> J. Agardh	GWS001026 - Lord Howe I., NSW, Australia. GWS 11 March 2001.	GQ471913/GQ471905 ND/ND
<i>Halymenia plana</i> Zanardini	GWS001572 - Point Lonsdale Lighthouse Reef, Vic., Australia. GWS 7 December 2002.	GQ471914/GQ471906 ND/ND
<i>Halymenia pseudofloresii</i> Collins & M. Howe	CL033701 (= CWS 03-43-1) - Harbour Pool, Walsingham, Bermuda. CWS & CEL 5 October 2003.	GQ471915/GQ471907 GQ862076/GQ471920
<i>H. pseudofloresii</i>	GWS011901 (= CWS 05-8-7, CL050202) - Walsingham Pond, Bermuda. CWS & CEL 19 July 2005.	ND/ND GQ862075/GQ471921
<i>H. pseudofloresii</i>	GWS011905 (= CWS05-3-1, CL050101) - Harbour Pool, Walsingham, Bermuda. CWS & CEL 17 July 2005.	ND/ND GQ862073/GQ471923
<i>H. pseudofloresii</i>	GWS011902 (= CWS05-9-5, CL050301) - Cliff Pool, Walsingham, Bermuda. CWS & CEL 5 October 2003.	ND/ND GQ862074/GQ471922
<i>H. pseudofloresii</i>	GWS011909 (= CWS 05-8-6, CL050201) - Walsingham Pond, Bermuda. CWS & CEL 19 July 2005.	ND/ND GQ862072/GQ471924
Halymenioid Vic	GWS001562 - Queenscliff Jetty, Port Phillip Heads, Vic., Australia. GWS 7 December 2002.	GQ471916/GQ471908 ND/ND
<i>Isabbottia ovalifolia</i> (Kylin) Balakrishnan		EF033616/EF033563 ND/ND
<i>Norrissia setchellii</i> (Kylin) Balakrishnan		DQ343694/ND ND/ND
<i>Pachymenia carnosia</i> (J. Agardh) J. Agardh		DQ343695/ND ND/ND
<i>Pachymenia lusoria</i> (Greville) J. Agardh	GWS002123 - Pahi, New Zealand. GWS 12 February 2004.	GQ471917/ND ND/ND
<i>Pachymenia orbicularis</i> (Zanardini) Setchell & N.L. Gardner	G0365 - Safety Bay, WA, Australia. GTK & GWS 7 November 1995.	GQ471918/GQ471909 ND/ND
<i>Pachymenia cf. orbicularis</i> (Zanardini) Setchell & N.L. Gardner		DQ343696/ND ND/ND
<i>Polyopes constrictus</i> (Turner) J. Agardh		DQ343697/ND ND/ND
<i>Polyopes tasmanicus</i> (Womersley & J.A. Lewis) Kawaguchi & J.A. Lewis	GWS001526 - Sandy Bay, south of Hobart, Tas., Australia. GWS 29 November 2002.	GQ471919/ND ND/ND
<i>Prionitis sternbergii</i> (C. Agardh) J. Agardh		EF033617/EF033617 ND/ND
<i>Zymurgia chondriopsidea</i> (J. Agardh) J.A. Lewis & Kraft		DQ343698/ND ND/ND

originally purchased by Wellesley College (Massachusetts) now maintained by CWS. When listed, herbarium abbreviations follow the online Index Herbariorum <<http://sweetgum.nybg.org/ih/>> and standard author initials are from Brummitt & Powell (1992).

Molecular methods

Samples used in molecular analyses are recorded in Table 1. Total DNA was extracted following Saunders (1993) with

modifications (Saunders 2008). For purposes of collection assignment to genetic species: COI-5P (Saunders 2005, 2008) was amplified with the primers GazF1 or GrF1 (ACTAATCATAARGATATYGG) and Cox1R1 (Saunders 2009) or GWSFa (CAAAYCAYAARGATATYGAAC) and GWSR (Saunders 2009); and UPA was amplified with p23SrVf1 (Sherwood & Presting 2007) and p23SnewR (TCAGCCTGTTATCCCTAG). For phylogenetic analyses, the LSU ribosomal DNA was amplified according to Harper & Saunders (2001), and the EF2 as in

Le Gall & Saunders (2007). All polymerase chain reaction (PCR) products were cleaned by gel electrophoresis (Saunders 1993) and sequenced using a Big Dye Terminator Cycle Sequencing Ready Reactions DNA sequencing kit (Applied Biosystems, Foster City, California, USA). For the LSU and EF2 the products were sequenced with their specific PCR primers, as well as additional internal primers as outlined in Harper & Saunders (2001) and Le Gall & Saunders (2007). Final sequences (excluding the 5' and 3' PCR regions) were assembled using Sequencher™ 4.2 (Gene Codes Corporation, Ann Arbor, Michigan, USA) on the basis of bidirectional data.

Multiple alignments including the data generated here and additional sequences from GenBank (see Table 1) were prepared in MacClade version 4.06 (Maddison & Maddison 2003). For species identification, the COI-5P and UPA alignments were six taxa and 661 bp and five taxa and 371 bp, respectively. For phylogenetic analyses three alignments were generated. The LSU alignment contained 20 taxa and 2787 sites, of which 115 were excluded as ambiguously aligned. The EF2 alignment included 11 taxa and 1684 sites with no indels. For phylogenetic analyses of these individual alignments, the program Modeltest (Posada & Crandall 1998) was used to identify model parameters and maximum likelihood was completed in PAUP* version 4.0b10 (Swofford 2003; heuristic search with 10 random additions, and with tree bisection–reconnection branch swapping in effect). Robustness was assessed through analyses of 500 bootstrap repetitions under maximum likelihood as outlined. In addition, Bayesian analyses of a combined alignment were completed in Mr. Bayes v3.0b4 (Huelsenbeck & Ronquist 2001) with data partitioned by gene (LSU vs EF2) and by codon for EF2. A GTR + I + G model was implemented with parameters unlinked. Sampling was performed every 1000 generations and analyses were run in parallel for 2 million generations. The appropriate burn-in for each run was determined by plotting the overall likelihood against generations before estimating the posterior probability distribution.

OBSERVATIONS AND DISCUSSION

Chlorophyta, Chlorophyceae, Tetrasporales, Palmellopsidaceae

Verdigellas peltata D.L. Ballantine & J.N. Norris 1994,
p. 369, figs 5–7

TYPE LOCALITY: Off Isla Mona, Puerto Rico, Caribbean Sea, western Atlantic.

COLLECTION: **Bermuda:** C.W. Schneider (CWS)/C.E. Lane (CEL) 06-5-3, 19 June 2006, Tobacco Bay, St George's Island, 32°23.333'N, 64°40.733'W, on rock from 2–3 m in a shaded grotto.

Remarks

A small population of this grass-green crust establishes this genus in Bermuda for the first time. Although a similar taxon is known from deeper offshore waters, *Palmophyllum*

crassum (Naccari) Rabenhorst (Frederick 1963; Searles & Schneider 1987), this species is easily differentiated from *Verdigellas* by its concentrically zonate lobes and more cartilaginous texture (Ballantine & Norris 1994). The Tobacco Bay crusts spread several centimeters over shaded rock, have spherical cells from 3–6 µm in diameter spread throughout a soft gelatinous matrix, the cells demonstrating the cup-shaped plastids typical for the genus. The crusts are attached over much of the ventral surface. Specimens were compared with material from the Bahamas (*Ballantine/ Aponte* 5220, 6 May 1995, Lee Stocking Island, Exumas, from the Nekton Gamma, 122 m [herb. CWS]).

This species was previously reported from the Bahamas (Ballantine & Aponte 2003), the Caribbean Sea (Ballantine & Norris 1994; Littler & Littler 2000), Florida (Dawes & Mathieson 2008) and Brazil (Bravin *et al.* 1999).

Bryopsidales, Udoteaceae

Cladocephalus luteofuscus (P.L. Crouan et H.M. Crouan)
Børgesen 1909, p. 44.

Fig. 1

BASIONYM: *Flabellaria luteofusca* P.L. Crouan & H.M. Crouan in Mazé & Schramm 1878, p. 88.

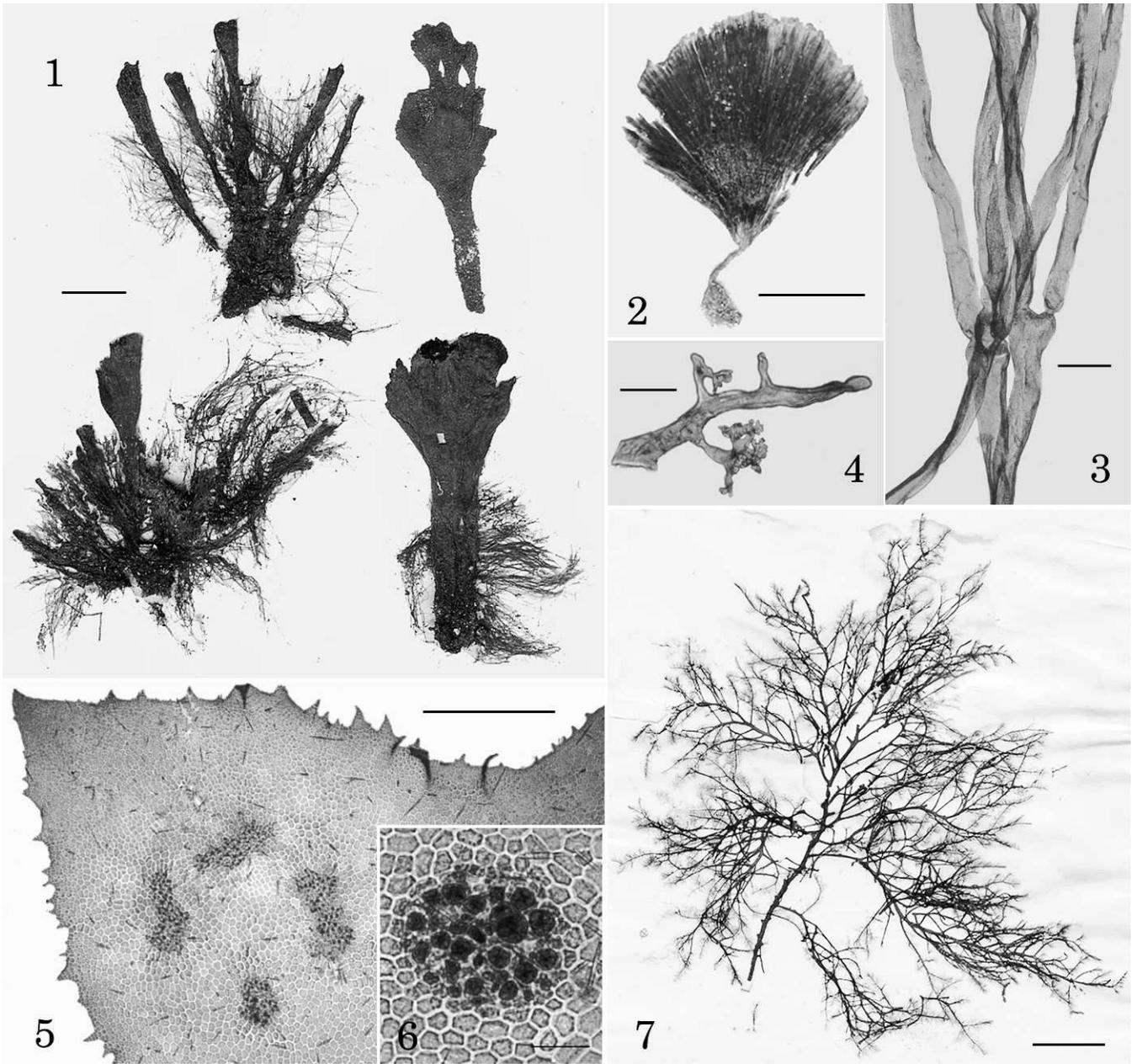
TYPE LOCALITY: Sainte-Martin, Guadeloupe, West Indies, western Atlantic.

COLLECTION: **Bermuda:** A.J. Bernatowicz (AJB) 53-350, 13 May 1953, Millbrook, Bermuda Island, 0–1 m under mangroves [MICH].

Remarks

A collection of specimens in MICH from Millbrook, the south shore bay of Mill Creek in Bermuda, was made by A.J. Bernatowicz in 1953 and the identification as *Cladocephalus luteofuscus* confirmed by W.R. Taylor in both 1956 and 1968. Curiously, this northern range extension was not included by Taylor (1960) in his comprehensive western Atlantic flora. We have also evaluated these specimens and conclude again that the original identification is correct. The margins of the flattened, marginally dissected blades (Fig. 1) have unconsolidated filaments; whereas, the remainder of the blades is covered by a cortex composed of unpigmented, divaricately and dichotomously branched filaments, a feature indicative of the genus (Howe 1905).

Aside from this new northernmost report from Bermuda, *C. luteofuscus* is known from Florida (Littler *et al.* 2008) to Venezuela (Ganesan 1990) and throughout much of the Caribbean (Littler & Littler 2000). It has also been recorded from the Seychelles in the Indian Ocean (Silva *et al.* 1996). In Bermuda, this species might be confused with some species of *Avrainvillea* or lightly calcified *Udotea*. Its congener, *Cladocephalus scoparius* M. Howe, is presently endemic to the Bahamas and has upright filaments formed in a brushlike capitulum reminiscent of *Penicillus* [Howe 1905, pl. 25 (type *P.B.-A.* 1334, Collins *et al.* 1906)], and not organized into a flattened entire or dissected blade like *C. luteofuscus* (Børgesen 1909, 1913). Figures for the two



Figs 1–7. Bermuda marine algae.

- Fig. 1.** *Cladocephalus luteofuscus* (AJB 53-350). Scale bar = 1 cm.
Fig. 2. *Udotea caribaea* (CWS/CEL 09-34-18). Scale bar = 2 cm.
Fig. 3. *U. caribaea* blade siphons [WRT 61-141 (MICH)]. Scale bar = 100 μ m.
Fig. 4. *U. caribaea* stipe cortical siphon [WRT 61-141 (MICH)]. Scale bar = 200 μ m.
Fig. 5. *Myriogramme prostrata*, tetrasporangial tip (CWS/CEL 03-31-7). Scale bar = 1 mm.
Fig. 6. *M. prostrata*, tetrasporangial sorus (CWS/CEL 03-31-7). Scale bar = 100 μ m.
Fig. 7. *Dasya antillarum* [WRT 21810 (MICH)]. Scale bar = 2 cm.

species of *Cladocephalus* in Littler & Littler (2000, p. 397) both appear to be indicative of *C. luteofuscus*.

***Udotea caribaea* D.S. Littler & Littler 1990, p. 211, fig 2**

Figs 2–4

TYPE LOCALITY: Tobacco Range, Belize, Caribbean Sea, western Atlantic.

COLLECTIONS: **Bermuda:** All but the last collected by D.W. Menzel, but bearing W.R. Taylor collection numbers: *WRT* 61-141, 23 February 1961, at edge of Challenger Bank, NE of center, haul 7, depth 52 m [MICH]; *WRT* 61-168, 23 February 1961, NNE border of Challenger Bank, haul 11, depth 55 m [MICH]; *WRT* 61-175, 25 February 1961, NNE border of Challenger Bank, haul 12, depth 52 m [MICH]; *WRT* 61-278, 7 April 1961, Challenger Bank, haul 42, depth

? [MICH]; *WRT* 61-288, 7 April 1961, southern section of Challenger Bank, haul 43, depth *c.* 65 m [MICH]; *CWS/CEL* 09-34-18, 20 March 2009, off middle buoy, Eastern Blue Cut, 32°23'20.6"N, 64°53'19.9"W, depth 15–16 m.

Remarks

Several deepwater collections of *Udotea caribaea* made from an offshore Bermuda seamount were discovered as undetermined collections of the genus in MICH. Subsequent to finding these, a new collection was recently made on the outer reef north of the Dockyard on Ireland Island North (Fig. 2). The specimens have the straight-tipped siphons that are tightly parallel (conglutinate), smooth and constricted at the dichotomies (Fig. 3) as described in the protologue (Littler & Littler 1990). They also match Caribbean specimens in siphon diameters and stipe cortical filament anatomy (Fig. 4), with the recent shallower collection having slightly larger blade siphons (to 60 µm). The Challenger Bank and recent plants are smaller (1–4 cm) than those from shallow water in the Caribbean (4–9 cm), and several show the distinctive concentric bands. The blades are composed of a single layer of siphons except at their bases.

Since its original report, *U. caribaea* has been reported as widespread throughout the Caribbean to 7 m in depth (Littler & Littler 2000; Wysor & Kooistra 2003; Suárez 2005), considerably less than the depths reported here. This species is most similar to *Udotea conglutinata* (J. Ellis & Solander) J.V. Lamouroux (Littler & Littler 1990), a species reported from shallow water in Bermuda (Collins & Hervey 1917; Howe 1918), but only sporadically collected since those reports. The new record from Bermuda extends the depth and biogeographic ranges of *U. caribaea* considerably.

Rhodophyta, Florideophyceae, Ceramiales, Wrangeliaceae

Ptilothamnion speluncarum (Collins & Hervey) D.L. Ballantine & M.J. Wynne 1998, p. 227, figs 1–6

BASIONYM: *Rhodochorton speluncarum* Collins & Hervey 1917, p. 147.

TYPE LOCALITY: Agar Island, Hamilton Harbour, Bermuda, western Atlantic.

COLLECTION: **Bermuda:** *CWS/CEL* 06-21-2, male, female, ⊕, 23 June 2006, Red Hole, St David's Island, 32°22'11.2"N, 64°38'59.4"W, depth 2–3 m.

Remarks

A massive fertile collection of this species was found covering a discarded linen tablecloth in a thick rolling bed of unattached *Heterodasya mucronata* (Harvey) M.J. Wynne in Red Hole, a natural drift accumulation site. The cystocarps, males and tetrasporangia are the first collected from Bermuda, the type locality. The reproductive characteristics of the Bermuda specimens validate those described and illustrated by Ballantine & Wynne (1998) from Puerto Rico and Guimarães & Fujii (2001) from Brazil. Although Ballantine & Wynne (1998) report

polysporangia, as well as tetrasporangia, in Puerto Rico, we have only found tetrahedrally divided sporangia in Bermuda thus far, as was also true for Brazilian specimens (Guimarães & Fujii 2001). Torres *et al.* (2004) previously reported monosporangia for *Ptilothamnion speluncarum* in Brazil. These could represent tetrasporangia before meiosis.

Delesseriaceae

Myriogramme prostrata (E.Y. Dawson, Neushul & Wildman) M.J. Wynne 1990, p. 330, figs 8–13

Figs 5, 6

BASIONYM: *Haraldia prostrata* E.Y. Dawson, Neushul & Wildman 1960, p. 25, figs 4–6.

TYPE LOCALITY: Islas San Benitos, Baja California, Pacific Ocean.

COLLECTIONS: **Bermuda:** *CWS* 03-31-7, ⊕, 3 April 2003, Tobacco Bay, St George's Island, 32°23.3'N, 64°40.7'W, depth 3 m; *CWS/CEL* 06-5-7, ⊕, 19 June 2006, Tobacco Bay, *loc. cit.*, depth 2–3 m; *CWS/CEL* 08-22-43, ⊕, 15 February 2008, off Gurnet Rock, mouth of Castle Harbour, 32°20.162'N, 64°39.731'W, depth 17.4 m.

Remarks

Prostrate, tetrasporangiate plants in conformity with *Myriogramme prostrata* were discovered in the shallow waters of Tobacco Bay on the north shore of Bermuda, as well as in deep water off Gurnet Rock on the south shore. Even if these specimens had not been tetrasporangiate, we most certainly would have assigned all of the Bermuda collections to *M. prostrata* on the basis of its vegetative characteristics, including dentate margins, each of which is in conformity with the protologue (Dawson *et al.* 1960) and the first report from the Atlantic Ocean (Costa Rica, Wynne 1990). However, the protologue and Wynne (1990) reports describe tetrasporangia forming in 'prominent, solitary, rounded sori, each occupying a large area near the end of an ultimate branch'. Guimarães (2006) illustrated her new report of *M. prostrata* for Brazil but showed only the detail of one branch tip that bears a subterminal tetrasporangial sorus. The sori in the Tobacco Bay plants are scattered over apical as well as less distal portions of the blades (Fig. 5), thus raising the question as to whether they are genuine *M. prostrata*. When Littler & Littler (2000), Ballantine *et al.* (2004) and Littler *et al.* (2008) reported plants from the Lesser Antilles, Puerto Rico and Venezuela, and Florida respectively, they noted tetrasporangia in 'discrete scattered sori' but did not report them as restricted to apical regions. Tetrasporangial sori in our plants vary from circular (Fig. 6) to oval, elongate to irregular (Fig. 5). It is possible that all the newly reported Caribbean and Florida plants, as well as those noted here from Bermuda, are *M. prostrata* and that the species indeed has sori not restricted to distal ends of branches. Further collections from Baja California and the western Caribbean might clarify the distinction.

Dasyaceae***Dasya antillarum* (M. Howe) A. Millar 1996, p. 155**

Fig. 7

BASIONYM: *Dasyopsis antillarum* M. Howe 1920, p. 577.

TYPE LOCALITY: Fort George Cay, Caicos Islands, Caribbean Sea.

COLLECTIONS: **Bermuda:** *M.M. Brooks*, ⊕, 1924, Tom Moore's Lake (= Walsingham Pond), Bermuda Island, identified by W.R. Taylor (no. 12810, as *D. ?antillarum*) [MICH]; *CWS/CEL* 02-13-5, 17 April 2002, Ferry Reach cove, St George's Island, 32°22.1'N, 64°41.8'W, on red mangroves.

Remarks

Collections of 3-cm-tall plants on red mangrove prop roots in the heavily silted Ferry Reach are the same as a larger specimen (12 cm) in MICH tentatively identified by W.R. Taylor as *Dasya antillarum* from Bermuda in 1924 (Fig. 7). Both of these collections match the protologue (Howe 1920, as *Dasyopsis antillarum*) specimens from the Caicos Islands and Bahamas. We have observed specimens identified as this species by Howe in MICH, and they compare favorably. The Bermuda plants have percurrent axes that develop indeterminate branches radially at the apex and secondarily become bilaterally organized in lower portions, the axes covered with pseudodichotomously branched determinate pseudolaterals less than 2 mm in length. These characteristics confirmed the species' placement in *Dasya* C. Agardh rather than *Eupogodon* Kützing [= *Dasyopsis* (Montagne) Montagne; see Silva *et al.* 1987] according to Millar (1996). Many of the acute-tipped indeterminate branches become arrested in development, giving them a subspinescent appearance, just as for the plants described by Howe (1920). The archival Walsingham Pond specimen has tetrasporangia that are formed in fusiform to narrowly ovoid stichidia on one-celled pedicels off pseudolaterals, and the globose sporangia are 24–27 µm in diameter after rehydration and mounting.

Dasya antillarum in Bermuda can be easily distinguished from the most common *Dasya* in the islands, the distinctly rigid and densely pilose *Dasya spinuligera* Collins & Hervey, as well as another heavily corticated local species, the long and lax *Dasya baillouviana* (S.G. Gmelin) Montagne, both of which remain radially branched throughout. One other species from Bermuda could be confused with *D. antillarum*. *Dasya ramosissima* Harvey has an alternate to subdichotomous branching pattern with the branches often appearing nearly corymbose when spread on paper. The axes are distinctively covered in dense pseudolaterals only in upper portions and bear ocellate tips, with the axes becoming naked below. These features can be observed in *P.B.-A.* nos 1098, 1099, specimens collected from the Key West, Florida type locality (Collins *et al.* 1903). *Dasya ramosissima* is equally rare as *D. antillarum* in the islands and we have seen only a single specimen that verifies its report in Bermuda (*W.R. Taylor* 56-838, 8 June 1956, Castle Island [MICH]).

In the western Atlantic, *D. antillarum* is found from the Bahamas and Florida and throughout the Caribbean (Guiry & Guiry 2008). Silva *et al.* [1987, as *Eupogodon antillarum* (M. Howe) P.C. Silva] reported this species from the Philippines. Like all of the species reported in this work, Bermuda represents a new northernmost locality for *D. antillarum*.

Rhodomelaceae***Chondria leptacremon* (Melville in G. Murray) De Toni 1903, p. 848**

Figs 8, 9

BASIONYM: *Chondriopsis leptacremon* Melville in G. Murray 1888, p. 333, pl. 284, figs 2a, 2b.

TYPE LOCALITY: Fort Taylor, Key West, Florida, western Atlantic.

COLLECTION: **Bermuda:** *CWS* 96-9-13, 5 July 1996, Walsingham Pond, Bermuda Island, 32°20.7'N, 64°42.8'W, depth 2–3 m.

Remarks

This extremely delicate species of *Chondria* was found growing epiphytically on *Halimeda incrassata* (J. Ellis) J.V. Lamouroux in a landlocked salt pond tidally fed by subterranean caves. Because of its small size, *Chondria leptacremon*, like other diminutive species reported here, was likely overlooked by early collectors. Its vegetative axes measure 270–375 µm in diameter, its clavate branches are basally constricted (Fig. 8) and apical cells are found embedded in blunt terminal depressions (Fig. 9). We have compared our vegetative collection with material from the Florida Keys [in MICH], the protologue and subsequent, more detailed descriptions (Taylor 1960), and can find no differences. This species was previously known from Florida, the Bahamas, the Caribbean Sea and Brazil (Taylor 1960; Ballantine & Aponte 1997; Guimarães 2006; Dawes & Mathieson 2008).

***Laurencia caraibica* P.C. Silva 1972, p. 205**

Figs 10, 11

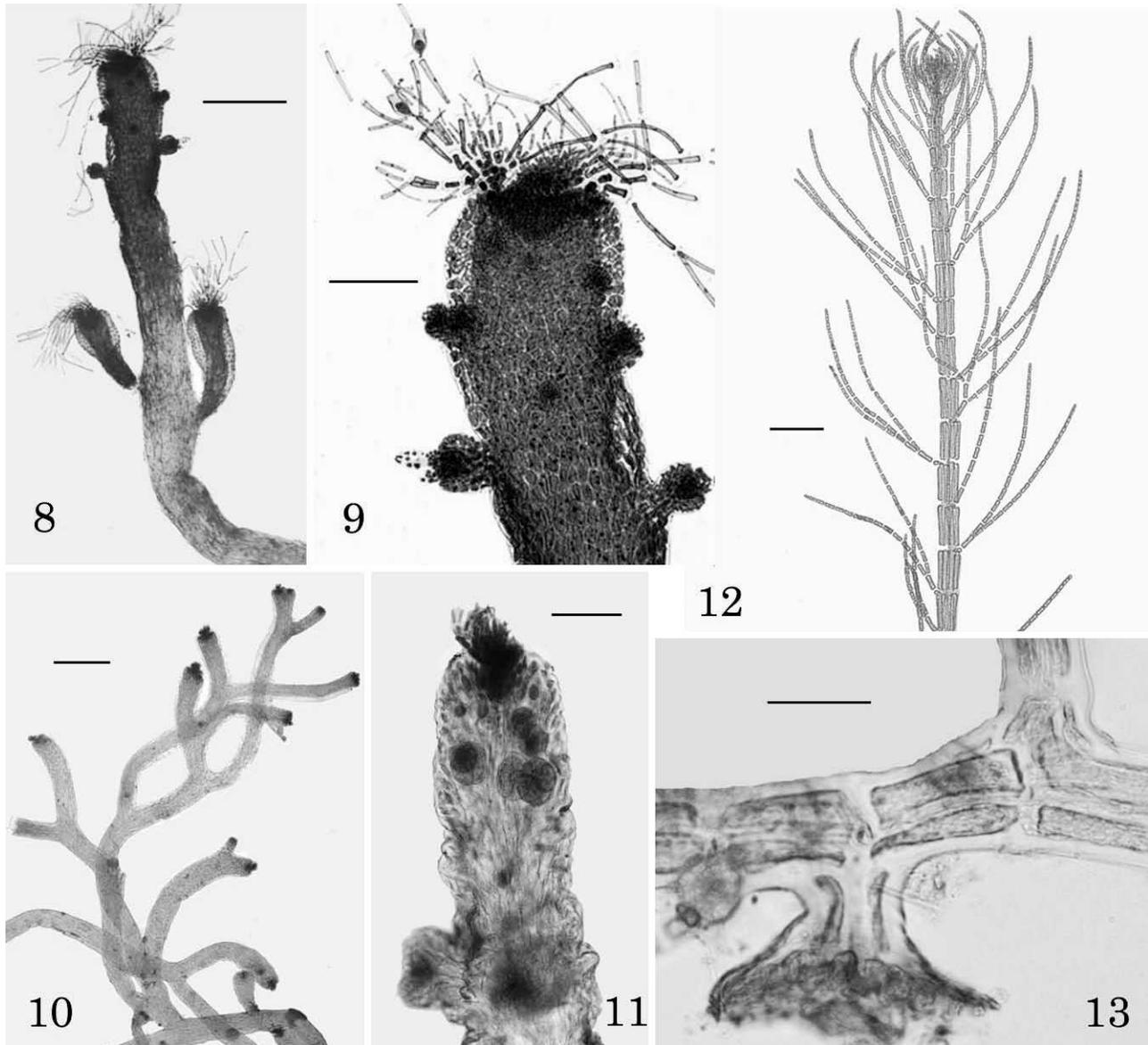
BASIONYM: *Laurencia nana* M. Howe 1920, p. 566 [replaced name]

TYPE LOCALITY: Abraham Bay, Mariguana [Mayaguana], Bahamas, western Atlantic.

COLLECTIONS: **Bermuda:** *CWS/CEL* 05-5-10, ⊕, 17 July 2005, Gibbet Island, Gibbon's Bay, 32°19.4'N, 64°44.6'W, depth 1–2 m on *Udotea*; *CWS* 06-3-5, ⊕, 18 June 2006, Somerset Long Bay Park, Somerset Island, 32°18'14.9"N, 64°52'18.6"W, depth 0.5–1.0 m on *Thalassia*; *CWS/CEL* 06-4-15, ⊕, 18 June 2006, West Whale Bay, Bermuda Island, 32°15'20.9"N, 64°52'24.4"W, on sand-inundated intertidal rock.

Remarks

This species was originally described as *Laurencia nana* M. Howe (Howe 1920, p. 566), but because it was a later



Figs 8–13. Bermuda marine algae.

Fig. 8. *Chondria leptacremom*, branched axis (CWS 96-9-13). Scale bar = 500 μ m.

Fig. 9. *C. leptacremom*, axis tip (CWS 96-9-13). Scale bar = 200 μ m.

Fig. 10. *Laurencia caraibica*, habit (CWS 06-3-5). Scale bar = 500 μ m.

Fig. 11. *L. caraibica*, tetrasporangia in parallel series tip (CWS/CEL 05-5-10). Scale bar = 100 μ m.

Fig. 12. *Veleoia magneana*, erect axis (CWS/RBS 83-4-50). Scale bar = 100 μ m.

Fig. 13. *V. magneana*, digitate hapteron on prostrate axis (CWS/RBS 83-4-50). Scale bar = 25 μ m.

homonym of *L. nana* (C. Agardh) Greville, Silva (1972) provided the new name. We have discovered lax epiphytic and fastigate mat-forming saxicolous tetrasporangiate collections of *Laurencia caraibica* that match the Howe (1920) description in habit and dimensions. The upright branches of this delicate decumbent plant frequently reattach with secondary haptera to other branches or the host, a diagnostic character for this species. The upright axes are terete, alternately to subdichotomously branched and 130–360 μ m in diameter (Fig. 10), the lax epiphytic forms being more slender (to 250 μ m diam.) than those growing on intertidal rock that approach the dimensions described by Howe (1920, 150–450 μ m diam.). Apices are

truncate, and when the tip of a branchlet is tetrasporangiate, the axes broaden toward the tips becoming clavate. When Fujii & Villaça (2003) reported the discovery of this species in Brazil, they studied an isotype collection of *L. caraibica* [US]. They reported that tetrasporangia were 53–76 μ m diameter, forming in a parallel arrangement (see Saito 1966, fig. 3), and that the outer cortex had secondary pit connections. Our Bermuda plants are similar with secondary pit connections and parallel tetrasporangia 34–80 μ m in diameter (Fig. 11).

A table provided by Boisset & Lino (1998) miscategorized *L. caraibica* as lacking secondary pit connections in the outer cortex and possessing tetrasporangia in a right-angle

arrangement using the report of Puerto Rican plants as their guide (Ballantine & Norris 1989). Interestingly, Fujii & Villaça (2003) questioned this latter report, suggesting that the Puerto Rican plants could be another species, presumably on the basis of information corroborated by the isotype (although this is not explicitly stated). Some of the apices in Bermuda specimens bear the sporangia in a single ring near the apex, a situation described by Ballantine and Norris. These are the first 'line' of tetrasporangia produced as other apices have additional rows of tetrasporangia produced in parallel lines similar to those illustrated by Fujii & Villaça (2003). Thus the Puerto Rican plants could merely have just started tetrasporangial production when collected by Ballantine & Norris (1989) and were subsequently misinterpreted as right-angle development by Boisset & Lino (1998) and Fujii & Villaça (2003).

In the Atlantic, *L. caraibica* is found from Brazil and throughout the Caribbean (Fujii & Villaça 2003; Fujii & Senties 2005), and now as far north as Bermuda. It is also reported from India, the Philippines (Silva *et al.* 1996), and the South Pacific (Lobban & Tsuda 2003).

***Veleroa magneana* A. Millar 2000, p. 158, figs 1–10.**

Figs 12, 13

TYPE LOCALITY: North East Herald Cay, Coral Sea, South Pacific Ocean.

COLLECTIONS: **Bermuda:** *CWS/R.B. Searles (RBS)* 83-4-50, 5 August 1983, east of St Catherine's Point, 32°23.9'N, 64°34.3'W, depth 18–21 m; *CWS/RBS* 85-20-19, 15 June 1985, southwest of Long Bar, west of High Point, Bermuda Island, 32°13.7'N, 65°01.0'W, depth 24–27 m.

Remarks

When Millar (2000) described *Veleroa magneana*, he distinguished it from other members of the genus by having decumbent axes that give rise to erect branches bearing simple to branched trichoblasts to 24 cells long. We have collected epiphytic specimens in deep offshore Bermudian waters that compare well in all vegetative features to this species from the tropical South Pacific. Prostrate axes on the Bermuda specimens are 38–60 µm in diameter, and they give rise dorsally to erect polysiphonous branches 26–34 µm in diameter with simple to alternately branched, uniseriate trichoblasts 17–20 cells long (Fig. 12). Millar (2000) observed slightly longer trichoblasts in the Pacific specimens, to 24 cells from base to apex. In the Coral Sea type material (Millar 2000), periaxial cells begin forming at the eighth to 10th axial cell from the apex on erect branches; whereas, those from Bermuda begin developing on the seventh to eighth axial cell. The basal cells of trichoblasts are round to ellipsoidal, with other cells of the trichoblasts being elongate cylindrical. The trichoblasts arch out from their bases and then back toward the erect axes. Multiseriate rhizoids are issued from ventral portions of the decumbent axes at segment nodes, one portion of the rhizoid being issued from the distal end of a periaxial cell, the other from the proximal end of the contiguous periaxial cell, then 'cabling' together (Fig. 13). Upon contact with a host plant, the rhizoids form multicellular digitate haptera (Fig. 13). These characteristics

match those described and illustrated in the protologue (Millar 2000). Despite the conformity of these many features, we do not have reproductive characteristics to compare. Therefore, we have no choice but to assign these deepwater epiphytes to *V. magneana*, extending its range from the South Pacific to the North Atlantic.

Only two other species of *Veleroa* are decumbent, *Veleroa adunca* (J. Agardh) Womersley & Parsons from Australia and Tasmania (Womersley 2003) and *Veleroa complanata* Afonso-Carrillo & Rojas-González, an endemic to the Canary Islands (Afonso-Carrillo & Rojas-González 2004). *Veleroa adunca* is shorter with thicker axes than *V. magneana* and much longer trichoblasts that always branch (Womersley 2003, Afonso-Carrillo & Rojas-González 2004). *Veleroa complanata*, the only other congeneric in the Atlantic, is significantly larger (to 30 mm tall) than *V. magneana* (to 4 mm tall), has axial dimensions 10 times greater and, among other features, is corticated (Afonso-Carrillo & Rojas-González 2004). Afonso-Carrillo & Rojas-González (2004, p. 88) provided a comparative table for the six known species in the genus.

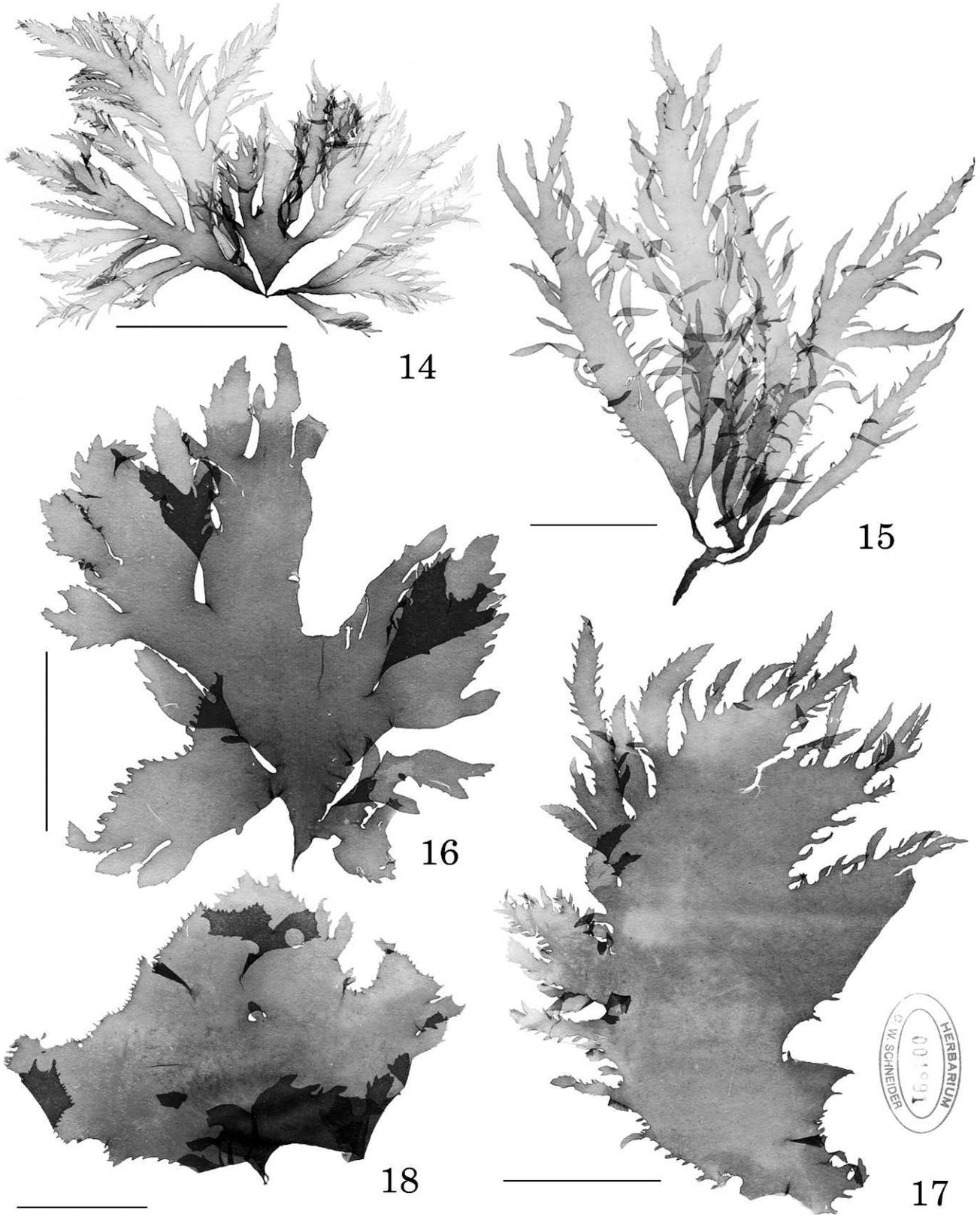
Halymeniales: Halymeniaceae

***Halymenia pseudofloresii* Collins & M. Howe 1916, p. 177**

Figs 14–18

TYPE LOCALITY: Walsingham grotto, Walsingham Park, Bermuda Island, Bermuda, western Atlantic (*P.B.-A.* no. 2099 [FH]).

SELECTED COLLECTIONS: **Bermuda:** *A.B. Hervey (ABH)* *P.B.-A.* 2099, 15 January 1915, Walsingham grotto, *loc. cit.*; *AJB* 51-658 as *Halymenia floresii* (Clemente) C. Agardh, 15 January 1951, Red Hole, St David's Island east; *A.R. Cavaliere*, July 1988, Whalebone Bay, St George's Island; *CWS/CEL* 01-22-11, 16 November 2001, Walsingham Pond, Bermuda Island, 32°20'48.2"N, 64°42'40.9"W, depth 8 m; *CWS/CEL* 03-16-2, 31 March 2003, Walsingham Pond, *loc. cit.*, 3–6 m; *CWS/CEL* 03-24-1, 2 April 2003, Harbour Pool, Walsingham Park vic. Castle Harbour, 32°20'52.3"N, 64°42'34.1"W, 0.5 m; *CWS/CEL* 03-43-1, 5 October 2003, Harbour Pool, Walsingham Park, *loc. cit.*, 0.5 m; *CWS/CEL* 03-44-3, cystocarpic, 5 October 2003, Cliff Pool, Walsingham Park, 32°20'50.2"N, 64°42'41.5"W, 1–3 m; *CWS/CEL* 05-3-1, 17 July 2005, Harbour Pool, Walsingham Park, *loc. cit.*, 0.5 m; *CWS/CEL* 05-4-3, 17 July 2005, Calabash Pool, Walsingham Park, 32°20'51.2"N, 64°42'35.0"W, 0.5 m; *CWS/CEL* 05-8-6, 19 July 2005, Walsingham Pond, *loc. cit.*, 6 m; *CWS/CEL* 05-8-7, 19 July 2005, Walsingham Pond, *loc. cit.*, 6 m; *CWS/CEL* 05-9-5, cystocarpic, 17 July 2005, Cliff Pool, Walsingham Park, *loc. cit.*, 1.0-6.5 m; *CWS* 05-23-1, 23 July 2005, sinkhole pool, Coney Island, 32°21'29.5"N, 64°42'53.5"W, 3 m; *CWS/CEL* 06-16-3, cystocarpic, 22 June 2006, Cliff Pool, Walsingham Park, *loc. cit.*, 2 m; *CWS/CEL* 08-18-3, 14 February 2008, Devil's Hole, off Harrington Sound, 32°19'53.3"N, 64°42'54.4"W, 10 m; *CWS* 08-24-4, 15 February 2008, Tucker's Town Bay chasm, off Castle Harbour, 32°20'01.5"N, 64°41'30.8"W, 1–2 m; *CWS* 08-37-1, ⊕, 18 February 2008, Idwal Hughes Pool, Walsingham Park, 32°20'46.5"N, 64°42'37.3"W, 1 m;



Figs 14–18. Morphological variation in *Halymenia pseudofloresii*. All scales bars = 5 cm.

Fig. 14. Narrow form (CWS/CEL 03-16-2).

Fig. 15. Narrow form (CWS/CEL 05-9-5).

Fig. 16. Intermediate form (CWS/CEL 03-28-3).

Fig. 17. Typical broad form (CWS/CEL 03-24-1).

Fig. 18. Typical broad form (CWS/CEL 03-28-3).

CWS 09-11-2, 16 March 2009, Calabash Pool, *loc. cit.*; CWS 09-32-2, 19 March 2009, Tucker's Town Bay chasm, *loc. cit.*; CWS 09-33-1, 19 March 2009, Tucker's Town public dock, 32°20'06.3"N, 64°41'28.9"W, 1 m.

Remarks

Halymenia pseudofloresii was described by Collins & Howe (1916, p. 177) on the basis of specimens collected 'in a grotto near Walsingham' on Bermuda Island, and Collins *et al.* (1916) included type material in their five Bermuda fascicles of the exsiccata *Phycotheca Boreali-Americana*. Among other things, Collins & Howe (1916) differentiated their new species from *H. floresii* (Clemente) C. Agardh and *Halymenia gelinaria* Collins & M. Howe by 'its deeper color, in the firmer subcoriaceous texture and verruculose surface of its older fronds, and in the mostly clavate-truncate and much elongate superficial cells of the older parts of the frond'. Nearly 100 years after its discovery, this species remains as a common year-round inhabitant of the several sinkhole pools (grottos) and ponds in the Walsingham Park area. Any number of small pools could be the 'grotto' where the type specimen was collected by Hervey, but we suggest it could possibly be a forested deep, azure pool at the mouth of a subterranean cave at the foot of a sizeable cliff in the park (Cliff Pool). In any case, because the small pools to large pond in Walsingham are interconnected by subterranean saltwater-filled caves, the entire area could be considered the type locality.

We have collected numerous specimens in Walsingham over the years containing the typical broad and less deeply dissected frond typical of *H. pseudofloresii*, some over a meter in length, as well as others with more narrowed pinnate branches that could easily be designated as *H. floresii*, a species also recognized in the Bermuda flora (Taylor 1960). Several of the field-collected specimens representing a variety of phenotypes, most from the type locality, were assessed for their divergence in COI-5P and UPA, two markers advocated for DNA barcoding (i.e., assigning unknown specimens to genetic species groups). The COI-5P was generated for five isolates of *H. pseudofloresii*, and a single isolate of *H. floresii* from the eastern Atlantic (Table 1) for comparative purposes. There were 661 base pairs (bp) of COI-5P for comparison with all five *H. pseudofloresii* identical or differing at a single site for an A vs R (ambiguity for A or G) indicating a single species; whereas, *H. floresii* differed from the previous by ca. 7%, consistent with distinct species. In agreement with the previous, the 371 bp of UPA available for comparison were identical in all five *H. pseudofloresii* collections. This tight cluster of narrowly pinnate (Figs 14, 15) to intermediate (Fig. 16) to typical broad (Figs 17, 18) fronds (to 3.8 dm wide and 5 dm long) effectively removes *H. floresii* (type locality, Cádiz, Spain) from the Bermuda flora and raises questions about the species assignment of other narrow, pinnately branched *Halymenia* specimens from the western Atlantic. To place *H. pseudofloresii* in a phylogenetic context, LSU, EF2 and combined analyses were completed. In all cases this species grouped closely with the type (Fig. 19) consistent with anatomical assignment to the genus *Halymenia*. What also became clear in our analyses

was that *Halymenia* is a polyphyletic genus requiring further taxonomic study, but this is not unique to this genus in the family (e.g., *Grateloupia ovata* Womersley & J.A. Lewis does not join the *Grateloupia* clade, and *Pachymenia* has species- and possibly genus-level issues).

Rhodymeniales: Champiaceae

Chylocladia schneideri D.L. Ballantine 2004, p. 127, figs 1–12

Figs 20–22

TYPE LOCALITY: Leeward of Guayacan Island, La Parguera, Puerto Rico, Caribbean Sea.

COLLECTIONS: **Bermuda:** ABH, 19 April 1913, Heron Bay, Bermuda Island [as *Lomentaria baileyana* (Harvey) Farlow] [NY]; CWS 96-4-9b, 2 July 1996, Coot Pond, Achilles Bay, St George's Island, 32°23.2'N, 64°40.7'W, depth 1 m; CWS/CEL 05-5-16, 17 July 2005, Gibbet Island, Gibbon's Bay, 32°19.4'N, 64°44.6'W, depth 1–2 m; CWS/CEL 05-26-14, 24 July 2005, southern Fairyland Creek, Bermuda Island, 32°17'41.9"N, 64°48'05.2"W, depth 2–3 m; CWS/CEL 08-36-3, 17 February 2008, Gravelly Bay, Bermuda Island, 32°19'02.5"N, 64°42'50.4"W, depth 0–1 m.

Remarks

Several collections of *Chylocladia schneideri* have been discovered growing epiphytically on a variety of macroalgae in shallow protected waters. These specimens are the first for the species since its original report from Puerto Rico (Ballantine 2004), and represent a significant northern extension of its range. An historic Bermuda collection made by A.B. Hervey was discovered in NY [*loc. cit.*] filed as *Lomentaria baileyana* (Harvey) Farlow (*det.* W.R. Taylor) (Fig. 20). Although all the plants discovered thus far in Bermuda are vegetative, morphological and anatomical characteristics demonstrate that they fit *C. schneideri*, the only species of this genus in the western Atlantic Ocean (Ballantine 2004; Wynne 2005). Mature axes on the Bermuda prostrate specimens are 350–600 µm (Fig. 21), secondarily attached by rhizoidal clusters issued from nodal regions and are made up of terete internodal segments that are three to four times as long as broad. In young axes, round, darkly staining cortical cells are issued from elongate cortical cells (Fig. 22). In older portions of axes, these cells are larger and no longer darkly staining. Before mounting on slides with the Karo[®]-aniline blue mounting medium (Schneider & Searles 1997), axes were minimally constricted at the diaphragms just as reported for the Puerto Rican plants (Ballantine 2004). Each of these features easily distinguishes *C. schneideri* from the small but somewhat larger and flattened *Champia parvula* v. *prostrata* L.G. Williams, a plant found in similar Bermuda habitats (Schneider & Searles 1997), and the similar-sized *L. corallicola* Børgesen (see below).

Lomentariaceae

Lomentaria corallicola Børgesen 1939, p. 113, figs 30–32

Figs 23, 24

TYPE LOCALITY: Kharg Island, Iran, Persian Gulf.

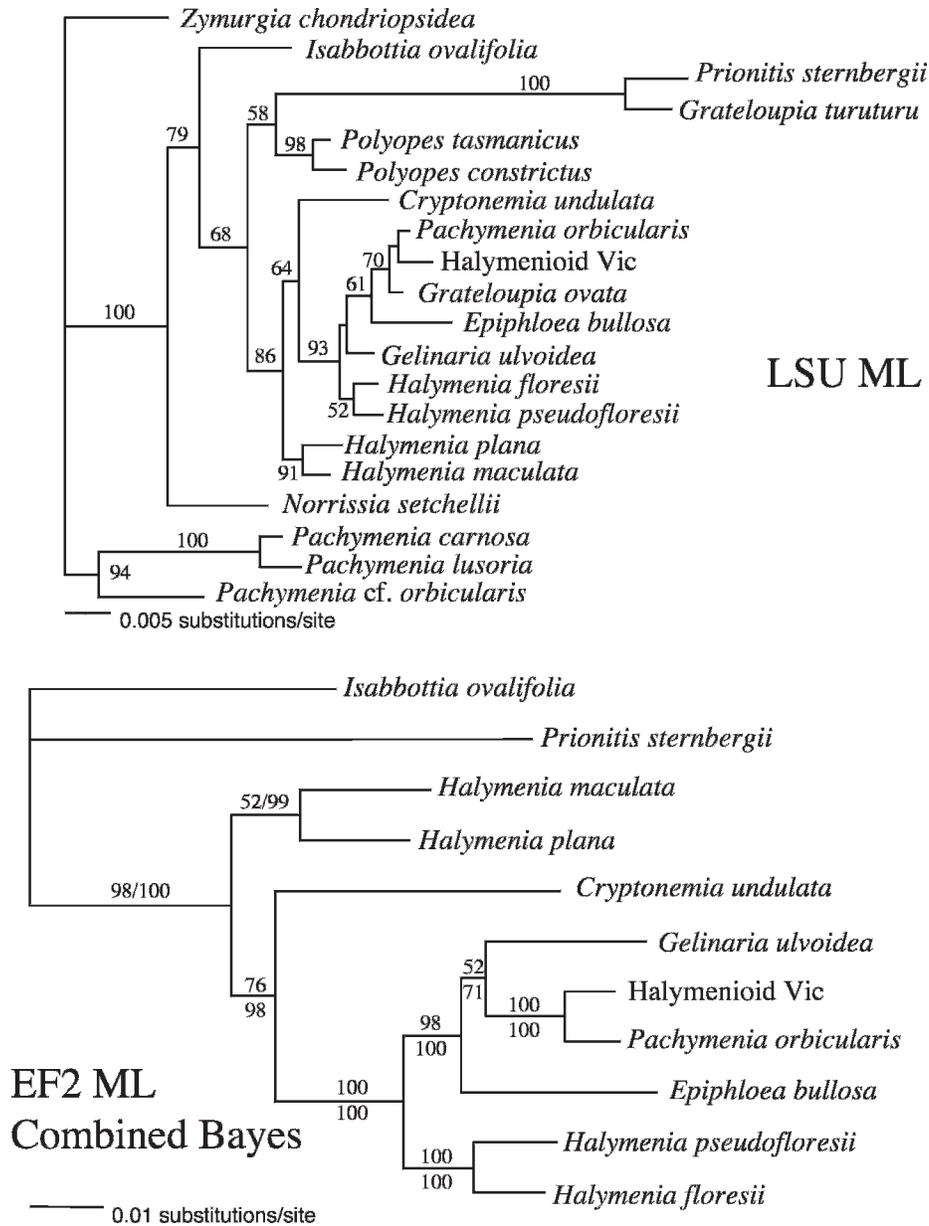


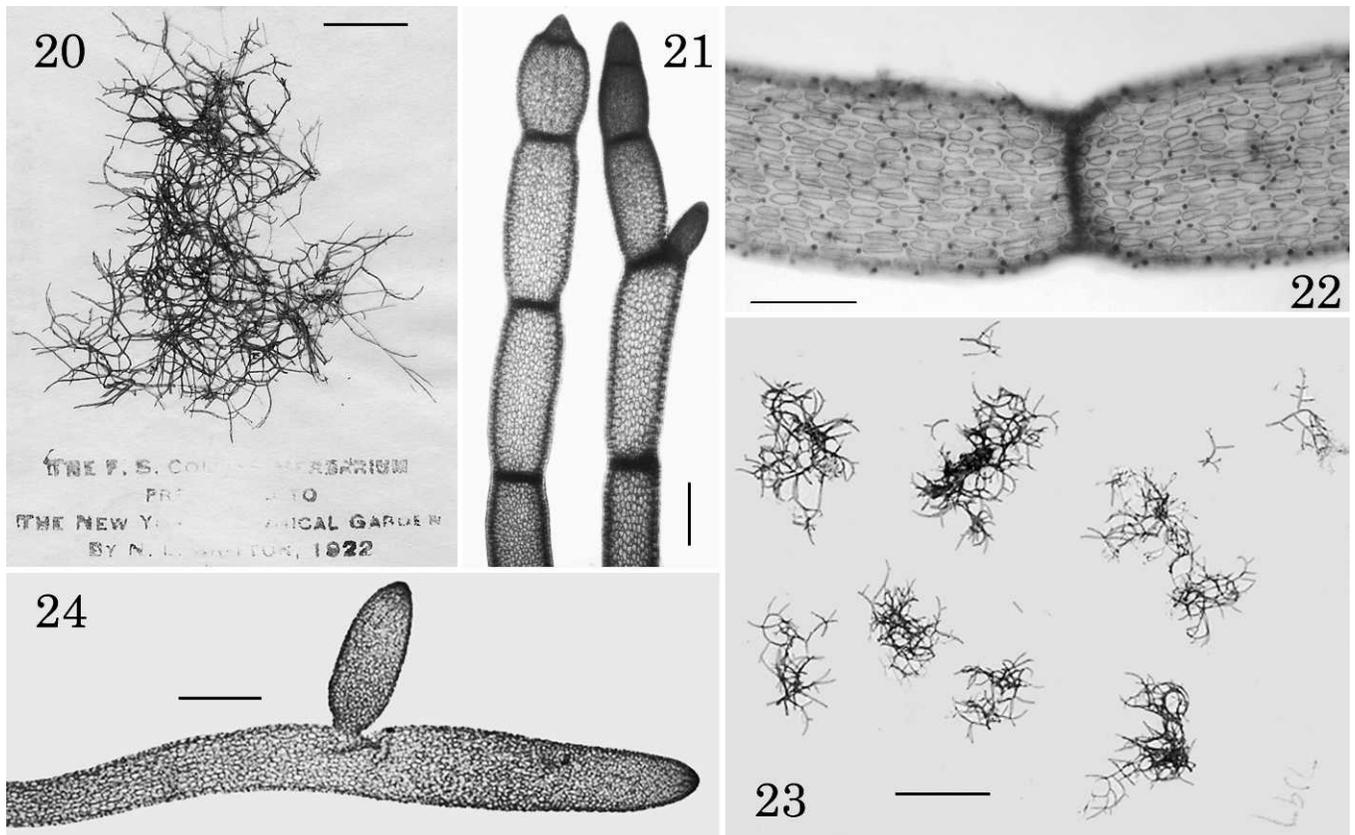
Fig. 19. Maximum likelihood analysis of the LSU alignment with bootstrap support (250 replicates) indicated at nodes (branches lacking values had < 50% support). Maximum likelihood analyses of EF2 alignment with bootstrap support as previous. Second support value indicates posterior probability support from Bayesian analyses of the combined LSU and EF2 alignment (the topology was the same as for the EF2-only analyses).

COLLECTIONS: Bermuda: *Frank S. Collins (FSC)* 7200, 2 May 1912, Hungry Bay, Bermuda Island [as *Lomentaria uncinata* var. *filiformis* (Harvey) Farlow] [NY]; *ABH* 7397, January 1914, Walsingham, Bermuda Island (as *L. uncinata* Meneghini ex Zanardini) [NY]; *AJB* 50-478, 19 December 1950, buoy mooring, Castle Rd., southeast side Castle Harbour (as *L. baileyana*) [MICH]; *AJB* 51-701, 19 January 1951, Turnup Breaker, southeast tip St David’s Island, depth 0 m (as *L. baileyana*) [MICH]; *CWS/RBS* 83-7-23, 7 August 1983, south of Warwick Long Bay, Bermuda Island, 32°13.8’N, 64°48.5’W, depth 40–44 m; *CWS/RBS* 85-1-18, male, 5 June 1985, south of Gibbs Hill lighthouse and Sinky Bay, Bermuda Island, 32°13.0’N, 64°50.5’W, depth 29 m; *CWS/CEL* 08-22-39, ⊕, 15 February 2008, off

Gurnet Rock, mouth of Castle Harbour, 32°20.162’N, 64°39.731’W, depth 17.4 m; *CWS/CEL* 09-23-9, 18 March 2009, Paget Lagoon, Paget Island, 32°22’29.8”N, 64°39’42.3”W, depth 0–1 m.

Remarks

Slender plants collected mostly in deep offshore waters fit the dimensions and spreading habit outlined for this species (Børgesen 1939; Cribb 1983; Yoneshigue 1985; N’Yeurt 2001). In the western Atlantic, *L. corallicola* could be confused only with the equally diminutive *Lomentaria rawitscheri* A.B. Joly, a species found in waters off Brazil (Joly 1957), Cuba (Suárez & Cortez 1983), Venezuela



Figs 20–24. Bermuda marine algae.

Fig. 20. *Chylocladia schneideri*, A.B. Hervey collection (as *Champia*, W.R. Taylor identification as *Lomentaria baileyana*), April 1913, Heron Bay, Bermuda [NY]. Scale bar = 1 cm.

Fig. 21. *C. schneideri*, apical portions of two axes (CWS/CEL 08-36-3). Scale bar = 500 μ m.

Fig. 22. *C. schneideri*, nodal region of two young axial cells demonstrating darkly staining cortical cells cut off elongate cortical cells (CWS/CEL 05-5-16). Scale bar = 200 μ m.

Fig. 23. *Lomentaria corallicola*, A.B. Hervey 7397 (as *L. uncinata*), January 1914, Walsingham, Bermuda [NY]. Scale bar = 1 cm.

Fig. 24. *L. corallicola*, apical portion of axis (CWS/CEL 85-1-16). Scale bar = 500 μ m.

(Ganesan 1990), Atlantic Colombia (Bula-Meyer & Norris 2001, as *L. corallicola* Børgesen) and Puerto Rico (Ballantine *et al.* 2002). Bula-Meyer & Norris (2001) argued that their specimens agreed well with *L. rawitscheri*, but they felt that species fell within the morphological range of *L. corallicola*. Not all workers accepted their synonymy. Ballantine *et al.* (2002) agreed with Yoneshigue (1985), who detailed both species from Brazil, that the differences between them were sufficient to retain each as a distinct taxon.

The spreading Bermuda plants have prostrate axes with arcuate and mostly second erect branches (Fig. 23), diameters ranging from 250 to 500 μ m, rounded apices (Fig. 24), some with tufts of rhizoids for attachment to the algal host on which they spread, all characters in conformity with *L. corallicola* (Børgesen 1939). *Lomentaria rawitscheri* has sharply tapering axes and branches in the type specimen, and the branches are quite broad in the middle portions (to 1 mm diameter), appearing spindle-shaped (July 1957). None of the Bermuda specimens shares this habit. A recent collection off Gurnet Rock was the first where tetrasporangia were found in Bermuda. These are immature (undivided), to 25 μ m diameter, mostly form in sori in stout, broadened ultimate branches arising from

prostrate axes. The protologue described tetrasporangia forming in similar ‘obovate-ellipsoidal’ ultimate branches with diameters of 50 μ m (Børgesen 1939, p.116).

Early reports of *Lomentaria* in Bermuda were attributed to *L. uncinata* Meneghini ex Zanardini and its variety *filiformis* (Harvey) Weber Bosse by Collins & Hervey (1917, p. 115), which were of ‘very small plants among *Poly-siphonia* ... on mangroves’. The only other report of *Lomentaria* from Bermuda was that by Howe (1918, p. 517), who referred only to the ‘slender ... delicate’ specimens collected by Collins and Hervey. We have observed several Collins and Hervey specimens deposited in NY as *L. uncinata* and var. *filiformis* [*loc. cit.*], including two of the three collections mentioned in Collins & Hervey (1917) (Fig. 23), and all represent *L. corallicola*. These diminutive Bermuda specimens are different from those plants described and illustrated in the protologue of *C. baileyana* v. *filiformis* Harvey (Harvey 1853) as ‘very slender, elongate [plants], with longer and less arching branches’ from Long Island, New York, USA, even though Farlow (1881) reported the slender variety as ‘common from Cape Cod southward’. Interestingly, when Cribb (1983) reported specimens of *L. corallicola* from the Great Barrier Reef, he suggested that specimens of *L. uncinata* var. *filiformis* from

the Somoan and Tonga Islands (Grunow 1874) 'may be conspecific with the Queensland material reported here [Australia]'. Two Bermuda specimens deposited in MICH by A.J. Bernatowicz (*loc. cit.*) as *L. baileyana* are also *L. corallicola*. This report of *L. corallicola* from Bermuda, then, represents only the second verified report of the species in the western Atlantic along with Brazil (Guimarães 2006) and has the effect of removing *L. baileyana* from the flora of Bermuda.

ACKNOWLEDGEMENTS

Support for the R/V *Seahawk* cruises was granted by the National Undersea Research Program, National Oceanic and Atmospheric Administration, Wilmington, North Carolina (SU-0683, SU-0683-2), and travel support to Bermuda was provided by a Charles A. Dana Professorship at Trinity College. Financial support for the molecular aspects of this project was provided by the Canadian Barcode of Life Network from Genome Canada through the Ontario Genomics Institute, NSERC and other sponsors listed at www.BOLNET.ca. Additional support was provided by the Canada Research Chair Program, the Canada Foundation for Innovation and the New Brunswick Innovation Foundation. All of the collectors listed in Table 1 are acknowledged for their important contributions to this project, as are Daniel McDevit, Tanya Moore, Brian MacDonald and Rodney Withall for generating the sequence data used in this report. We particularly thank Estibaliz Berecibar for sending eastern Atlantic *Halymenia floresii* on short notice for sequencing. Dr Richard Searles (Duke University) made some of the early collections. Special thanks to Dr Michael Wynne for hosting CWS' visit to the University of Michigan Herbarium, and for pointing out two Bermuda species not previously recorded in the literature. He carefully edited the final draft. We acknowledge loans of herbarium specimens from MICH and NY. Chris Flook, LeeAnne Hinton and Patrick Talbot (Bermuda Aquarium) provided logistical support while in Bermuda. This is contribution no. 162 to the Bermuda Biodiversity Project (BBP) of the Bermuda Aquarium, Natural History Museum and Zoo (BAMZ).

REFERENCES

AFONSO-CARRILLO J. & ROJAS-GONZÁLEZ B. 2004. Observations on reproductive morphology and new records of Rhodomelaceae (Rhodophyta) from the Canary Islands, including *Veleroa complanata* sp. nov. *Phycologia* 43: 79–90.

BALLANTINE D.L. 2004. *Chylocladia schneideri* sp. nov. (Champia-ceae, Rhodophyta) from Puerto Rico, Caribbean Sea. *Cryptogamie, Algologie* 25: 125–132.

BALLANTINE D.L. & APONTE N.E. 1997. A revised checklist of the benthic marine algae known to Puerto Rico. *Caribbean Journal of Science* 33: 150–179.

BALLANTINE D.L. & APONTE N.E. 2003. An annotated checklist of deep-reef benthic marine algae from Lee Stocking Island, Bahamas (western Atlantic), I. Chlorophyta and Heterokontophyta. *Nova Hedwigia* 76: 113–127.

BALLANTINE D.L. & NORRIS J.N. 1989. Notes on the marine algae of Puerto Rico. V. New additions to the flora. *Caribbean Journal of Science* 25: 1–8.

BALLANTINE D.L. & NORRIS J.N. 1994. *Verdigellas*, a new deep-water genus (Tetrasporales, Chlorophyta) from the tropical western Atlantic. *Cryptogamic Botany* 4: 368–372.

BALLANTINE D.L. & WYNNE M.J. 1998. *Ptilothamnion speluncarum* (Collins & Herv.) comb. nov. (Ceramiaceae, Rhodophyta) from Puerto Rico. *Cryptogamie, Algologie* 19: 223–229.

BALLANTINE D.L., RUIZ H. & WYNNE M.J. 2002. Notes on the marine algae of Puerto Rico. VII. Seven new records of benthic Rhodophyta. *Caribbean Journal of Science* 38: 252–256.

BALLANTINE D.L., RUIZ H. & APONTE N.E. 2004. Notes on the benthic marine algae of Puerto Rico. VIII. Additions to the flora. *Botanica Marina* 47: 335–340.

BOISSET F. & LINO J.C. 1998. *Laurencia epiphylla* sp. nov. (Ceramiaceae, Rhodophyta) from the Mediterranean Sea. *Cryptogamie, Algologie* 19: 213–222.

BØRGESEN F. 1909. The species of *Avrainvillea* hitherto found on the shores of the Danish West Indies. *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening i Kjøbenhavn* 1908: 27–44, 8 figs, pl III.

BØRGESEN F. 1913. The marine algae of the Danish West Indies, Part 1: Chlorophyceae. *Dansk Botanisk Arkiv* 1: 1–160 [map].

BØRGESEN F. 1939. Marine algae from the Iranian Gulf especially from the innermost part near Bushire and the Island Kharg. In: *Danish scientific investigations in Iran, Part 1* (Ed. by K. Jessen & R. Spärck), pp. 47–141. Einar, Munksgaard: Copenhagen.

BRAVIN I.C., TORRES J., GURGEL C.F.D. & YONESHIGUE-VALENTIN Y. 1999. Novas ocorrências de chlorofíceas marinhas de profundidade para o Brasil. *Hoehnea* 26: 121–133.

BRUMMITT R.K. & POWELL C.E. 1992. *Authors of plant names*. Royal Botanic Gardens, Kew. 732 pp.

BULA-MEYER G. & NORRIS J.N. 2001. Notes on new records of red algae from the Colombian Caribbean. *Botanica Marina* 44: 351–360.

COLLINS F.S. & HERVEY A.B. 1917. The algae of Bermuda. *Proceedings of the American Academy of Arts & Sciences* 53: 1–195.

COLLINS F.S. & HOWE M.A. 1916. Notes on species of *Halymenia*. *Bulletin of the Torrey Botanical Club* 43: 169–182.

COLLINS F.S., HOLDEN I. & SETCHELL W.A. 1903. *Phycotheca Boreali-Americana* (Exsiccata), Algae of North America. Fascicle XXII. Algae of Bermuda. Nos. 1051–1100. Malden, Mass.

COLLINS F.S., HOLDEN I. & SETCHELL W.A. 1906. *Phycotheca Boreali-Americana* (Exsiccata), Algae of North America. Fascicle XXVII. Nos. 1301–1350. Malden, Mass.

COLLINS F.S., HOLDEN I. & SETCHELL W.A. 1916. *Phycotheca Boreali-Americana* (Exsiccata), Algae of North America. Fascicle XLII. Algae of Bermuda. Nos. 2051–2100. Malden, Mass.

CRIBB A.B. 1983. *Marine algae of the Great Barrier Reef, part I: Rhodophyta*. Australian Coral Reef Society, Handbook no. 2. Watson Ferguson & Co., Brisbane. 173 pp., 71 pls

DAWES C.J. & MATHIESON A.C. 2008. *The seaweeds of Florida*. University Press of Florida, Gainesville, Florida. [1]2–591, [592] pp., pls I–LI pp.

DAWSON E.Y., NEUSHUL M. & WILDMAN R.D. 1960. New records of sublittoral marine plants from Pacific Baja California. *Pacific Naturalist* 1: 3–30.

DE TONI G.B. 1903. *Sylloge algarum omnium hucusque cognitarum. Vol. IV. Florideae. Sectio III*. Patavii [Padua]. 775, 775 bis, 776, 777 bis, 777–1521 + 1523–1525 pp.

FARLOW W.G. 1881. *Marine algae from New England and adjacent coast*. Rept. U.S. Comm. Fish Fisheries for 1879, Washington, DC. 209 pp., 15 pls.

FREDERICK J.J. 1963. *The marine algae of the Bermuda platform*. Ph.D. thesis. University of Michigan, Ann Arbor. 92 pp.

FUJII M.T. & SENTIES A. 2005. Taxonomia do complexo *Laurencia* (Rhodomelaceae, Rhodophyta) no Brasil, com ênfase nas espécies dos estados de São Paulo e do Espírito Santo. *Monografias Ficológicas* 2: 69–135.

FUJII M.T. & VILLAÇA R. 2003. On the occurrence of *Laurencia caraibica* (Ceramiaceae, Rhodophyta) in Atol das Rocas, Brazil. *Hidrobiológica* 13: 33–38.

GANESAN E.K. 1990. *A catalog of benthic marine algae and seagrasses of Venezuela*. Fondo Editorial Conicit, Caracas. 237 pp., 15 maps.

- GRUNOW A. 1874. Algen der Fidschi-, Tonga- und Samoa-Inseln, gesammelt von Dr. E. Graffe. *Journal des Museums Godeffroy (Hamburg)* 3: 23–50.
- GUIMARÃES S.M.P.B. 2006. A revised checklist of benthic marine Rhodophyta from the state of Espírito Santo, Brazil. *Boletim do Instituto de Botânica* 17: 143–194.
- GUIMARÃES S.M.P.B. & FUJII M.T. 2001. *Ptilothamnion speluncarum* (Ceramiaceae, Rhodophyta): estudo das estruturas reprodutivas femininas confirma a presença do gênero no Brasil. *Hoehnea* 28: 297–305.
- GUIRY M.D. & GUIRY G.M. 2008. AlgaeBase, www electronic publication, National University of Ireland, Galway. <http://www.algaebase.org> (06 August 2008).
- HARPER J.T. & SAUNDERS G.W. 2001. Molecular systematics of the Florideophyceae (Rhodophyta) using nuclear large and small subunit rDNA sequence data. *Journal of Phycology* 37: 1073–1082.
- HARVEY W.H. 1853. Nereis boreali-americana. Part II. Rhodospiraeae. *Smithsonian Contributions to Knowledge* 5: 1–258, pls. XIII–XXXVI.
- HOWE M.A. 1905. Phycological studies—II. New Chlorophyceae, new Rhodophyceae, and miscellaneous notes. *Bull. Torrey Bot. Club* 32: 563–586, pls. 23–29.
- HOWE M.A. 1918. Algae. In: *Flora of Bermuda* (Ed. by N.L. Britton), pp. 489–540. Charles Scribner's Sons, New York.
- HOWE M.A. 1920. Algae. In: *The Bahama flora* (Ed. by N.L. Britton & C.F. Millspaugh), pp. 553–618. New York.
- HUELSENBECK J.P. & RONQUIST F. 2001. MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics* 17: 754–755.
- JOLY A.B. 1957. Contribuição ao conhecimento da flora fitológica marinha da Baía de Santos e arredores. *Boletim de Faculdade de Filosofia, Ciências e Letras, Universidade de São Paulo, Botânica* 14: 1–199 + pls I–XIX.
- LE GALL L. & SAUNDERS G.W. 2007. A nuclear phylogeny of the Florideophyceae (Rhodophyta) inferred from combined EF2, small subunit and large subunit ribosomal DNA: establishing the new red algal subclass Corallinophycidae. *Molecular Phylogenetics and Evolution* 43: 1118–1130.
- LITTLER D.S. & LITTLER M.M. 1990. Systematics of *Udotea* species (Bryopsidales, Chlorophyta) in the tropical western Atlantic. *Phycologia* 29: 206–252.
- LITTLER D.S. & LITTLER M.M. 2000. *Caribbean reef plants*. OffShore Graphics, Inc., Washington, DC. 542 pp.
- LITTLER D.S., LITTLER M.M. & HANISAK M.D. 2008. *Submersed plants of the Indian River Lagoon*. OffShore Graphics, Inc., Washington, DC. 286 pp.
- LOBBAN C.S. & TSUDA R.T. 2003. Revised checklist of benthic macroalgae and seagrasses of Guam and Micronesia. *Micronesica* 35–36: 54–99.
- MADDISON W.D. & MADDISON D.R. 2003. MacClade v. 4.06., Sinauer Associates, Sunderland, Massachusetts.
- MAZÉ H. & SCHRAMM A. 1878 (*1870–1877*). *Essai de classification des algues de la Guadeloupe*. 2e édition. Basse-Terre (Guadeloupe). [Errata] + 283 pp.
- MILLAR A.J.K. 1990. Marine red algae of the Coffs Harbour region, northern New South Wales. *Australian Systematic Botany* 3: 293–593.
- MILLAR A.J.K. 1996. *Dasya roslyniae* sp. nov. (Dasyaceae, Rhodophyta), with a discussion on generic distinctions among *Dasya*, *Eupogodon*, *Rhodoptilum*, and *Pogonophorella*. *Journal of Phycology* 32: 145–157.
- MILLAR A.J.K. 2000. *Veleroa magneana* (Brongniartelleae, Ceramiaceae), a new red algal species from the Coral Sea, South Pacific. *Cryptogamie, Algologie* 21: 157–165.
- MURRAY G. 1888. Catalogue of the marine algae of the West Indian region. *Journal of Botany [London]* 26: 193–196, 237–243, 303–307, 331–338, 358–363, pl. 284.
- N'YEURT A.D.R. 2001. Marine algae from the Suva Lagoon and reef, Fiji. *Australian Systematic Botany* 14: 689–869.
- POSADA D. & CRANDALL K.A. 1998. Modeltest: testing the model of DNA substitution. *Bioinformatics* 14: 817–818.
- SAITO Y. 1966. On the secondary pit-connections among cortical cells of some Japanese species of *Laurencia*, with special reference to their systematic significance. *Bulletin of the Japanese Society of Phycology* 14: 70–75.
- SAUNDERS G.W. 1993. Gel purification of red algal genomic DNA: an inexpensive and rapid method for the isolation of polymerase chain reaction-friendly DNA. *Journal of Phycology* 29: 251–254.
- SAUNDERS G.W. 2005. Applying DNA barcoding to red macroalgae: a preliminary appraisal holds promise for future applications. *Philosophical Transactions of the Royal Society B* 360: 1879–1888.
- SAUNDERS G.W. 2008. A DNA barcode examination of the red algal family Dumontiaceae in Canadian waters reveals substantial cryptic diversity. 1. The foliose *Dilsea-Neodilsea* complex and *Weeksia*. *Botany* 86: 773–789.
- SAUNDERS G.W. 2009. Routine DNA barcoding of Canadian Gracilariales (Rhodophyta) reveals the invasive species *Gracilaria vermiculophylla* in British Columbia. *Molecular Ecology Resources* 9(Suppl. 1): 140–150.
- SAUNDERS G.W., LANE C.E., SCHNEIDER C.W. & KRAFT G.T. 2006. Unraveling the *Asteromenia peltata* species complex with clarification of the genera *Halichrysis* and *Drouetia* (Rhodymeniaceae, Rhodophyta). *Canadian Journal of Botany* 84: 1581–1607.
- SCHNEIDER C.W. 2003. An annotated checklist and bibliography of the marine macroalgae of the Bermuda islands. *Nova Hedwigia* 76: 275–361.
- SCHNEIDER C.W. 2004. Notes on the marine algae of the Bermudas. 6. Some rare or newly reported Ceramiaceae (Rhodophyta), including *Crouania elisiae* sp. nov. *Phycologia* 43: 563–578.
- SCHNEIDER C.W. & LANE C.E. 2005. Notes on the marine algae of the Bermudas. 7. Additions to the flora including *Chondracanthus saundersii* sp. nov. (Rhodophyta, Gigartinaceae) based on *rbcL* sequence analysis. *Phycologia* 44: 72–83.
- SCHNEIDER C.W. & LANE C.E. 2007. Notes on the marine algae of the Bermudas. 8. Further additions to the flora, including *Griffithsia aestivana* sp. nov. (Ceramiaceae, Rhodophyta) and an update on the alien *Cystoseira compressa* (Sargassaceae, Heterokontophyta). *Botanica Marina* 50: 128–140.
- SCHNEIDER C.W. & LANE C.E. 2008. Notes on the marine algae of the Bermudas. 9. The genus *Botryocladia* (Rhodophyta, Rhodymeniaceae), including *B. bermudana* *B. exquisita* and *B. flookii* spp. nov. *Phycologia* 47: 614–629.
- SCHNEIDER C.W. & SEARLES R.B. 1997. Notes on the marine algae of the Bermudas. 2. Some Rhodophyta, including *Polysiphonia tongatensis* and a discussion of the *Herposiphonia secundaltevella* complex. *Cryptogamie, Algologie* 18: 187–210.
- SCHNEIDER C.W. & WYNNE M.J. 2009 [*2008*]. Notes on the marine algae of the Bermudas. 10. *Woelkerlingia sterreri* sp. nov. (Rhodophyta, Wrangeliaceae), a first record of the genus in the western Atlantic. *Caribbean Journal of Science* 44: 303–310.
- SCHNEIDER C.W., LANE C.E. & SAUNDERS G.W. 2006. *Crassitigula walsinghamii* (Sebdeniaceae, Halymeniales), a new red algal genus and species from Bermuda based upon morphology and SSU rDNA sequence analyses. *European Journal of Phycology* 41: 115–124.
- SEARLES R.B. & SCHNEIDER C.W. 1987. Observations on the deep water flora of Bermuda. *Hydrobiologia* 151/152: 261–266.
- SHERWOOD A.R. & PRESTING G.G. 2007. Universal primers amplify a 23S rRNA plastid marker in eukaryotic algae and cyanobacteria. *Journal of Phycology* 43: 605–608.
- SILVA P.C. 1972. Remarks on algal nomenclature V. *Taxon* 21: 199–205.
- SILVA P.C., MEÑEZ E.G. & MOE R.L. 1987. Catalog of the benthic marine algae of the Philippines. *Smithsonian Contributions to the Marine Sciences* 27: 1–179.
- SILVA P.C., BASSON P.W. & MOE R.L. 1996. Catalogue of the benthic marine algae of the Indian Ocean. *University of California Publications in Botany* 79: 1259 pp.
- SUÁREZ A.M. 2005. Lista de las macroalgas marinas Cubanas. *Revista de Investigaciones Marinas* 26: 93–148.
- SUÁREZ A.M. & CORTEZ I. 1983. Riqueza del fitobentos en una zona de la costa norte de la Habana. *Revista de Investigaciones Marinas* 4: 3–21.
- SWOFFORD D.L. 2003. PAUP*. Phylogenetic analyses using parsimony (* and other methods)., Sinauer Associates, Sunderland, Massachusetts.

- TAYLOR W.R. 1960. *Marine algae of the eastern tropical and subtropical coasts of the Americas*. University of Michigan Press, Ann Arbor. 879 pp.
- TORRES J., BARRETO PEREIRA S.M. & YONESHIGUE-VALENTIN Y. 2004. Ceramiaceae (Rhodophyta) de áreas recifais do estado de Pernambuco, Brasil. *Hoehnea* 31: 119–149.
- WOMERSLEY H.B.S. 2003. *The marine benthic flora of southern Australia—Part IIID. Ceramiales—Delesseriaceae, Sarcomeniaceae, Rhodomelaceae*. Flora of Australia Supplementary Series Number 18. Australian Biological Resources Study, Canberra and State Herbarium of South Australia. 533 pp.
- WYNNE M.J. 1990. Observations on *Haraldia* and *Calloseris*, two rare genera of Delesseriaceae (Rhodophyta) from the western Atlantic. *Contributions to the University of Michigan Herbarium* 17: 327–334.
- WYNNE M.J. 2005. A checklist of benthic marine algae of the tropical and subtropical western Atlantic: second revision. *Nova Hedwigia, Beiheft* 129: 1–152.
- WYSOR B. & KOOISTRA W.H.C.F. 2003. An annotated list of marine Chlorophyta from the Caribbean coast of the Republic of Panama. *Nova Hedwigia* 77: 487–523.
- YONESHIGUE Y. 1985. *Taxonomie et ecologie des algues marines dans la région de Cabo Frio (Rio de Janeiro, Brésil)*. Ph.D. thesis. Université d'Aix-Marseille II, France. 467 pp.

Received 27 May 2009; accepted 10 September 2009
Associate editor: David Ballantine