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Crassitegula walsinghamii (Sebdeniaceae, Halymeniales), a new red algal genus and species from Bermuda based upon morphology and SSU rDNA sequence analyses

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Dorsiventral, mat-forming plants superficially similar to *Flahaultia tegetiformans* (Gigartinales, Solieriaceae), a Caribbean species known only in the vegetative condition, were collected in several Bermuda habitats. Morphological analysis of these specimens distinguished them from *F. tegetiformans*. Reproductive morphology and analyses of sequences of the nuclear encoded small subunit rDNA show them clustering with *Sebdenia* (Halymeniales). The plants are described as *Crassitegula walsinghamii* gen. et sp. nov., a new nemathecial member of the Sebdeniaceae.

Introduction

Along the neck of land that separates Castle Harbour from Harrington Sound on Bermuda Island in Hamilton Parish, a number of limestone sinkholes are tidally fed through underground caverns connected to the sea and sound. These sinkholes formed when subterranean caves collapsed over geologic time (Thomas *et al.*, 1991). Walsingham Pond is the largest sinkhole, covering 0.79 ha with a maximum depth of 6.18 m (Thomas *et al.*, 1991). The pond and associated smaller sinkhole pools in the Idwal Hughes Nature Reserve area are noted collection sites for seaweeds (Collins & Hervey, 1917) and significantly, the type localities for five taxa: *Halymenia pseudofloresii* Collins & M. Howe, *Sargassum cymosum* var. *farlowii* Grunow, *Ceramium leptozonum* M. Howe, *S. bermudense* var. *stagnale* W.R. Taylor ex C.W. Schneider, and *Chondracanthus saundersii* C.W. Schneider & C.E. Lane.

During two SCUBA dives in Walsingham Pond in November 2001, the first collections of a unique mat-forming, dorsiventral alga (Figs 1–4) were made, and this species was found in the same habitat on subsequent visits. At first glance, the Bermuda plants resemble an enigmatic Caribbean

species, *Flahaultia tegetiformans* W.R. Taylor, a taxon not known from Bermuda. Taylor (1974) selected the Sylvia Lawn coral reef in St Ann Parish as the type locality for this "ecologically...significant plant in the Jamaican flora," as this site had a conspicuous population of overlapping "mat-like colonies" (Taylor, 1974, figs 14–24), like those we found in Walsingham Pond. The Walsingham populations were located on a shaded ledge, 3–4 m deep depending on the tidal level, and are, thus far, the only ones found developing extensive mats in Bermuda. Unfortunately, during Hurricane Fabian on 6 September 2003, elevated Castle Harbour waters overflowed this land-locked pond and the surrounding nature reserve. Flooding caused the refrigerated food supply of an adjacent inn to wash into Walsingham Pond, fueling anoxic water conditions shortly thereafter. These post-Fabian conditions destroyed much of the flora and fauna in this protected habitat where previously there had been clear waters with spectacular macroalgae and few grazing herbivores. Six months after the hurricane, the subtidal in Walsingham Pond was completely devoid of algae, including the site where normally at that season a flourishing mat-like population of the new alga described below would be supported. Although a great many algal species had recovered in Walsingham by July 2005,

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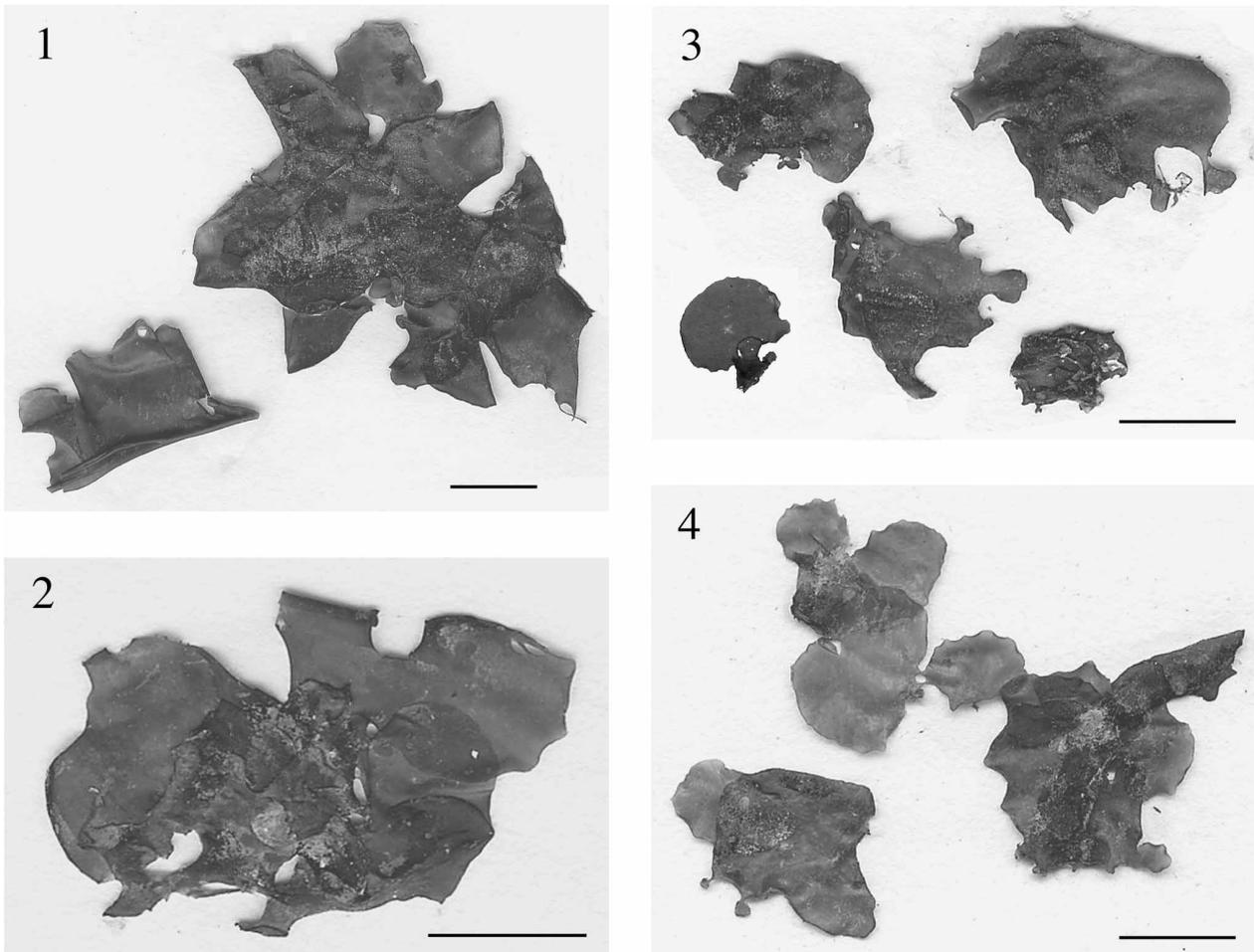
Figs 1–4. *Crassitegula walsinghamii* gen. et sp. nov. Fig. 1. Holotype, tetrasporic specimen (*CWS/CEL* 01-14-12 [MICH]). Fig. 2. Paratype, tetrasporic specimen (*CWS/CEL* 01-22-24). Figs 3, 4. Paratypes demonstrating marginal proliferations (*CWS/CEL* 02-9-31). Scale bars: 1 cm.

the mat-forming species was again not found in the pond. Whether this population will recover remains to be seen, but specimens gathered prior to the hurricane and those taken from other habitats in the islands were adequate to determine that this alga was previously unknown. In this paper, we describe the morphology and reproduction of the Bermuda plants and provide a comparison with the superficially similar *F. tegetiformans*. Analyses of gene sequences of the small subunit (SSU) rDNA were vital in determining the ordinal and familial placement of the new taxon.

Materials and methods

Morphological methods

Specimens of the new taxon were dried on silica gel for molecular analysis and pressed fresh onto cotton paper with fragments preserved in 5% formalin-sea water as herbarium vouchers. Site locations were taken using a Garmin™ GPS III Plus. Dried herbarium specimens were scanned at 300×300 dpi. Photomicrographs were taken using a Zeiss microscope equipped with an 11.2 Spot InSight 2 digital camera. Digital images were composed in Adobe Photoshop™ 6.0.1. Pen and ink

drawings were made with the aid of a Zeiss camera lucida. Herbarium abbreviations follow Holmgren *et al.* (1990) and initials for authorities' given names are from Brummitt & Powell (1992). Voucher specimens are deposited in MICH, MSM, NY, UNB and Craig Schneider's personal herbarium. The holotype was deposited in MICH. For comparison with the Bermuda specimens, we studied an isotype of *F. tegetiformans* [*V.J. Chapman* (=*WRT* A.1618), 15.iv.1954, Sylvia Lawn, St Ann Parish, Jamaica (MICH)], as well as other Taylor specimens (MICH) used in preparing the protologue.

Molecular methods

In the laboratory, dried isolates from Walsingham Pond (*GWS* 001245, *GWS* 001260) were ground under liquid nitrogen and stored at $-20°C$. DNA was extracted (Saunders, 1993) and the SSU rDNA was PCR-amplified using the primers outlined in Saunders & Kraft (1994, 1996). The PCR products were agarose gel-purified with the Wizard™ PCR Preps DNA Purification System (Promega, Madison, WI, USA). Sequencing of DNA was completed with the BigDye® Terminator Cycle Sequencing Kit (PE Applied Biosystems (ABI), Foster City, CA, USA) and data

Table 1. List of taxa used in SSU rDNA analysis and GenBank accession numbers

| Taxon	Accession No.
Nemastomatales	
Adelophycus corneus (J. Agardh) Kraft	AF515285
Nemastoma dichotoma J. Agardh	Unpubl. data
Platoma cyclocolpum (Montagne) F. Schmitz	AF515292
Predaea aurora Kraft & G.W. Saunders	AF515296
Predaea kraftiana A. Millar & Guiry	AF515297
Schizymenia dubyi (Chauvin ex Duby) J. Agardh	U33136
Wetherbeella australica (Womersley & Kraft) G.W. Saunders & Kraft	AF515290
Wetherbeella foliosa (Womersley & Kraft) G.W. Saunders & Kraft	AF515291
Rhodymeniales	
Asteromenia peltata (W.R. Taylor) Huisman & A. Millar	AY437710
Botryocladia ebriosa A. Millar	AF085255
Cephalocystis leucobotrys A. Millar, G.W. Saunders, I.M. Strachan & Kraft	U23950
Chrysymenia ornata (J. Agardh) Kylin	AF085257
Chrysymenia wrightii (Harvey) Yamada	AF117129
Erythrocolon podagricum (Harvey) J. Agardh	U23953
Erythrymenia minuta Kylin	AF085272
Fryeella gardneri (Setchell) Kylin	AF085273
Gloiosaccion brownii Harvey	AF085259
Hymenocladia chondricola (Sonder) J.A. Lewis	AF117128
Hymenocladiopsis crustigena R.L. Moe	AF085274
Irvinea ardreana (J. Brodie & Guiry) Guiry	AF085254
Rhodymenia leptophylla J. Agardh	U09621
Sparlingia pertusa (Postels & Ruprecht) G.W. Saunders, I.M. Strachan & Kraft	AF085261
Halymeniales, Halymeniaceae	
Carpopeltis phyllophora (Hooker f. & Harvey) F. Schmitz	U33124
Corynomorpha clavata (Harvey) J. Agardh	AY437700
Epiphloea bullosa (Harvey) De Toni	AY437701
Grateloupia luxurians (A. Gepp & E. Gepp) De Clerck & Gavio	U33132
Grateloupia intestinalis (Harvey) Setchell ex P.G. Parkinson	AY437702
Halymenia plana Zanardini	U33133
Norrissia setchellii (Kylin) Balakrishnan	AY437703
Pachymenia carnosa (J. Agardh) J. Agardh	AF515289
Pachymenia cf. *orbicularis* (Zanardini) Setchell & N.L. Gardner	AY437704
Polyopes tenuis Womersley & J.A. Lewis	AY437706
Zymurgia chondriopsidea (J. Agardh) J.A. Lewis & Kraft	AF515304
Sebdeniaceae	
'*Lesleigha* sp.' Kraft mscr. [nom. nud.]	AF515286
Lord Howe 'unknown'	AY437707
Sebdenia flabellata (J. Agardh) P.G. Parkinson	U33138
Tsengiaceae	
Tsengia comosa (Harvey) Womersley & Kraft	AF515303
Tsengia laingii (Kylin) Womersley & Kraft	AF515302
Tsengia lanceolata (J. Agardh) G.W. Saunders & Kraft	AF515288

*It has been established that this taxon is not a member of the genus *Chrysymenia* J. Agardh and is probably representative of *Cryptarachne* (Harvey) Kylin (cf. Saunders *et al.*, 1999).

were collected with the ABI PRISM 3100 Genetic Analyzer (AME Bioscience, Toroed, Norway).

The SSU sequence for *GWS* 001245 was submitted to GenBank (AY964057). Comparison of a partial sequence for a variable region on the other specimen (*GWS* 001260) showed it to be identical to the submitted sequence. The new SSU sequence was added to an alignment containing sequences for taxa related to, and included in, the Halymeniales downloaded from GenBank (Table 1). Preliminary analyses established unequivocally that our collections belong to this order (unpublished data).

The resulting alignment of 40 taxa contained 1799 sites of which 67 were considered ambiguously aligned or complementary to external PCR primer sequences and therefore were removed prior to analysis. The appropriate model for these data was determined in Modeltest (v 3.06; Posada & Crandall, 1998); the general time reversible model was selected with a gamma distribution and invariant sites. The program Mr. Bayes (v. 2.01; Huelsenbeck & Ronquist, 2001) was used for Bayesian inference of phylogeny under the previous model. Four Markov chains were used, the temperature was set to 0.2 and 10^6 generations were run with sampling every 100 generations. Log-likelihood values stabilized around 50,000 generations and we used the final 6000 trees (4000 burn-in) to calculate the posterior probabilities. Parsimony and distance analyses were completed in PAUP 4.0b10 (Swofford, 2002). Unweighted parsimony and minimum evolution
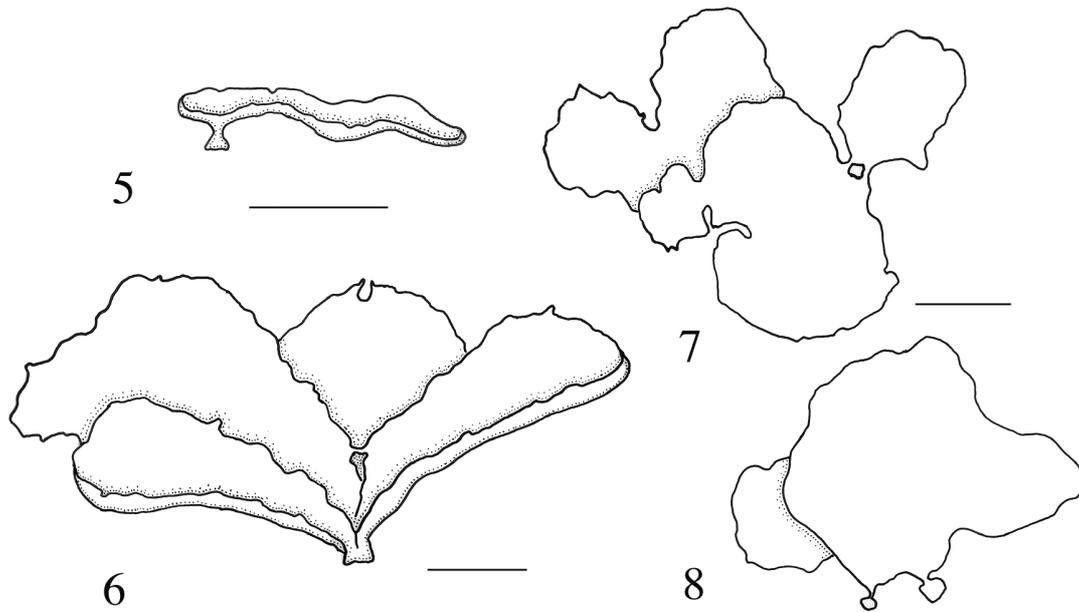
Figs 5–8. *Crassitegula walsinghamii* gen. et sp. nov. Fig. 5. Young, unproliferated specimen in side view (*CWS/CEL* 03-50-7). Scale bar: 0.5 cm. Fig. 6. Mature specimen in side view (*CWS/CEL* 03-46-15). Scale bar: 1 cm. Figs 7, 8. Proliferating specimens, surface view (*CWS/CEL* 02-9-31). Scale bar: 0.5 cm.

distance (parameters as identified in Modeltest) analyses were completed under a heuristic search using 50 random additions and the tree bisection-reconnection branch swapping option. Robustness of these phylogenies was assessed with 2000 bootstrap replicates (10 random additions) (Felsenstein, 1985). The final topologies were rooted along the branch separating the Halymeniales and Rhodymeniales rather than the Nemastomatales, based on the earlier results of Saunders *et al.* (2004).

Results and discussion

The Bermuda specimens are superficially similar in habit to the type and other specimens of *F. tegetiformans* in the protologue (Taylor, 1974: 67–70, figs 14–24). Like *F. tegetiformans*, the Bermuda specimens have thick, flat, reniform, dorsiventral thalli (Figs 3–5) that proliferate from the margins and occasionally produce submarginal haptera by which the plants attach to rock and other blades of the mat-like population (Figs 6–8). The population can be several layers thick, resembling a roof of overlapping tiles covering the rock (Figs 1, 2, 7, 8). After first locating the mat-like population in Walsingham Pond, we subsequently found a few individual reniform specimens in Harrington Sound. These showed early developmental stages prior to marginal blade and submarginal secondary holdfast proliferations (Fig. 5), features also described and illustrated by Taylor (1974) for *F. tegetiformans*. As opposed to inshore overlapping mats, offshore, dredged specimens of *F. tegetiformans* were "individual plants or small aggregations on bits of shell and

coral", a habit comparable to Harrington Sound and North Rock specimens.

Despite their obvious similarities to *F. tegetiformans*, the Bermuda plants are twice as large (blades maximum diameter 3.0 cm *v.* 1.5 cm) and show clear anatomical differences to the Caribbean species. Dorsiventral blades from Bermuda are up to 450 µm thick (Fig. 9), while those of *F. tegetiformans* are 50–165 µm thick. Bermuda specimens have a 6–8-celled cortex, grading from small (3–6 µm diameter), spherical to elongated and deeply pigmented outer cells to several layers of inner cortical cells that are large (45–55 µm diameter) and hyaline (Fig. 10). In some areas, particularly below carposporophytes, the innermost cortical cells are stretched apart as the tissue swells, becoming stellate. The cortex of *F. tegetiformans* is composed of three layers, the outermost spherical to slightly elongate cells (3–5 µm diameter) grading to slightly larger, 7–11 µm diameter, unpigmented inner cortical cells. The medulla of the Bermuda alga is loosely organized with medullary filaments (Figs 9, 11, 12), while that of *F. tegetiformans* is densely interwoven. Furthermore, despite having submarginal holdfasts that secondarily affix them to the substratum or lower blades in the mat, the Bermuda specimens do not have the distinctive, branched, horizontally produced finger-like projections that Taylor (1974, figs 22–24) used to discriminate his Jamaican species. Our specimens have occasional unbranched projections that will probably develop into new blades, and initially led us to consider them as *F. tegetiformans*. However, it is clear from
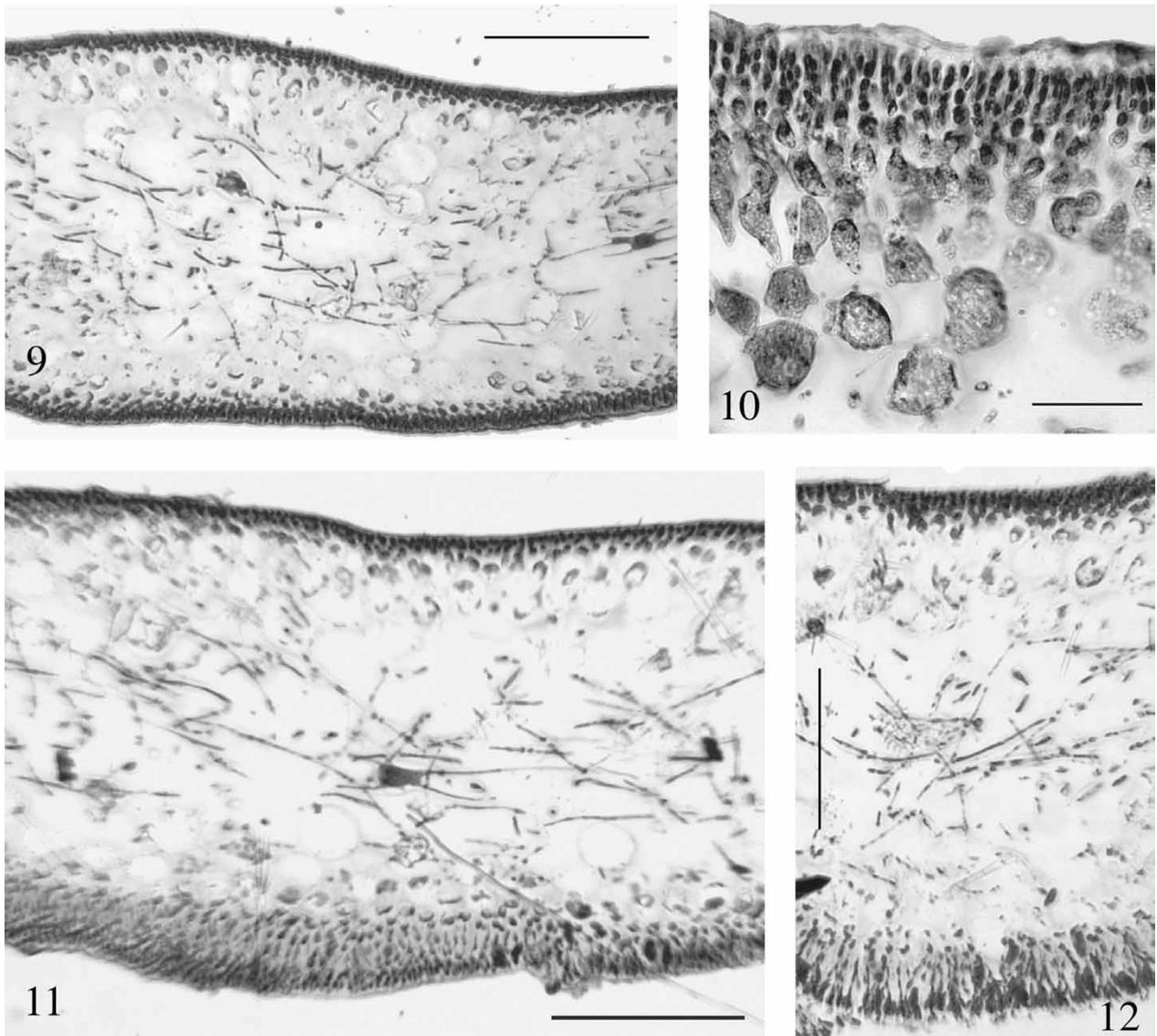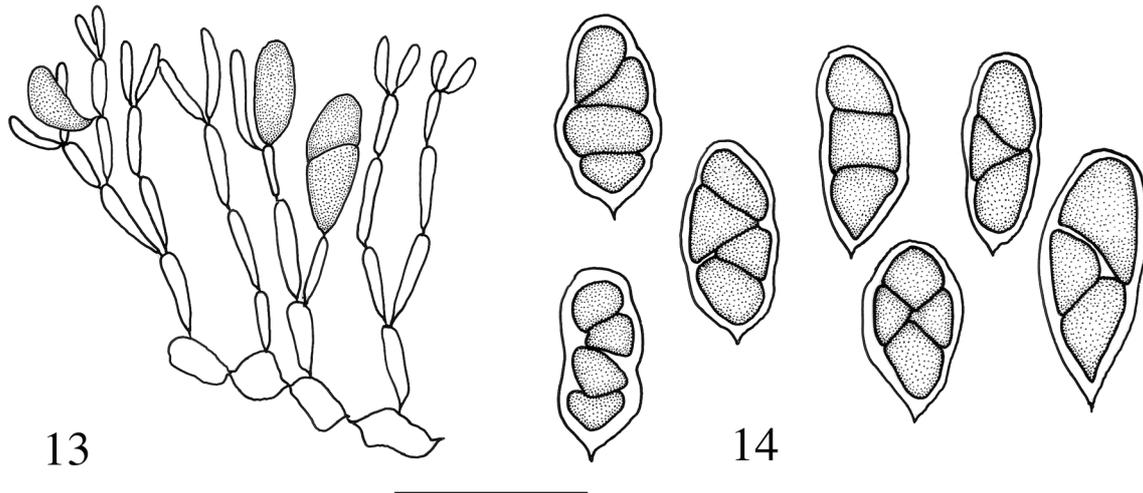
Figs 9–12. *Crassitegula walsinghamii* gen. et sp. nov. Fig. 9. Cross section of thallus, holotype (*CWS/CEL* 01-14-12). Scale bar: 200 µm. Fig. 10. Inner and outer cortex, holotype (*CWS/CEL* 01-14-12). Scale bar: 50 µm. Figs 11, 12 Tetrasporangial thallus with nemathecia on ventral surfaces (*CWS/CEL* 01-22-5). Scale bars: 200 µm.

the morphological distinctions that the Bermuda plants do not belong to *F. tegetiformans*.

In the absence of reproductive characteristics, Taylor (1974) could only tentatively assign his new species to a genus, based upon its morphological similarity to *Flahaultia appendiculata* Bornet from the Mediterranean. Subsequent records of *F. tegetiformans* from other Caribbean sites (Bula Meyer, 1986; Ballantine & Aponte, 1997; Littler & Littler, 2000) are also confined to vegetative specimens only. Taylor's generic assignment placed his new species in the Solieriaceae. Specimens from Bermuda have tetrasporangia embedded in the outer cortex of the ventral surface (Figs 11–13) and are irregularly cruciately divided, at times almost appearing zonate (Fig. 14). *Flahaultia* and the Solieriaceae have true zonately divided tetrasporangia (Bornet, 1892; Kylin, 1932; Gabrielson & Kraft, 1984). Tetrasporangial initials

in the Bermuda specimens are formed as lateral branches of subsurface cortical cells (Fig. 13). In areas of tetrasporangial formation, outer cortical cells divide and elongate greatly, collectively forming a raised nemathecium (Figs 11, 12). The attenuated cortical cells give the nemathecium a less dense structure than non-reproductive portions, so they appear more lightly pigmented than non-nemathecial surfaces. Tetrasporangial development is similar to that in non-nemathecial *Sebdenia* (J. Agardh) Berthold (Balakrishnan, 1961; Hansen, 1989), which has scattered tetrasporangia in its outer cortex (Kylin, 1932).

Since the molecular analyses of two Walsingham Pond samples are unequivocally consistent in their placement, we only present the Bayesian phylogeny but apply the distance and parsimony bootstrap values for comparison (Fig. 15). In all cases, the Bermuda specimens were resolved within the

Figs 13, 14. *Crassitegula walsinghamii* gen. et sp. nov. (*CWS/CEL* 01-22-5). Scale bar: 25 μm. Fig. 13. Nemathecial paraphyses with developing sporangia. Fig. 14. Mature tetrasporangia with a variety of irregularly cruciate divisional patterns, some appearing zonately divided.

Sebdeniaceae, solidly allied with an undescribed plant from Lord Howe Island, Australia (AY437707, Saunders *et al.*, 2004). If Taylor (1974) was correct that his Caribbean species was a *Flahaultia* and in the Solieriaceae, then it is only in habit that the seaweeds in question exhibit remarkable convergence. Although the Bermuda specimens and the undescribed Lord Howe alga are unequivocally allied and positioned within the Sebdeniaceae, their SSU divergence exceeds that observed between many sister genera in the orders included in our analyses (Fig. 15).

At present, *Sebdenia* is the only recognized genus in the Sebdeniaceae, although another sequence ['*Lesleigha*' nom. nud. (AF515286), see Saunders & Kraft, 2002; Saunders *et al.*, 2004] nested within the clade (Fig. 15). This will represent a new genus from Hawaii (G.T. Kraft, pers. comm.). The several known species of *Sebdenia* range from dichotomously branched, terete tubes (Schneider & Wynne, 1991; Adams, 1994) to broad, flat, simple to lobed blades (Taylor, 1945; Dawson *et al.*, 1964; Hansen, 1989). None have dorsiventral organization of the specimens from Bermuda, nor are nemathecia currently known in the genus.

Sexual reproduction in the Bermuda specimens is consistent with that in *Sebdenia*. Spermatangia are formed in male thalli from elongated outer cortical cells in large, slightly elevated patches covering both dorsal and ventral surfaces as well as margins (Fig. 16). During male development, surface cortical cells divide anticlinally to form a pair of attenuate cells that either function as spermatangial mother cells or divide once again to form the latter (Fig. 17). Each spermatangial mother cell produces terminal,

spherical to obovid, minute spermatia (1 μm diameter).

What we have been able to discover about female development in a single mature Bermuda specimen (portion of the holotype) parallels that in *Sebdenia* (Sjöstedt, 1926; Balakrishnan, 1961; Codomier, 1972; Hansen, 1989). Thus far, we have not located carpogonial branches. Cells in the inner cortex swell and function as auxiliary cells (Fig. 18, ac). After presumed fertilization, a diploid nucleus is transferred via a connecting filament (ooblast) to the auxiliary cell that divides anticlinally forming a cup-shaped gonimoblast initial towards the cortex surface (Fig. 18). At this stage, cells contiguous to the auxiliary cell cut off densely staining nutritive cells (Figs 18, 19) that presumably provide support to the developing gonimoblast. The cystocarp continues to develop outwardly and the growing carposporophyte elevates the surface while surrounding cortical cells stretch to form a loose involucre. The surface cortical cells above the cystocarps divide into anticlinal chains and remain as a compact, non-ostiolate surface (Fig. 19). At maturity, all of the cells of the carposporophyte except for the gonimoblast initial develop into irregular to spherical carposporangia (Fig. 19).

The suite of vegetative and reproductive morphological characters shows that our Bermuda alga is an undescribed member of the Sebdeniaceae. The phylogenetic analyses confirm placement in this family. Based upon its SSU rDNA sequences, *Sebdenia*, the only member of the Sebdeniaceae (Kylin, 1932), is phylogenetically distinct and cannot accommodate this dorsiventral
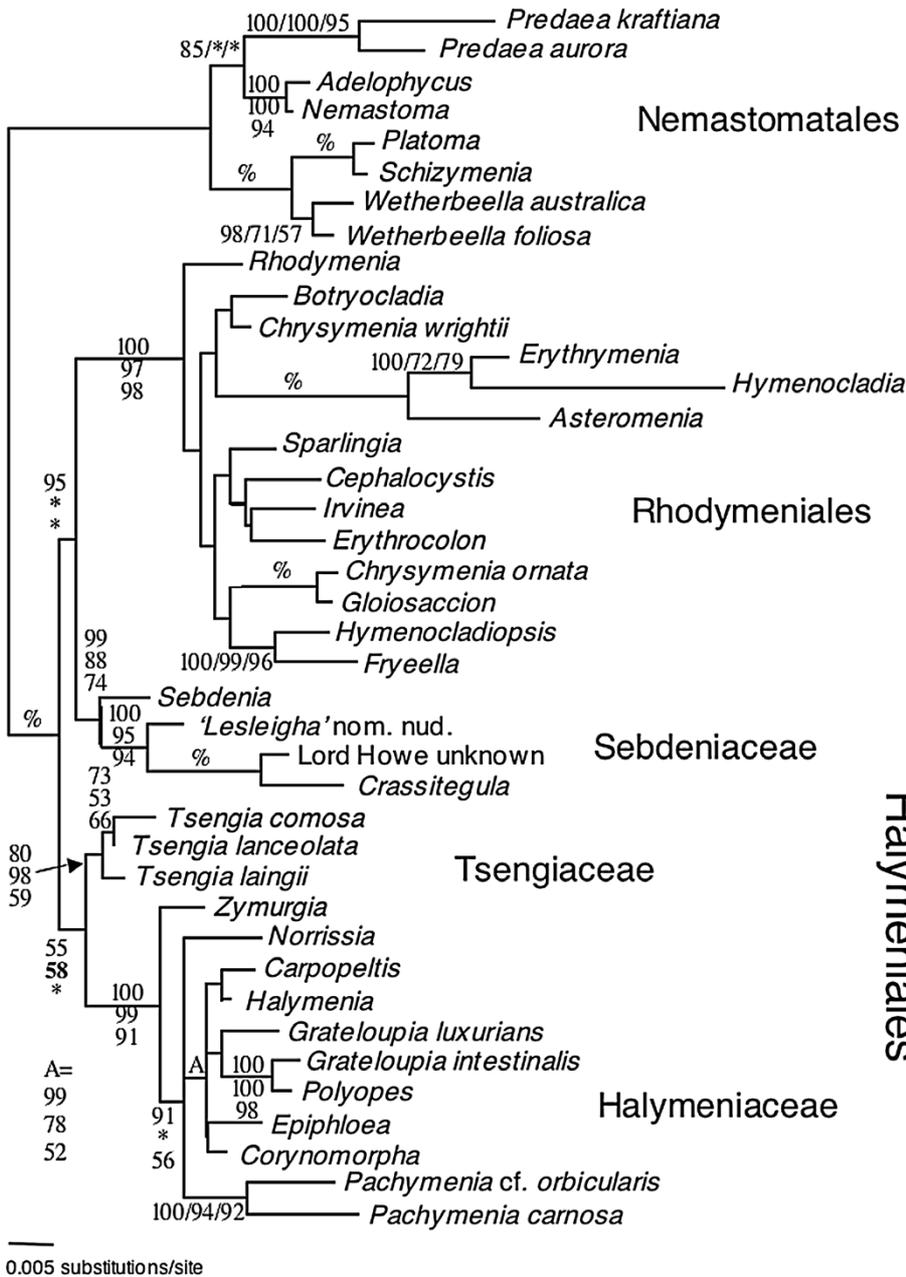
Fig. 15. Best phylogeny inferred under Bayesian inference for the SSU alignment. Values at branches indicate posterior probabilities, and distance and parsimony bootstrap support, respectively. The % mark indicates 100% support under all analyses; *indicates <50% in a particular analysis along that branch; bold text (**58**) reflects support for a monophyletic Halymeniales, i.e. including the Sebdeniaceae, under distance analyses. Many relationships within the Halymeniaceae and Rhodymeniaceae were variably and weakly supported under the analyses and those support values are excluded for purposes of presentation.

species. We therefore establish the following new genus for it:

Crassitegula C.W. Schneider, C.E. Lane & G.W. Saunders, gen. nov.

TYPUS, *C. walsinghamii* C.W. Schneider, C.E. Lane & G.W. Saunders, sp. nov.

Thalli dorsiventraliter ordinati cum laminis flabellatis vel reniformibus ad subcirculares et ovatos, a haptero submarginali primitus affixi, laminae veteres efferentes haptera secondaria a pagina ventrali, ad laminas alias vel substratum affixa; laminae novas laminas a marginibus pullulantes, aliqui cum laminis aliis in idem plano conjungentes; medulla filamentosa, ex filis hyalinis ramosis plerumque parallelis ad axem constans ad cellulas corticales interiores; cortex interior ad

cellulas parviores et plures pigmentosas gradatim redactus extrinsecus; tetrasporangia a cellulis interioribus corticalibus evoluta, irregulariter cruciata divisa, in nematheciis elevatis formata ab cellulis attenuatis corticalibus involuta; cystocarpia in pagina dorsali formantia, pagina laminae a spissescenti corticis supra cystocarpium leviter elevata; cellulae totae gonimoloborum evolutae in carposporangia; carposporophyta a cellulis corticalis elongatis involucra laxa formantibus circumcincta; spermatangia elongata in pannis elevatis in paginis dorsalibus et ventralibus formantia, spermatia terminalia producentia.

Thalli dorsiventrally organized with flabellate or reniform to subcircular and ovate blades, initially attached by a submarginal holdfast, the older
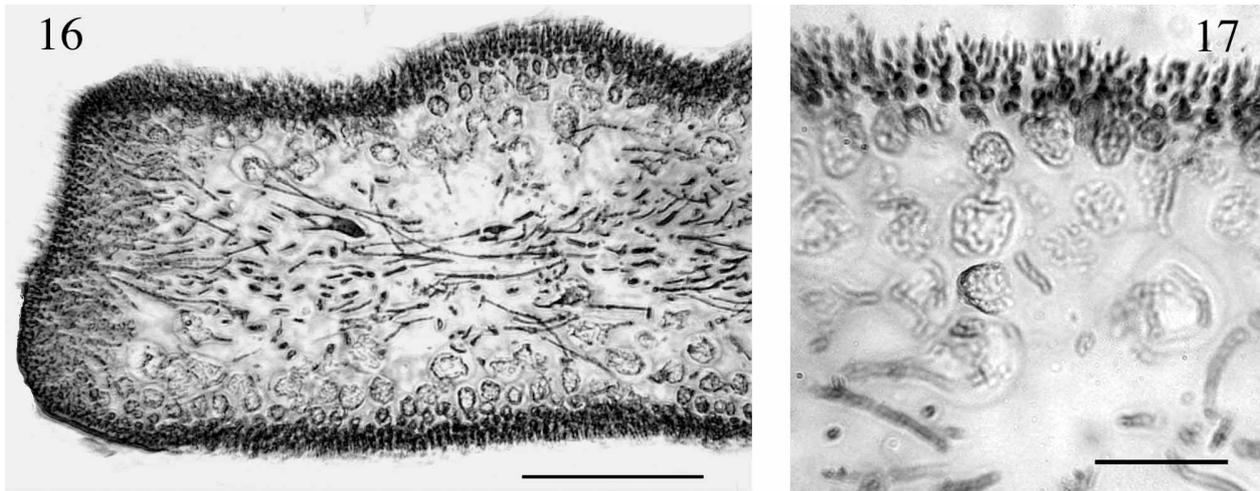
Figs 16, 17. *Crassitegula walsinghamii* gen. et sp. nov. (*CWS/CEL* 03-46-15). Fig. 16. Spermatangial thallus with sori on dorsal and ventral surfaces, as well as margins. Scale bar: 200 μm. Fig. 17. Spermatangial mother cells in raised outer cortex. Scale bar: 50 μm.
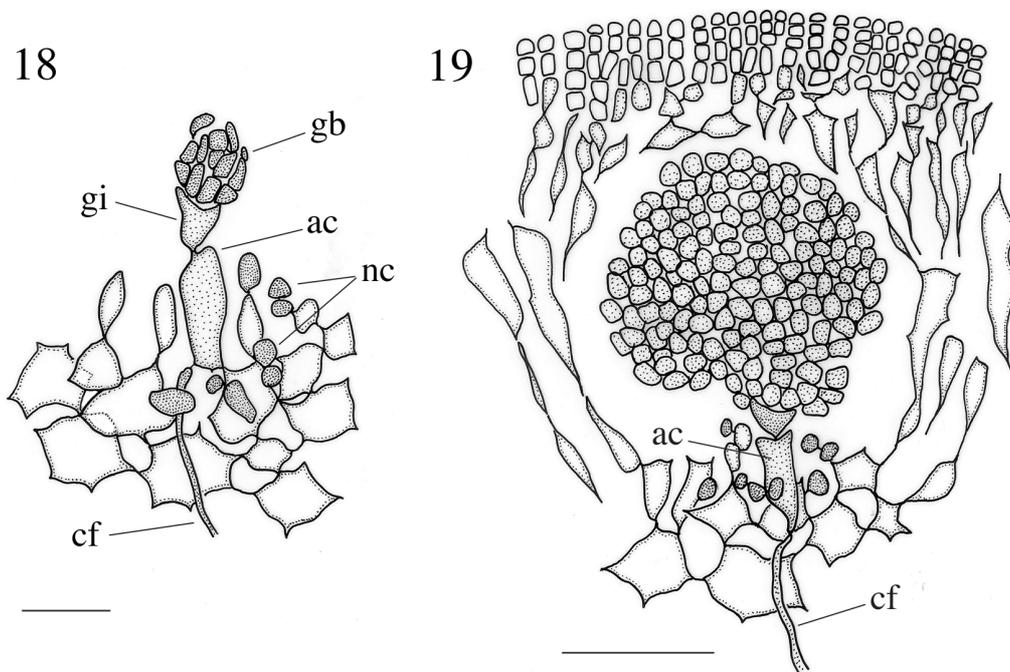
Figs 18, 19. *Crassitegula walsinghamii* gen. et sp. nov., holotype (*CWS/CEL* 01-14-12). Fig. 18 Auxiliary cell (ac) with gonimoblast initial (gi) and early stage of the gonimoblast development (gb). Darkly staining nutritive cells (nc) are shown cut off from adjacent cortical cells, and the connecting filament (cf) is still evident at the proximal end of the auxiliary cell. Scale bar: 25 μm. Fig. 19. Mature cystocarp with non-ostiolate pericarp. Scale bar: 50 μm.

blades sending down secondary holdfasts from the ventral surface, attaching to other blades or the substratum; blades proliferating new blades from the margins, some fusing with other blades in the same plane; medulla filamentous, comprised of hyaline, mostly periclinal, branched filaments, attached to inner cortical cells; inner cortex grading to progressively smaller and more pigmented layers of outer cortical cells; tetrasporangia developed from cortical cells, irregularly cruciate, formed in raised nemathecia enveloped by attenuated cortical cells; cystocarps forming on the dorsal surface, slightly elevating the surface of the blade by thickening the cortex; all cells of the gonimolobes developing into carposporangia; carposporophytes surrounded by elongated cortical cells forming loose involucres; elongate spermatangia formed in elevated patches on dorsal and ventral surfaces, producing spermatia terminally.

Diagnosis. Differing from *Sebdenia* in its dorsiventral habit, nemathecial tetrasporangia, and SSU rDNA sequences.

Etymology. *crassus* (L.) = thick, and *tegula* (L.) = tile, tiled roof.

A monotypic genus containing the following species:

Crassitegula walsinghamii C.W. Schneider, C.E. Lane & G.W. Saunders, sp. nov.

Thalli saxatales, prostrati, dorsiventraliter ordinati, firmi et levigati in textura, haematitici; laminae originaliter reniformes ad transverse ovatos, 1–3 cm latae, in initio a hapteronibus brevis submarginalibus affixae, lamina primaria tum prolifica laminas novas a marginibus, aliquot cum laminis aliis in idem plano coalescens; laminae imbricatae et affixae inter se a hapteronibus secondariis ex pagina ventrali aliquandro producientibus; laminae 400–450 µm crassae cum marginibus fere quadratis, medulla filamentosa laxa cum filis longis attenuatis plerumque parallelis ad axem 2–6 µm in diametro et ad extrema ramosa expansis; cortex 6–8-stomatica cum cellulas irregulares ad subglobosas magnas interiores corticales 45–55 µm in diametro, ad cellulas minores exteriores corticales redactus, cellulae superficiei irregulariter rotundae ad globosas et parvas, 3–6 µm diametro; tetrasporangia obovata, irregulariter zonata ad cruciata divisa, 10–15 µm diametro, 20–35 µm longitudino, in cellulis exterioribus corticalibus in pannis elevatis paginae ventralis inclusa; thalli sexuales dioecii, spermatangia a cellulis transformatis elongatis exterioribus corticalibus producentia; spermatia globosa ad elongata, 0.5–1 µm diametro; carposporophyta dispersa et in cortice dorsali inclusa, ad 125 µm diametro; carposporangia subglobosa ad irregulariter angulatas, 7.5–12.5 µm diametro.

Thalli saxicolous, prostrate, dorsiventrally organized, firm and smoothly textured, brownish-red; blades originally reniform to transversely ovate, 1–3 cm wide, initially attached by short, submarginal holdfasts, the primary blade then proliferating new blades from the margins, some fusing with other blades in the same plane; blades overlapping and affixed to one another by occasional secondary holdfasts issued from the ventral surface; blades 400–450 µm thick with nearly squared-off margins (Fig. 16), medulla loosely filamentous with long, thin, mostly periclinal filaments 2–6 µm in diameter and flaring somewhat at the branching ends; cortex 6–8 layered with irregular to subglobose large inner cortical cells 45–55 µm diameter, grading to smaller outer cortical cell layers, the surface cells irregularly rounded to spherical and small, 3–6 µm in diameter; tetrasporangia obovate, irregularly cruciately divided, 10–15 µm diameter, 20–35 µm long, amongst elongated outer cortical cells in raised surface patches on the ventral surface; thalli dioecious, spermatangia produced from transformed elongated outer cortical cells; spermatia spherical to elongate, 0.5–1 µm diameter; carposporophytes scattered and embedded in the dorsal cortex, to 125 µm diameter; carposporangia subglobose to irregularly angled, 7.5–12.5 µm diameter.

Dried specimens do not adhere well to herbarium paper.

Type collection. *CWS/CEL* 01-14-12, 12.xi.2001, Walsingham Pond, Hamilton Parish, Bermuda I., 32°20.7'N, 64°42.8'W, on vertical wall at 3 m.

Holotype. MICH, tetrasporic (Fig. 1) and cystocarpic (Figs 18, 19).

Isotype. UNB (*GWS* 001245, GenBank acc. no. AY964057), tetrasporic.

Additional collections (Paratypes). *CWS/CEL* 01-22-24, tetrasporic, 16.xi.2001, Walsingham Pond, *ibid.*, depth 4 m; *GWS* 001260, *ibid.*; *CWS/CEL* 02-9-31, 15.iv.2002, Walsingham Pond, *ibid.*, depth 3 m (MICH, MSM, NY); *CWS/CEL* 03-46-15, male, 6.x.2003, Shark Hole, Harrington Sound, 32°20.3'N, 64°42.3'W, depth 2 m; *CWS/CEL* 03-50-7, 7.x.2003, Abbot's Cliff, Harrington Sound, 32°20.3'N, 64°42.7'W, depth 1.5 m in a cave opening; *CWS/CEL* 05-10-12, 20.vii.2005, North Rock, north of Bailey Bay Flats, 32°28.3'N, 64°46.1'W, depth 18 m.

Etymology. *walsinghamii* (L.), named after the type locality, Walsingham Pond.

References

ADAMS, N.M. (1994). *Seaweeds of New Zealand*, Canterbury University Press, Christchurch, NZ.

BALAKRISHNAN, M.S. (1961). Studies on Indian Cryptonemiales—III *Halymenia* C.A. Ag. *J. Madras Univ. B*, **31**: 183–217.

BALLANTINE, D.L. & APONTE, N.E. (1997). Notes on the benthic marine algae of Puerto Rico. VI., Additions to the flora. *Bot. Mar.*, **40**: 39–44.

BORNET, E.L (1892). Les algues de P.-K.-A. Schousboe récoltées au Maroc et dans le Mediterranée de 1815 à 1829. *Mém. Soc. nat'l. Sci. nat. & math Cherbourg*, **28**: 165–376.

BRUMMITT, R.K. & POWELL, C.E. (editors) (1992). *Authors of Plant Names*, Royal Botanic Gardens, Kew.

BULA MEYER, G. (1986). Las macroalgas de los arrecifes coralinos de la Islas del Rosario, costa Caribe de Colombia. *Bol. Ecotróp.*, **14**: 3–20.

CODOMIER, M.L. (1972). Sur la reproduction sexuée du *Sebdenia rodrigueziana* (J. Feldm.) comb. nov. (Gigartinales, Sebdeniacées). *C.R. Acad. Sci., Paris, Sér. D*, **274**: 2299–2301.

COLLINS, F.S. & HERVEY, A.B. (1917). The algae of Bermuda. *Proc. Amer. Acad. Arts Sci.*, **53**: 1–195.

DAWSON, E.Y., ACLETO, C. & FOLDVIK, N. (1964). The seaweeds of Peru. *Nova Hedw., Beih.*, **13**: 1–111, 81 pls.

FELSENSTEIN, J. (1985). Confidence limits on phylogenies: an approach using the bootstrap. *Evolution*, **39**: 783–791.

GABRIELSON, P.W. & KRAFT, G.T. (1984). The marine algae of Lord Howe Island (N.S.W.): the family Solieriaceae (Gigartinales, Rhodophyta). *Brunonia*, **7**: 217–251.

HANSEN, G.I. (1989). *Schizymenia dawsonii* and its relation to the genus *Sebdenia* (Sebdeniaceae, Rhodophyta). *Taxon*, **38**: 54–59.

HOLMGREN, P.K., HOLMGREN, N.H. & BARNETT, L.C. (1990). *Index Herbariorum, I. The Herbaria of the World*, 8th edn. New York Botanical Garden, New York.

HUELSENBECK, J.P. & RONQUIST, F.R. (2001). MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics*, **17**: 754–755.

KYLIN, H. (1932). Die Florideenordnung Gigartinales. *Lunds Univer. Årsskr.*, N.F. Avd. 2, 28: 1–88.

LITTLER, D.S. & LITTLER, M.M. (2000). *Caribbean Reef Plants. An Identification Guide to the Reef Plants of the Caribbean, Bahamas, Florida and Gulf of Mexico*. Offshore Graphics, Inc., Washington, D.C.

POSADA, D. & CRANDALL, K.A. (1998). Modeltest: testing the model of DNA substitution. *Bioinformatics*, **14**: 817–818.

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. *J. Phycol.*, **29**: 251–254.

SAUNDERS, G.W. & KRAFT, G.T. (1994). Small-subunit rRNA gene sequences from representatives of selected families of the Gigartinales and Rhodymeniales (Rhodophyta). 1. Evidence for the Plocamiales ord. nov. *Can. J. Bot.*, **72**: 1250–1263.

SAUNDERS, G.W. & KRAFT, G.T. (1996). Small-subunit rRNA gene sequences from representatives of selected families of the Gigartinales and Rhodymeniales (Rhodophyta). 2. Recognition of the Halymeniales ord. nov. *Can. J. Bot.*, **74**: 694–707.

SAUNDERS, G.W. & KRAFT, G.T. (2002). Two Australian species of *Predaea* (Nemastomataceae, Rhodophyta) with taxonomic recommendations for an emended Nemastomatales, and expanded Halymeniales. *J. Phycol.*, **38**: 1245–1260.

SAUNDERS, G.W., STRACHAN, I. & KRAFT, G.T. (1999). The families of the order Rhodymeniales (Rhodophyta): a molecular-systematic investigation with a description of Faucheaceae fam. nov. *Phycologia*, **38**: 23–40.

SAUNDERS, G.W., CHIOVITTI, A. & KRAFT, G.T. (2004). Small-subunit rRNA gene sequences from representatives of selected families of the Gigartinales and Rhodymeniales (Rhodophyta). 3. Recognizing the Gigartinales *sensu stricto*. *Can. J. Bot.*, **82**: 43–74.

SCHNEIDER, C.W. & WYNNE, M.J. (1991). Lectotypification of *Sebdenia flabellata* (J. Agardh) Parkinson (Gigartinales, Rhodophyta). *Taxon*, **40**: 471–474.

SJÖSTEDT, L.G. (1926). Floridean studies. *Lunds Univ. Årsskr.*, N.F., Avd. 2, **22**: 1–95.

SWOFFORD, D.L. (2002). PAUP*. Phylogenetic Analysis Using Parsimony (* and Other Methods). Version 4. Sinauer Associates, Sunderland, Massachusetts.

TAYLOR, W.R. (1945). Pacific marine algae of the Allan Hancock Expeditions to the Galapagos Islands. *Allan Hancock Pac. Exped.*, **12**: 1–528.

TAYLOR, W.R. (1974). Notes on algae from the tropical Atlantic Ocean – VII. *Rev. Algol. Nouv. Sér.*, **11**: 58–71.

THOMAS, M.L.H., EAKINS, K.E. & LOGAN, A. (1991). Physical characteristics of the anchialine ponds of Bermuda. *Bull. Mar. Sci.*, **48**: 125–136.