

Halichrysis corallinarius sp. nov. (Rhodymeniaceae, Rhodophyta) from Puerto Rico, Caribbean Sea

David L. Ballantine,^{1*} Gary W. Saunders² and Hector Ruiz¹

¹Department of Marine Sciences, University of Puerto Rico, Mayagüez, Puerto Rico 00681 and ²Department of Biology, University of New Brunswick, Fredericton, New Brunswick, Canada, E3B 6E1

SUMMARY

A new species, *Halichrysis corallinarius* sp. nov. is described from coral reef habitats in southwest Puerto Rico as well as from Grand Cayman Island. The new species produces strap-shaped thalli supported above the substrata by abundant peg-like stipes. The lobed branches are frequently anastomosed with colonies measuring to 4.0 cm broad with individual axes measuring to 7.0 mm across. Algae possess up to five layers of medullary cells with frequent open spaces in the medulla. Tetrasporangia, measure to 19 × 25 µm, and are borne in sori limited to ventral surfaces. Gametophytes are monoecious and hemispherical carposporophytes are produced dorsally, measuring to 900 µm in diameter and 600 µm high.

Key words: Caribbean, *Halichrysis corallinarius*, molecular systematics, Puerto Rico, Rhodophyta, Rhodymeniaceae, Rhodymeniales.

INTRODUCTION

Morphologically the genus *Halichrysis* is characterized by generally iridescent peltate or prostrate plants with a dorsiventral organization. Spreading branches are frequently anastomosed and overlapping, as well as possessing a polystromatic medulla with small intercalating cells among the larger medullary cells (Huisman & Millar 1996; Saunders *et al.* 2006). Reproductively, three-celled carpogonial branches are reportedly in pairs on enlarged supporting cells, cystocarps lack *tela arachnoidea* (i.e. a mesh-like network of narrow filaments between the pericarp and developing gonimoblast, cf. Saunders *et al.* 2006), but possess a 'réseau muqueux' (i.e. mucilaginous strands, cf. Huvé & Huvé 1977; Saunders *et al.* 2006) and tetrasporangia are usually borne terminally on filaments that differentiate from existing cortical cells (Saunders *et al.* 2006). The genus currently includes five species (Guiry & Nic Dhonncha 2004; Saunders *et al.* 2006): *Halichrysis concrescens* (J. Agardh) G. De Toni, *H. depressa* (J. Agardh) F. Schmitz, *H. japonica* Segawa, *H. micans*

(Hauptfl.) P. Huvé & H. Huvé and *H. thivyae* (E.Y. Dawson) Eiseman & R.L. Moe. With the exception of *H. depressa*, which is found in the eastern Atlantic, the remaining *Halichrysis* species either have a Pacific or Indian Ocean distribution.

The status of three species previously assigned to *Halichrysis* has been clarified by Saunders *et al.* (2006). *Halichrysis coalescens* (Farl.) R.E. Norris & A. Millar in R.E. Norris was originally based on *Herpophyllon coalescens* Farl. and transferred to *Drouetia coalescens* (Farl.) G. De Toni; however, Saunders *et al.* indicated that it is not allied with *Halichrysis* and recommended that the species remain in *Drouetia*, which they argue represents an independent lineage within the Rhodymeniales. *Halichrysis irregularis* (Kütz.) A. Millar (in Millar & Prud'homme van Reine 2005) was based on *Iridea irregularis* Kütz. and considered to be synonymous with *Drouetia coalescens*. However, Saunders *et al.* (2006) provided contrary evidence and suggested that *Iridaea irregularis* may represent a new species of *Halichrysis*. *Halichrysis peltata* (W.R. Taylor) P. Huvé & H. Huvé was originally based on material from Venezuela (as *Faucheia peltata* W.R. Taylor). This species is also known from the southeast United States (Schneider & Searles 1991) and Puerto Rico (Ballantine & Wynne 1986). Huisman and Millar (1996) subsequently transferred the species to *Asteromenia*.

Recent collections made in cryptic coral reef habitats in southwestern Puerto Rico (western Atlantic), as well as from a single collection at Grand Cayman Island, have revealed a new distinctive species that conforms to *Halichrysis*.

MATERIALS AND METHODS

Specimens collected by scuba were preserved in 10% formalin/seawater. Sections (30 µm thick) were made

*To whom correspondence should be addressed.

Email: dballant@uprm.edu

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using an American Optical Cryo-Cut freezing microtome (American Optical Co., New York, NY, USA). Microscopic preparations were stained in acidified 1% aniline blue and mounted in 60% Karo corn syrup on microscope slides. Photomicrographs were taken with a SPOT RE digital camera through an Olympus BMAX light microscope (Olympus Optical Company, Tokyo, Japan). The plates were assembled from digital photographs using Adobe Photoshop CS2 (Adobe Systems, San Jose, CA, USA). The holotype is deposited in the US with isotypes at MICH, MSM and UNB. Paratype specimens have been deposited at MICH, MSM, UNB and US. Herbarium abbreviations follow Holmgren *et al.* (1990) and authority designations are according to Brummitt and Powell (1992).

Samples for molecular investigation (Table 1) were ground under liquid nitrogen and stored in sealed vials at -20°C . DNA was extracted from these isolates as outlined in Saunders (1993). The large subunit (LSU) rDNA and DNA barcode *cox1-5'* were amplified with published primers and protocols as necessary (Harper & Saunders 2001; Saunders 2005). The polymerase chain reaction (PCR) products were agarose gel-purified with the Wizard⁺ PCR preps DNA purification system (Promega, Madison, WI, USA) and DNA sequencing was completed with the dRhodamine terminator cycle sequencing ready reaction kit (PE Applied Biosystems (ABI), Foster City, CA, USA). Sequence data were collected with the ABI PRISM 3100 genetic analyzer.

The new data were combined with previously published sequence data for LSU and the DNA barcodes (DB) as follows: *Asteromenia anastomosans* (Weber Bosse) G.W. Saunders, C.E. Lane, C.W. Schneid. & Kraft (LSU – DQ068299; DB – AY970630, AY970631, AY970632); *A. bermudensis* G.W. Saunders, C.E. Lane, C.W. Schneid & Kraft (LSU – DQ068297; DB – AY970560, AY970561, AY970562, AY970563, AY970564, AY970565); *A. exanimans* G.W. Saunders, C.E. Lane, C.W. Schneid & Kraft (LSU – DQ068301); *A. peltata* (W.R. Taylor) Huisman & A. Millar (LSU – DQ068298); *A. psuedocoalescens* G.W. Saunders, C.E. Lane, C.W. Schneid & Kraft (LSU – DQ068300; DB – AY970629); *Botryocladia leptopoda* (J. Agardh) Kylin (LSU – DQ345756); *Erythrymenia minuta* Kylin (LSU – DQ068295); *Erythrymenia obovata* F. Schmitz ex. Mazza (LSU – DQ068296); *Hymenocladia chondricola* (Sond.) J.A. Lewis (LSU – DQ068294); *Halichrysis corallinarius* sp. nov. (DB – AY970628); and *Irvinea ardreana* (J. Brodie & Guiry) Guiry (LSU – DQ343714). The final alignments had 20 taxa with 2849 nucleotide positions (207 sites excluded for being ambiguously aligned or for having homology to the 3' PCR primer position) and 18 taxa and 710 positions (46 excluded for being homologous to the PCR primers) for the LSU and DNA barcode, respectively. The LSU alignment was subjected to bayesian analyses (Mr Bayes v3.1.1;

Table 1. Collection details for samples included in molecular analyzes

Name	Voucher no.	Collection details	GenBank LSU	GenBank DB
<i>Asteromenia bermudensis</i>	6450	Puerto Rico; D. Ballantine 1.21. 2005	ND	EF101933
G.W. Saunders, C.E. Lane, C.W. Schneid. & Kraft	6448	Puerto Rico; D. Ballantine 1.21. 2005	ND	EF101934
<i>Chrysomenia ornata</i> (J. Agardh) Kylin	G0281	Jervis Bay, NSW, Australia; A. Millar & P. Richards 1.2. 1995.	DQ343670	ND
<i>Coelarthrum opuntia</i> (Endl.) Børgesen	G0303	Port Phillip Bay (in the rip), Vic., Australia; GWS & G.T. Kraft 5.4. 1995.	DQ343671	ND
<i>Halichrysis concrescens</i> (J. Agardh) G. De Toni	GWS002090	Lord Howe I., Australia; GWS 3.2. 2004.	DQ343672	ND
<i>Halichrysis micans</i> (Hauptf.) P. Huvé et H. Huvé	GWS001065	Lord Howe I., Australia; GWS 14.3. 2001.	DQ343673	EF101937
<i>Halichrysis corallinarius</i> sp. nov.	6268	Puerto Rico; H. Ruiz 11.7. 2004.	DQ343674	AY970628†
	6304	Puerto Rico; H. Ruiz 9.2. 2004	ND	EF101935
	6320	Puerto Rico; H. Ruiz 9.28. 2004	ND	EF101936
<i>Rhodymenia ardissonaei</i> Feldmann	GWS001223	Greece; GWS 22.8. 2001.	DQ343675	ND
South Africa 'Drouetia'	KZnb2258	Sodwana, South Africa; O. DeClerck, T. Schils, H. Verbruggen & E. Demeulenare 6.11. 2003.	DQ343676	ND
<i>Sparlingia pertusa</i> (Postels & Ruprecht) G.W. Saunders, I.M. Strachan et Kraft	GWS000581	Bamfield, Canada; GWS 6.5. 1999.	DQ343677	ND
Unknown	GWS002041	Lord Howe I., Australia; Rodney Withall 31.1. 2004.	DQ343678	EF101938
WA unknown	G0402	Abrolhos I., Australia; GTK & GWS 10.11. 1995.	DQ343679	EF101939

†Determined in an earlier study (Saunders 2005). ND indicates gene not determined for that sample; DB, DNA barcode region – *cox1-5'*; LSU, nuclear large subunit ribosomal DNA.

Huelsenbeck & Ronquist 2001) using the generalized time reversible (GTR) + I + G model and two million generations (analyses completed in triplicate). Trees were sampled every 100 generations with log-likelihood scores stabilized at approximately 25 000 generations – the first 5000 of a possible 20 000 trees were discarded as burnin. The remaining trees were imported into PAUP to generate a majority rule consensus tree to estimate posterior probabilities. The DNA barcode alignment was analyzed under neighbor-joining (NJ) as implemented in PAUP (v.4.0b10; Swofford 2002) with a GTR model to provide a visual representation of within versus between species variation (this is not presented as a phylogenetic analysis).

RESULTS

Halichrysis corallinarius D.L. Ballant, G.W. Saunders & H. Ruiz sp. nov. Figures 1–12.

Description

Algae thallos ligulatos formantes; thalli prostrati multistipitibus 1–2 (–3.5) mm longis et paxilliformibus affixi atque e superficiebus ventralibus producti; algae expansae et lobatae; coloniae algarum usque ad 40 cm latae et axes singuli usque ad 7.0 mm latae; ramificatio irregulatum a marginibus; rami lobati paulatim expansi distaliter et frequenter anastomosantes; rami juniores supra laminas maiores frequenter crescentes; thalli 250–300 µm crassi 3 stratis cellularum corticalium et usque ad 5 stratis cellularum medullarum; cellulae medullosae maximae usque ad 100 × 200 µm. Cavities apertae in medulla communes; cellulae medullosae circum spatia aperta glandicellulas vel pryiformes usque ad 8 µm longas vel elongatas usque ad 14.0 µm longas frequenter sustinentes; tetrasporangia in soris superficialibus irregulatum formatis portata, usque ad 8 mm lata in superficiebus ventralibus; cellulae matrices tetrasporangiorum in filamentis cellularum elongatarum portatae, 1–3 tetrasporangia distaliter abscindentes.; tetrasporangia ovata et cruciatim divisa, usque ad 19 × 25 µm; gametophyta monoceia; carposporophyta cystocarpia valde conspicua et hemisphaerica usque ad 900 µm diametro et 600 µm alta in superficiebus dorsalibus producentia.

Algae form strap-shaped thalli which grow in a prostrate manner attached by abundant 1–2 (–3.5) mm long peg-like stipes produced from ventral surfaces; algae are spreading and lobed with entire colonies to 4.0 cm broad and individual axes to 7.0 mm across; branching occurs irregularly from margins; the lobed branches slightly expanded distally and frequently anastomosed; younger branches frequently overgrow older blades; thalli are 250–300 µm thick with three cortical cell layers and to five layers of medullary cells,

the largest medullary cells measuring to 100 × 200 µm; open cavities are common in the medulla and medullary cells surrounding the open spaces frequently support pyriform, to 8 µm long, or elongated gland cells, to 14 µm long; tetrasporangia are borne in irregularly shaped superficial sori, to 8 mm across, on ventral surfaces; tetrasporangial mother cells are borne on filaments of elongated cells and support one to three tetrasporangia distally; tetrasporangia are ovate and cruciately divided, measuring to 19 × 25 µm; gametophytes are monoecious; carposporophytes produce highly conspicuous hemispherical cystocarps on dorsal surfaces which measure to 900 µm in diameter and 600 µm high.

Holotype

D.L.B. 6340, Turrumote Reef, La Parguera, Puerto Rico (17°56.097 N, 67°01.130 W), 11 m (Coll. H. Ruiz) 5.x. 2004 (Alg. Coll. US – 209166). Isotypes in MICH and MSM.

Paratypes

Edge of insular shelf, offshore from La Parguera, Puerto Rico (17°53.423 N, 66°59.320 W): *D.L.B. 6268*, 23 m (Coll. D.L. Ballantine, H. R) 11.vii. 2004; *D.L.B. 6465*; 20 m (Coll. H. R) 17.ii. 2005; *D.L.B. 6483*, 23 m (Coll. H. R), 12.iv. 2005; *D.L.B. 6486, ibid.*, 13.iv. 2005; Media Luna Reef, La Parguera, Puerto Rico (17°56.10′N; 67°02.94′W): *D.L.B. 6304*, 6 m (Coll. H. R) 2.ix. 2004; *D.L.B. 6372*, 12 m, 16.xi. 2004; *D.L.B. 6381, ibid.*, 24.xi. 2004; *D.L.B. 6587, ibid.*, 28.vi. 2005.

Turrumote Reef, La Parguera: *D.L.B. 6309*, 21 m (Coll. H. R) 13.ix. 2004; *D.L.B. 6316*, 14 m (Coll. H. R) 28.ix. 2004.

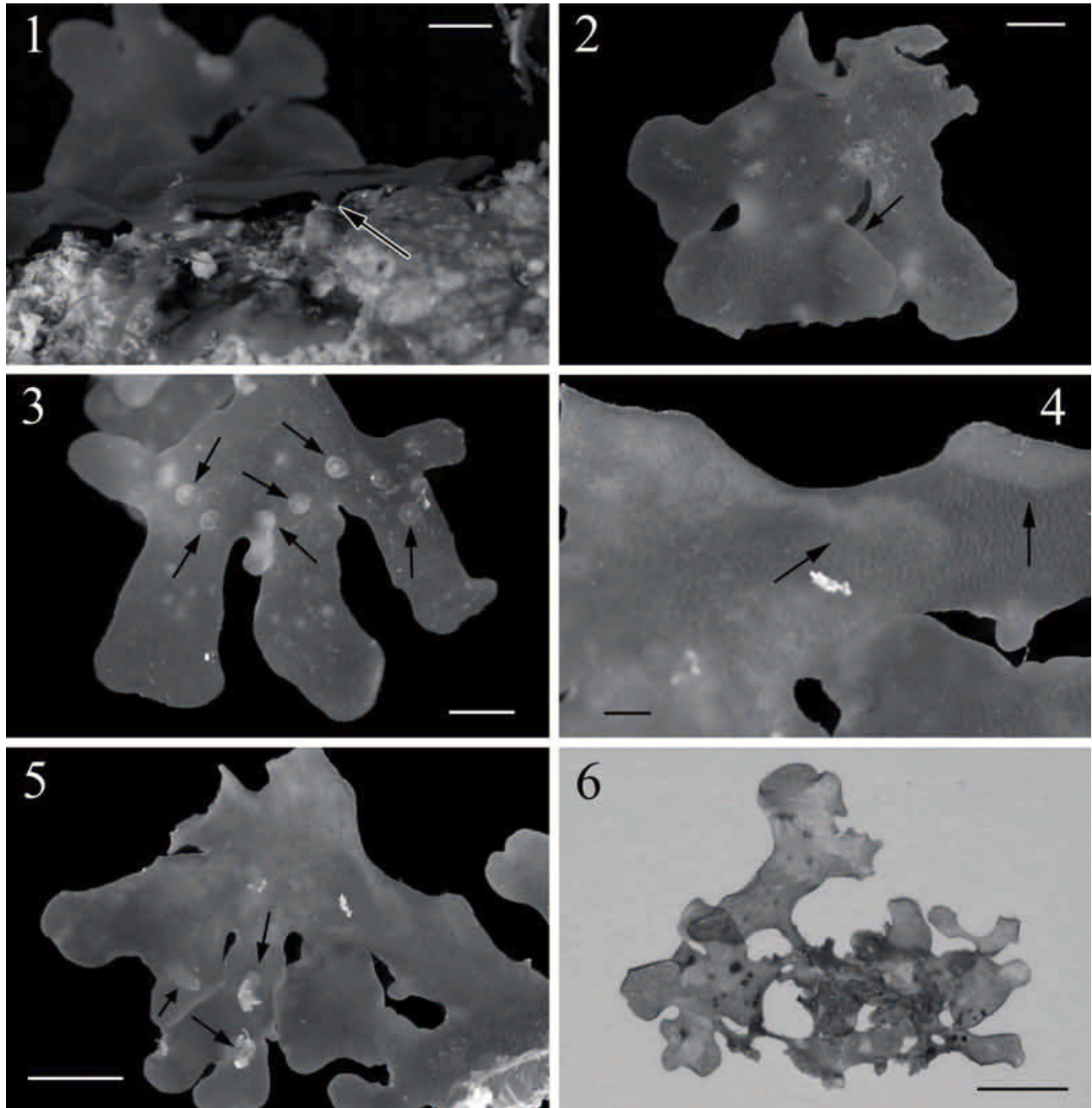
Cayman Islands: Grand Cayman Island, Andros Wall: *D.L.B. 5916*, 14 m (Coll. H. R) 5.viii. 2003.

Etymology

The specific epithet refers to the fact that the new species has been observed exclusively in coral reef habitats.

Observations

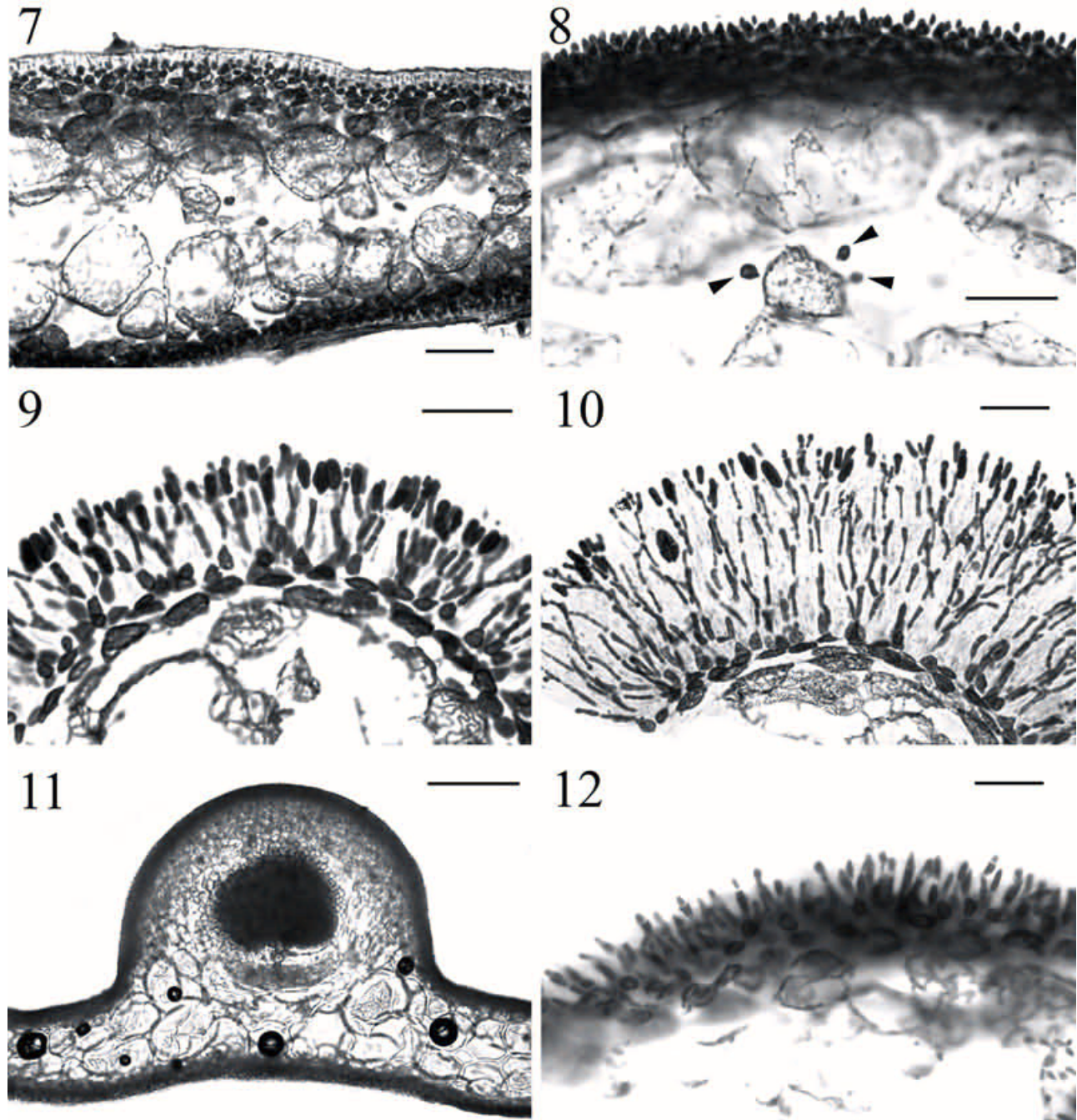
Specimens of *Halichrysis corallinarius* were collected in coral reef habitats from depths of 6–23 m. Algae form strap-shaped thalli (Figs 1–6), which grow in a prostrate manner, mostly elevated above (and roughly parallel to) the substratum by abundant 1–2 (–3.5) mm long peg-like stipes produced from ventral surfaces (Fig. 5). Algae are spreading and lobed (Figs 2,3,5,6) with entire colonies to 5.5 cm broad and individual axes to 7.0 mm across. Branching occurs irregularly from the margins. The lobed branches are slightly expanded distally (Figs 2,3) and frequently anasto-



Figs 1–6. *Halichrysis corallinarius* sp. nov. 1. Habit of living plant. Arrows denote attachment sites. (*D.L.B.* 5483). Scale bar = 2 mm. 2. Habit of living plant. Arrow shows point of blade overlap. (*D.L.B.* 6483). Scale bar = 2 mm. 3. Dorsal surface of living plant showing abundant and conspicuous hemispherical cystocarps (arrows). (*D.L.B.* 6268). Scale bar = 2 mm. 4. Ventral surface of living tetrasporangial plant. Arrows point to tetrasporangial nematocysts. (*D.L.B.* 6486). Scale bar = 1.0 mm. 5. Ventral surface of living plant showing peg-like stipes (arrows). (*D.L.B.* 6486). Scale bar = 5 μ m. 6. Habit of the holotype specimen (*D.L.B.* 6340). Scale bar = 5 mm.

mose. Older plants form extensive colonies, which may include anastomosis with neighboring thalli. On mature plants, younger branches frequently overgrow older blades (Fig. 2). Plants are internally composed of three cortical cell layers and up to five medullary layers of cells and the entire blade thickness ranges from 250 to

350 μ m (Fig. 7). The outermost cortical layer consists of spherical, averaging 5.6 μ m in diameter, to somewhat radially elongated cells, 5 μ m \times 8 μ m long. The middle cortical layer is of spherical cells, to 8 μ m in diameter, and the inner cortical layer consists of oval, to 10 \times 16 μ m cells. The outermost medullary cells are



Figs 7–12. *Halichrysis corallinarium* sp. nov. 7. Transection through blade showing polystromatic medulla and internal spaces (*D.L.B.* 6486). Scale bar = 50 μm . 8. Transection through blade showing medullary cells which support gland cells (arrowheads) (*D.L.B.* 5604). Scale bar = 50 μm . 9. Transection section through tetrasporangial nematocyst showing terminal tetrasporangia (*D.L.B.* 6309). Scale bar = 50 μm . 10. Transection section through a second tetrasporangial nematocyst showing terminal tetrasporangia (*D.L.B.* 6309). Scale bar = 50 μm . 11. Transection through cystocarp showing compact gonimoblast borne above basal layer of nutritive cells (*D.L.B.* 6268). Scale bar = 250 μm . 12. Transection through blade bearing spermatangia (*D.L.B.* 5486). Scale bar = 25 μm .

oval in shape and measure to $28 \times 52 \mu\text{m}$. These grade into larger medullary cells inwardly, which measure to $100 \times 200 \mu\text{m}$ (Fig. 7). Smaller diameter cells, mostly $50\text{--}100 \mu\text{m}$ in diameter are irregularly located in the central medulla (Figs 7,8). Among the medullary cells

are small open areas or cavities (Figs 7,8). Medullary cells surrounding these open spaces frequently support pyriform, to $8 \mu\text{m}$ long, or elongated gland cells, to $14 \mu\text{m}$ in length and which measure $5 \mu\text{m}$ in diameter (Fig. 8).

(Saunders 2005), within species differences were between 0 and 3 nucleotides, whereas divergences between closely related species were greater than 30 differences (e.g. *Asteromenia anastomosans* and *A. pseudocoalescens* with 31 differences; Fig. 13). *Halichrysis micans* and the new entity from Puerto Rico had 39–40 differences supporting the LSU and anatomical data in recognizing the latter as an independent species of *Halichrysis*.

DISCUSSION

The genera *Asteromenia*, *Drouetia*, *Maripelta* and *Sciadophycus* display morphological similarities to *Halichrysis*. *Maripelta* and *Asteromenia* both differ in possessing intercalary tetrasporangia, which are not associated with differentiation of contiguous cortical filaments (Saunders *et al.* 2006), and the former possesses a monostromatic medulla (Eiseman & Moe 1981; Huisman & Millar 1996). *Sciadophycus* differs in possessing a monostromatic medulla, stellate blades and cystocarps that possess *tela arachnoidea* (Dawson 1944). *Drouetia* differs from *Halichrysis* in possessing tetrasporangial sori on upper surfaces, in the development of the tetrasporangial nemathecium and in the lack of small intercalating cells in the medulla (Saunders *et al.* 2006). The new species is assigned to *Halichrysis* on the basis of its molecular alignment with other *Halichrysis* species (Fig. 13) and on morphological and anatomical attributes. The latter include its dorsiventrally organized prostrate blades, polystromatic medulla, possessing small intercalary cells in the medulla, cystocarps lacking *tela arachnoidea* but possessing 'réseau muqueux', location of tetrasporangial sori on ventral surfaces and mode of nemathecium development. In *Halichrysis*, the elongated cells within tetrasporangial nemathecium have previously been misinterpreted as adventitious paraphyses as opposed to being transformed cortical cells (Saunders *et al.* 2006). In this light, the development in height of thicker nemathecium (although only observed on one occasion; Fig. 10) is problematic as it involves either renewed vegetative growth during nemathecium development (prior to sporangial differentiation) or variable levels of cortical thickness in different parts of the thallus (perhaps thicker in older thallus regions). Secondary growth of nemathecium filaments upon release of the first order of tetrasporangia as observed in *Chamaebotrys erectus* Schils & Huisman (Schils *et al.* 2003) could also explain this observation. We were unable to observe intermediate stages in the development of the expanded nemathecium, and thus this issue is unresolved.

The new species differs from all presently known *Halichrysis* species by being monoecious (where known) and in possessing gland cells (Table 2). Otherwise the new species differs by means of a combination of

Table 2. Comparison of vegetative morphological and reproductive characters in recognized species of *Halichrysis*

Species	Habit	Stipe length (mm)	Blade/colony length/diam. (cm)	Blade thickness (μm)	Tetrasporangia size (W X L, μm)	Cystocarp size (diam., μm); shape	Monoecious/dioecious	Size medullary cells (μm)	Intercalating cells of medulla	References
<i>H. conrescens</i>	Prostrate	5	80–230	22 x 25	Approximately 800 (based on single torn section of type); subhemispherical	Unknown	Unknown	To 85 x 150	Simple to short chains	Saunders <i>et al.</i> (2006)
<i>H. depressa</i>	Foliaceous, partially prostrate	17	420–750	68 x 96	1300–1600; depressed (slightly raised from thallus surface)	Dioecious?	Dioecious?	To 165 x 550	Simple to extensive chains	Huvé and Huvé (1977); Sansón <i>et al.</i> (2002); Saunders <i>et al.</i> (2006) Segawa (1941)
<i>H. japonica</i>	Horizontally repent	10	800	Unknown	Unknown	Unknown	Unknown	Intercalating cells in long rows	Schneider (1975); Cribb (1983); Yamada (1932); Saunders <i>et al.</i> (2006)	
<i>H. micans</i>	Prostrate	7	300–500	To 15 x 40	1000–1300; hemispherical	Unknown	Unknown	To 100 x 200	Simple to short chains and extensive clusters	Saunders <i>et al.</i> (2006) Dawson (1963); Eiseman and Moe (1981)
<i>H. thiyae</i>	Concave blades above contorted stipe	30	4	Unknown	1000	Dioecious?	Dioecious?	To 100 x 200	Simple; presence of gland cells	This paper
<i>H. corallinarius</i>	Prostrate, multiple holdfasts	1–2	250–350	To 19 x 25	900; subhemispherical	Monoecious	Monoecious	To 100 x 200	Simple; presence of gland cells	

morphological characters. *Halichrysis corallinarius* differs from *H. micans* in blade thickness (to 350 μm in the new species and to 500 μm in the latter (Saunders *et al.* 2006). Additionally, tetrasporangia in *H. micans* are much larger, to 40 versus to 25 μm in the new species (Cribb 1983). Owing to the similarity in LSU sequence of the new species to *H. micans*, DNA barcode analyses with *cox1-5'* were carried out and it was established that the species were closely related but nonetheless clearly distinct (see Saunders 2005). In *Halichrysis depressa*, tetrasporangia are up to 96 μm long and are generally positioned singly on the modified cortical cells (Sansón *et al.* 2002) as opposed to one to three tetrasporangia per modified cortical cell in the new species. Saunders *et al.* (2006) further observed that medullary cells of the lectotype of *H. depressa* are to 165 μm in width \times to 550 μm in length (vs to 150 \times 200 μm in the new species) and that the cortex was four to six cell layers (vs three layers in the new species). *Halichrysis japonica* was described on the basis of a single specimen and assigned to the genus with a query (Segawa 1941) and thus is poorly known. Based on the little information available for *H. japonica*, it differs from the new species by producing 'rhizoidal processes' from the ventral surface (Segawa 1941) as opposed to multiple short cylindrical stipes.

Halichrysis concrescens possesses thinner blades (80–230 μm vs 250–350 μm in the new species) and in having intercalary cells arranged in short chains or filaments (vs being solitary in the new species (Saunders *et al.* 2006). *Halichrysis thivyae* differs from the new species by its production of blades from a longer (to 3 cm) stipe and in possession of a rostrate cystocarp.

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REFERENCES

Ballantine, D. L. and Wynne, M. J. 1986. Notes on the marine algal flora of Puerto Rico. I. Additions to the flora. *Bot. Mar.* **29**: 131–5.

- Brummitt, R. K. and Powell, C. E. (Eds). 1992. *Authors of Plant Names*. Royal Botanic Gardens, Kew.
- Cribb, A. B. 1983. *Marine Algae of the Southern Great Barrier Reef – Rhodophyta*. Australian Coral Reef Society, Brisbane. Handbook No. 2, 173 pp + 71 pls.
- Dawson, E. Y. 1944. Some new and unreported sublittoral algae from Cerros Island, Mexico. *Bull. Soc. Cal. Acad. Sci.* **43**: 102–12.
- Dawson, E. Y. 1963. Marine red algae of Pacific Mexico, Part 6. Rhodymeniales. *Nova Hedwigia* **5**: 437–76.
- Eiseman, N. J. and Moe, R. L. 1981. *Maripelta atlantica* sp. nov. (Rhodophyta Rhodymeniales) a new deep-water alga from Florida. *J. Phycol.* **17**: 299–308.
- Guiry, M. D. and Nic Dhonncha, E. 2004. *AlgaeBase*, Version 4.1. World-wide electronic publication, National University of Ireland, Galway. <http://www.algaebase.org> [12.v.2006].
- Harper, J. T. and Saunders, G. W. 2001. The application of sequences of the ribosomal cistron to the systematics and classification of the florideophyte red algae (Florideophyceae, Rhodophyta). *Cah. Biol. Mar.* **42**: 25–38.
- Holmgren, P. K., Holmgren, H. H. and Barnett, L. C. 1990. *Index Herbariorum, Part I. The Herbaria of the World*. New York Botanical Garden, Bronx, New York. x + 693 pp. [Regnum vegetabile vol. 120].
- Huelsenbeck, J. P. and Ronquist, F. R. 2001. MRBAYES: bayesian inference of phylogenetic trees. *Bioinformatics* **17**: 754–5.
- Huisman, J. M. and Millar, A. J. K. 1996. *Asteromenia* (Rhodymeniaceae, Rhodymeniales), a new red algal genus based on *Faucheia peltata*. *J. Phycol.* **32**: 138–45.
- Huvé, P. and Huvé, H. 1977. Notes de nomenclature algale 1. Le genre *Halichrysis* (J. Agardh emend. J. Agardh 1876) Schousboe mscr. in Bornet 1892 (Rhodymeniales, Rhodymeniaceae). *Soc. Phycol. de France* **22**: 99–107.
- Millar, A. J. K. and Prud'homme van Reine, W. F. 2005. Marine benthic macroalgae collected by Vieillard from New Caledonia and described as new species by Kützing. *Phycologia* **44**: 536–49.
- Sansón, M., Reyes, J., Afonso-Carrillo, J. and Muñoz, E. 2002. Sublittoral and deep-water red and brown algae new from the Canary Islands. *Bot. Mar.* **45**: 35–49.
- 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**: 251–4.
- Saunders, G. W. 2005. Applying DNA barcoding to red macroalgae: a preliminary appraisal holds promise for future applications. *Phil. Trans. R. Soc. B* **360**: 1879–88.
- Saunders, G. W., Strachan, I. and 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., Lane, C. E., Schneider, C. W. and Kraft, G. T. 2006. Unraveling the *Asteromenia peltata* species

- complex with clarification of the genera *Halichrysis* and *Drouetia* (Rhodymeniaceae, Rhodophyta). *Can. J. Bot.* **84**: 1581–607.
- Schils, T., Huisman, J. M. and Coppejans, E. 2003. *Chamaebotrys erectus* sp. nov. (Rhodymeiales, Rhodophyta) from the Socotra Archipelago, Yemen. *Bot. Mar.* **46**: 2–8.
- Schneider, C. W. 1975. North Carolina marine algae. V. Additions of the flora of Onslow Bay, including the reassignment of *Faucheia peltata* Taylor to *Weberella* Schmitz. *Br. Phycol. J.* **10**: 129–38.
- Schneider, C. W. and Searles, R. B. 1991. *Seaweeds of the Southeastern United States. Cape Hatteras to Cape Canaveral*. Duke University Press, Durham.
- Segawa, S. 1941. New or noteworthy algae from Izu. *Sci. Papers Inst. Algal Res. Fac. Sci. Hokkaido Imperial Univ.* **2**: 251–71.
- Swofford, D. L. 2002. *PAUP: Phylogenetic Analysis Using Parsimony*, Version 4.08a. Computer Program Distributed by the Illinois Natural History Survey, Champaign, IL.
- Yamada, Y. 1932. Notes on some Japanese algae IV. *J. Fac. Sci. Hokkaido Univ. Ser. 5* **2**: 267–76 + plates III–IX.