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Research article

The pseudodichotomous *Dasya sylviae* sp. nov. (Delesseriaceae, Ceramiales) from 60–90 m mesophotic reefs off Bermuda

Craig W. SCHNEIDER [1,*], Margaret M. CASSIDY [2] & Gary W. SAUNDERS [3]

[1,2] Department of Biology, Trinity College, Hartford, CT 06106, USA.
[3] Centre for Environmental & Molecular Algal Research, Department of Biology, University of New Brunswick, Fredericton, New Brunswick E3B 5A3, Canada.

[*] Corresponding author: cschneid@trincoll.edu
[2] Email: margaret.cassidy@trincoll.edu
[3] Email: gws@unb.ca

Abstract. The red alga *Dasya sylviae* C.W.Schneid., M.M.Cassidy & G.W.Saunders sp. nov. is described from mesophotic depths of 60–90 m off Bermuda. Genetic sequences (COI-5P, *rbc*L) and morphological characteristics show that this species is distinct from other known pseudodichotomous species of *Dasya*. Of ten current species in the genus reported from Bermuda, only three, *D. collinsiana* M.Howe, *D. cryptica* C.W.Schneid., Quach & C.E.Lane and *D. punicea* (Zanardini) Menegh., share the overall pattern of pseudodichotomous branching in their axes; however, key morphological features easily distinguish them from *D. sylviae* sp. nov. The species most similar in habit to *D. sylviae* sp. nov. is *D. crouaniana* J.Agardh (type locality West Indies), but it bears shorter pseudolateral branches, and broader and longer tetrasporangial stichidia than the new species. Unique among the species of *Dasya*, *D. sylviae* sp. nov. lacks post-sporangial cover cells in tetrasporangial stichidia.

Keywords. Western Atlantic, *Dasya*, mesophotic zone, Rhodophyta.

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Introduction

Since joining the 2016 Nekton XL Catlin cruise of the R/V *Baseline Explorer*, the mesophotic collections of macroalgae taken off the coast of Bermuda have yielded a growing list of species new to science (Richards *et al.* 2018; Schneider *et al.* 2018, 2019a, 2019b, 2020). In the present paper, we report another new species, this a member of the genus *Dasya* C.Agardh that was abundantly collected at several offshore reef sites from depths of 60–90 m (Stefanoudis *et al.* 2018: fig. 53, as *Dasya* sp.).

The genus *Dasya* presently hosts 90 species from throughout the world's temperate and tropical seas (Guiry & Guiry 2020). Its axial growth is sympodial with a main leading axis being continually displaced to one side by a new axis forming from a lateral bud near the apex. The resulting lateral axis takes over as the new main axis, a pattern that is repeated over and over in axial development (Parsons 1975).

Based on appearance and not development, species of *Dasya* mostly look to have alternate indeterminate branching patterns. However, some species of *Dasya* have sympodial branching patterns that appear to be dichotomous or pseudodichotomous (subdichotomous), and they are described as having this type of branching (e.g., Schneider *et al.* 2017; Howe 1918; Huisman 2018). In these species, the former main axis is not as suppressed by the newly produced lateral axis as in the case of most species of *Dasya* and often grows nearly as long as the new leading axis, in some species to a greater degree than in others. Of the ten species historically reported from Bermuda (Schneider 2003; Schneider *et al.* 2017), only three, *D. collinsiana* M.Howe, *D. cryptica* C.W.Schneid., Quach & C.E.Lane and *D. punicea* (Zanardini) Menegh., have an at least partial pseudodichotomous branching pattern appearance of their indeterminate axes. A morphological comparison was conducted to compare all of the known large species of the genus demonstrating mostly or partially pseudodichotomous branching with collections discovered in deep water off Bermuda demonstrating pseudodichotomous branching. Using both morphological comparisons and molecular data from the offshore samples, we were able to determine that the mesophotic specimens represent a species of *Dasya* new to science.

Material and methods

On the 2016 Nekton XL Catlin cruise of the R/V *Baseline Explorer* (*BEX*) off the coast of Bermuda, collections from living low-profile reefs in the mesophotic zone (Stefanoudis *et al.* 2018) were made by a team of technical rebreather divers (Global Underwater Explorers (GUE), High Springs, Florida, USA) equipped with closed-circuit JJ-CCR CE Edition rebreathers (JJ-CCR ApS, Copenhagen, Denmark) modified to GUE configuration, and Triton 1000-2 class submersibles (Vero Beach, Florida, USA) with mechanical collecting arms. Approximately 30 specimens of a common species of *Dasya* were taken at five collecting sites from depths of 60–90 m. Vouchers of type specimens are deposited in the herbaria noted in the Material examined section below; herbarium abbreviations follow the online Index Herbariorum (Thiers, continuously updated). Collection site locations on the *BEX* were recorded using a Beier Radio DP1 (dynamic positioning, Beier Integrated Systems, Mandeville, Louisiana, USA) to receive shipboard GPS. After living specimens were chosen for DNA analysis, they were photographed using a Canon Powershot s90 digital camera (Canon Inc., Tokyo, Japan), and fragments of each were then dried in silica gel for later DNA extraction. The remainder of the DNA specimens were dried on herbarium paper as permanent vouchers. Hand-cut sections were mounted in 30% corn syrup with acidified 1% aniline blue in a ratio of 20:1. Dried specimens were scanned on an Epson ET-2650 scanner (Seiko Epson Corporation, Suwa, Nagano, Japan), and photomicrographs were taken using a Zeiss Axioskop 40 microscope (Oberkochen, Germany) equipped with a Spot Idea 28.2 5MP digital camera (Diagnostic Instruments, Sterling Heights, Michigan, USA).

Specimens generated for use in our molecular analysis are listed in Table 1. When quick drying single or multiple isolates of associated field collection numbers, the silica gel samples were designated with unique 'BDA' numbers. DNA extractions of BDA numbers followed Saunders & McDevit (2012) and PCR amplification and sequencing of COI-5P and *rbc*L were as detailed in Saunders & Moore (2013). These markers initially identified five specimens assignable to a new genetic group. To place this new species into a wider phylogenetic context, additional COI-5P and *rbc*L sequences were generated for a variety of species of *Dasya* and the taxonomically related genera *Dasysiphonia* I.K.Lee & J.A.West, *Heterosiphonia* Mont. and *Rhodoptilum* J.Agardh from Canada, Australia and the US (Table 1). To expand further our analyses, COI-5P and *rbc*L data were also downloaded from GenBank for additional taxonomically related species, and their accession numbers are included in Fig. 1. Two single-gene alignments were generated: COI-5P with 28 sequences of 664 bp (base pairs) and *rbc*L with 36 sequences and 1272 bp. These alignments were analysed separately in Geneious ver. 2021.0.1 (https://www.geneious.com; Kearse *et al.* 2012) with maximum likelihood (GTR+I+G) using RAxML (Stamatakis 2014) with partitioning by codon and 500 bootstrap replicates. Since no conflicts were detected, a concatenated COI-5P and

Table 1 (continued on next page). Collection data for isolates with newly generated GenBank accession numbers included in the molecular analyses of this study. [1] = our *rbc*L-3P sequence generated here was linked to *rbc*L-5P data available in GenBank (KX913353) for *Dasya spinuligera* Collins & Herv.

Species	Voucher no.	BOLD no.	Collectors	Coll. date	Country	Province/State	Locality	°Latitude	°Longitude	COI-5P	*rbc*L
Dasya baillouviana (S.G.Gmel.) Mont.	*GWS*012466	ABMMC14293-10	K. Dixon	21 Aug. 2010	Canada	Nova Scotia	South Harbour, Cape Breton Island	46.867237	-60.447124	HQ919472	MW698713
Dasya 'baillouviana'	*CWS/TRP* 16-17-4 (BDA2013)	ABMMC22695-16	C. Schneider, T. Popolizio	3 Aug. 2016	Bermuda		Spittal, offshore of Midocean Point	32.3200000	-64.658056	—	MW698701
Dasya ceramioides Harv.	*GWS*014838	ABMMC7112-10	G. Kraft, G. Saunders	14 Jan. 2010	Australia	Victoria	Queenscliff Jetty, Port Phillip Heads	-38.2669	144.6678	HM917437	MW698711
Dasya clavigera (Womersley) M.J.Parsons	*GWS*014853	ABMMC7125-10	G. Kraft, G. Saunders	14 Jan. 2010	Australia	Victoria	Queenscliff Jetty, Port Phillip Heads	-38.2669	144.6678	HM917445	MW698723
Dasya corymbifera J.Agardh	CWS/CEL 10-26-10 (BDA0422)	BERMR252-10	C. Schneider, C. Lane, D. McDevit, T. Popolizio	24 Aug. 2010	Bermuda		Shark Hole, Harrington Sound, Bermuda I.	32.337083	-64.703889	KX913329	MW698710
Dasya sessilis Yamada	*GWS*011955	ABMMC7065-10	G. Saunders, T. Abe, N. Yotsukura	2 Dec. 2008	Japan		Kikoni (site of old marine station)	41.70075	140.52399	HM917402	MW698715
Dasya sp. 1AUS	*GWS*002588	ABMMC5285-09	G. Saunders	22 Jan. 2005	Australia	Tasmania	Snug Park	-43.06615	147.2645	HM916129	MW698700
Dasya sp. 2GWS	*GWS*014969	ABMMC7219-10	G. Saunders, K. Dixon	18 Jan. 2010	Australia	Tasmania	Windmill Point, George Town	-41.1097	146.81699	HM917514	MW698716
Dasya sp. 2TAS	*GWS*025124	OZSEA508-10	G. Saunders, K. Dixon	11 Nov. 2010	Australia	Western Australia	Canal Rocks	-33.66935	114.99531	MW699759	MW698705
Dasya sp. 3WA	*GWS*024888	OZSEA514-10	G. Saunders, K. Dixon	10 Nov. 2010	Australia	Western Australia	Cozy Corner (Knobby Pt.)	-34.25595	115.02777	MW699759	MW698703
Dasya sp. 4WA	*GWS*024893	OZSEA443-10	G. Saunders, K. Dixon	10 Nov. 2010	Australia	Western Australia	Cozy Corner (Knobby Pt.)	-34.25595	115.02777	MW699763	MW698708
Dasya spinuligera Collins & Herv.	CWS/CEL 10-15-6 (BDA0210)	BERMR131-10	C. Schneider, C. Lane, D. McDevit, T. Popolizio	21 Aug. 2010	Bermuda		Gates Fort, St. George's Harbour	32.37878	-64.66339	KX913327	MW698714[1]
Dasya sylviae C.W.Schneid., M.M. Cassidy & G.W.Saunders **sp. nov.**	*CWS/TRP* 16-11-1 (BDA1969)	ABMMC22688-16	C. Schneider, T. Popolizio	28 Jul. 2016	Bermuda		Ledge North northeast of St. George's I.	32.4799333	-64.594805	MW699758	MW698704
	CWS/TRP 16-11-10 (BDA1982)	ABMMC22692-16	C. Schneider, T. Popolizio	28 Jul. 2016	Bermuda		Ledge North northeast of St. George's I.	32.4799333	-64.594805	MW699765	—
	CWS/TRP 16-12-2 (BDA1992)	ABMMC22693-16	C. Schneider, T. Popolizio	29 Jul. 2016	Bermuda		Ledge North northeast of St. George's I.	32.48270	-64.587531	MW699761	—
	CWS/TRP 16-17-2 (BDA2011)	ABMMC22694-16	C. Schneider, T. Popolizio	3 Aug. 2016	Bermuda		Spittal, offshore of Midocean Point	32.320000	-64.658056	MW699766	—

Table 1 (continued). Collection data for isolates with newly generated GenBank accession numbers included in the molecular analyses of this study.

Species	Voucher no.	BOLD no.	Collectors	Coll. date	Country	Province/State	Locality	°Latitude	°Longitude	COI-5P	*rbc*L
Dasya sylviae C.W.Schneid., M.M. Cassidy & G.W.Saunders **sp. nov.**	*CWS/TRP* 16-21-14 (BDA2030) **Isotype**	ABMMC22698-16	C. Schneider, T. Popolizio	11 Aug. 2016	Bermuda		Spittal, offshore of Midocean Point	31.3205555	-64.658889	MW699769	—
	CWS/TRP 16-21-14 (BDA2031) **Holotype**	ABMMC22699-16	C. Schneider, T. Popolizio	11 Aug. 2016	Bermuda		Spittal, offshore of Midocean Point	31.3205555	-64.658889	—	MW698721
Dasya tenuis M.J.Parsons & Womersley	*GWS*025517	OZSEA485-10	G. Saunders, K. Dixon	14 Nov. 2010	Australia	Western Australia	Blackwall Reach, Swan River	-32.02101	115.78316	MW699764	MW698709
Dasysiphonia japonica (Yendo) H.-S.Kim	*GWS*030121	ABMMC16707-12	A. Savoie	18 Apr. 2012	USA	Massachusetts	Garbage Beach Breakwater, Woods Hole	41.52518	-70.67256	KC158582	MW698722
Dasysiphonia sp. 1WA	*GWS*024416	OZSEA529-10	G. Saunders, K. Dixon	7 Nov. 2010	Australia	Western Australia	Little Beach	-34.97163	118.19599	MW699762	MW698707
Dasysiphonia sp. 2WA	*GWS*024798	OZSEA536-10	G. Saunders, K. Dixon	9 Nov. 2010	Australia	Western Australia	Cape Leeuwin Lighthouse	-34.37167	115.1363	MW699760	MW698706
Heterosiphonia callithamnium (Sond.) Falkenb.	*GWS*024726	OZSEA533-10	G. Saunders, K. Dixon	9 Nov. 2010	Australia	Western Australia	Cape Leeuwin Lighthouse	-34.37167	115.1363	MW699772	—
	*GWS*024727	OZSEA534-10	G. Saunders, K. Dixon	9 Nov. 2010	Australia	Western Australia	Cape Leeuwin Lighthouse	-34.37167	115.1363	MW699771	MW698720
Heterosiphonia crassipes (Harv.) Falkenb.	*GWS*023911	OZSEA543-10	G. Saunders, R. Withall	26 Nov. 2010	Australia	New South Wales	Yellow Rock, Lord Howe I.	-31.515	159.0344	MW699767	MW698717
Heterosiphonia plumosa (J.Ellis) Batters	*GWS*040690	ABMMC21928-16	G. Saunders, T. Bringloe	9 Jun. 2016	Norway		Kleppesjoen	60.18474	5.14938	MN184231	MN184525
Heterosiphonia densiuscula Kylin	*GWS*028128	ABMMC15502-11	G. Saunders, K. Dixon	7 Jul. 2011	Canada	British Columbia	Murchison I., east end, Gwaii Haanas	52.60585	-131.43289	MW699770	MW698719
Heterosiphonia sp. 2AUS	*GWS*016476	ABMMC8255-10	G. Saunders, L. Kraft, K. Dixon	29 Jan. 2010	Australia	Tasmania	Stanley Breakwater	-40.76731	145.30583	MW699756	MW698702
Rhodoptilum plumosum (Harv. & Bailey) Kylin	*GWS*036815	ABMMC21032-15	G. Saunders, M. Bruce, T. Bringloe	11 Jul. 2015	Canada	British Columbia	Smythe Passage East (*Macrocystis* bed), Haida Gwaii	54.06791	-132.51958	MW699768	MW698718

*rbc*L alignment was constructed (38 sequences, 1936 bp) with analyses as described for the single gene alignments, but with partitioning by gene and codon and with 1000 bootstrap replicates (Fig. 1). In all cases, the trees were rooted on the lineage defined as the *Heterosiphonia* group (Choi *et al.* 2002).

Results

Phylogenetic analysis

In the speciose genus *Dasya* worldwide, there is a total of eight known corticated species taller than 3 cm at maturity that bear indeterminate axes appearing mostly or partially pseudodichotomously branched. A comparative review of these species is summarized in Table 2. None of these bear a suite of characteristics that is comparable with the mesophotic specimens collected off Bermuda.

We successfully generated COI-5P (664 bp) for five individuals of this novel species and all had identical sequences except for one substitution in BDA2011, or 0–0.15% divergence within this species. The nearest neighbor identified through a BLAST search in GenBank was *Dasya adela* Heggøy, Rueness & Sjøtun that demonstrated a 6% divergence. Similarly, we generated an *rbc*L sequence for two specimens, which were identical over 1358 bp and 2.9% divergent from *D. adela*. Phylogenetic analyses placed the new genetic group solidly in a clade with *D. adela* and an undescribed species from the euphotic zone off Bermuda (Fig. 1, *Dasya* sp. 1Bda). Of further note, none of the genera included in the current tree were monophyletic except for the monospecific *Rhodoptilum*, which nonetheless fell solidly in a group with the generitype of *Dasya*, *D. baillouviana* (S.G.Gmel.) Mont. (Fig. 1). Clearly considerable taxonomic work remains to be done on the genera included in our phylogenetic analyses, but this does not detract from our clear discovery of a novel species best included in the genus *Dasya*. Therefore, based upon our molecular comparisons and phylogenetic analysis, we here describe the following unique mesophotic species of *Dasya* for Bermuda and the western Atlantic.

Taxonomic treatment

Phylum Rhodophyta Wettst.
Subphylum Eurhodophytina G.W.Saunders & Hommers.
Class Florideophyceae Cronquist
Subclass Rhodymeniophycidae G.W.Saunders & Hommers.
Order Ceramiales Oltm.
Family Delesseriaceae Bory
Subfamily Dasyoideae De Toni
Genus *Dasya* C.Agardh nom. cons.

Dasya sylviae C.W.Schneid., M.M.Cassidy & G.W.Saunders sp. nov.
Fig. 2

Diagnosis

Differing from most species of *Dasya* by its pronounced pseudodichotomous branching pattern (Fig. 2A–C), and from its most similar congener in habit, *D. crouaniana* J.Agardh, by its longer pseudolaterals, narrower and shorter tetrasporangial stichidia and axes fully covered with pseudolaterals to barely denuded proximal axes. The new taxon differs from all species of *Dasya* by its lack of post-sporangial cover cells.

Etymology

The species is named after Dr Sylvia A. Earle, pioneering phycologist, scientist and open-water diver, 50 years after she led the first all-female team of aquanauts in Tektite II on the floor of the Caribbean Sea (Earle 1972a, 1972b).

Table 2 (continued on next page). A morphological comparison of corticated pseudodichotomous *Dasya* spp. taller than 3 cm.

	D. anastomosans	***D. carteri***	***D. collinsiana***	***D. crouaniana***	***D. cryptica***	***D. haitiana***	***D. punicea***	***D. rosylniae***	***D. sylviae* sp. nov.**
Plant height (cm)	3–6(–20)	to 11	1–3(–5+)	to 7	4–5	5–9	5–10	to 10	4–17
Branching pattern	pseudo-dichotomous	irregularly pseudo-dichotomous	alternate, irregular, to somewhat pseudo-dichotomous	widely pseudo-dichotomous to irregular	pseudo-dichotomous	pseudo-dichotomous	pseudo-dichotomous to irregular	alternate to pseudo-dichotomous and irregular	pseudo-dichotomous
Axial cortication	complete	complete	mostly complete	complete	complete	complete	complete	heavily corticated to several segments from apex	complete
Axial diameter (mm)	1–3	to 3	0.5–0.75	0.5–0.7	1–2	0.5–0.6	0.4–1.2	1.8	0.3–0.8
Apices of main axes	tapering slightly to tips, branch ends recurved	tapering distally	tapering distally		tapering slightly to tips, branch ends recurved		tapering distally	tapering distally	tapering slightly to tips
Pseudolaterals	monosiphonous	monosiphonous	monosiphonous	monosiphonous	monosiphonous	monosiphonous and polysiphonous	monosiphonous	monosiphonous few with polysiphonous bases	monosiphonous
Disposition	random	–	spiraled	random	random	spiraled	sub-verticillate	spiraled	random
Axial coverage	dense coverage, denuded in proximal axes of older plants	dense coverage, denuded in proximal axes of older plants	dense coverage up to the last 2–3 dichotomies, lighter above	dense coverage distally, mostly with lower half completely denuded	dense coverage, denuded in proximal axes of older plants	dense coverage, denuded in proximal axes of older plants	densely covered distally, naked proximally	denuded of monosiphonous laterals for much of their length	denuded only in most proximal area of older plants
Branching	1–3 times from basal portions	1–4(–5) times pseudo-dichotomously branched near base	5–8 times divaricately pseudo-dichotomous	2–3 times dichotomously	2–4 times from basal portions	–	2–3 times dichotomously near base	5 times dichotomous	to 7 times irregularly dichotomous
Overall length (mm)	2–5	to 3	to 0.9	1–2	2–4	–	2.0–4.4	0.8	1.7–5.5
No. cells base to apex	31–44				30–70	–	–	–	25–102
Basal cell diameter (µm)	15–44	12–14	100–130	18–20	12–33	–		to 44	21–37
Basal cell length (µm)	14–45	–	wider than long	20–40	24–48	–		–	12–30
Suprabasal cell diameter (µm)	7–14	tapering	–	–	6–16	–	20–40	–	19–32
Suprabasal cell length (µm)	18–33	–	–	–	1–38	–	50–80	–	8–32
Median cell diameter (µm)	13–15	8–12	to 75	–	14–18	–	–	–	9–22

Table 2 (continued). A morphological comparison of corticated pseudodichotomous *Dasya* spp. taller than 3 cm.

	D. anastomosans	*D. carteri*	*D. collinsiana*	*D. crouaniana*	*D. cryptica*	*D. haitiana*	*D. punicea*	*D. rosylniae*	*D. sylviae* sp. nov.
Median cell length (µm)	50–60	2.5	to 2 diameters	4 times as long as broad	75–92	–	–	–	27–102
Apical cell diameter (µm)	4–12	8–12	45–55	5–12	5–18	–	12	–	8–19
Apical cell length (µm)	10–24		90–110	to 30	11–43	–	–	–	32–127
Tetrasporangium diameter (µm)	32–45	35–40	30–40	18–30	30–50	60–70(–80)	30–40	to 40	21–29
Tetrasporangial stichidium	linear lanceolate	lanceolate	ovate-lanceolate, often curved	lanceolate to elongated cylindrical	linear lanceolate	lanceolate and slightly curved	ovate to lanceolate	ovate to lanceolate	lanceolate to narrowly elliptical
Diameter (µm)	50–100	–	90–130	80–120	60–80	70–200	70–90	120	73–80
Length (µm)	210–400	–	300–500	to 1000	340–1040	300–700	300–400	to 640	269–305
No. fertile segments/ stichidium	10–13	15	–	–	10–27	–	–	to 12	10–12
No. sporangia/ fertile segment	3–5	4	–	–	4(–5)	5	5	6	3–5
Post-sporangial cover cells	1(–2)	2(–3)	3	–	1	(2–)3	–	3	absent
Spermatangial stichidium	–	–	–	lanceolate to elongated cylindrical	–	–	–	linear lanceolate	lanceolate to narrowly elliptical
Diameter (µm)	–	–	24–36	60–70	–	–	–	50–60	46–69
Length (µm)	–	–	60–100	150–225	–	–	–	to 425	192–258
Type locality	Indonesia	Western Australia	Bermuda	West Indies	Bermuda	Haiti	Italy	New South Wales	Bermuda
References	Schneider *et al.* 2017	Huisman 2018	Howe 1918; Littler & Littler 2000; present study	Taylor 1928; Littler & Littler 2000; Dawes & Mathieson 2008	Schneider *et al.* 2017	Fredericq & Norris 1986	Taylor 1960; Littler & Littler 2000; López-Piñero & Ballantine 2001	Millar 1996	present study

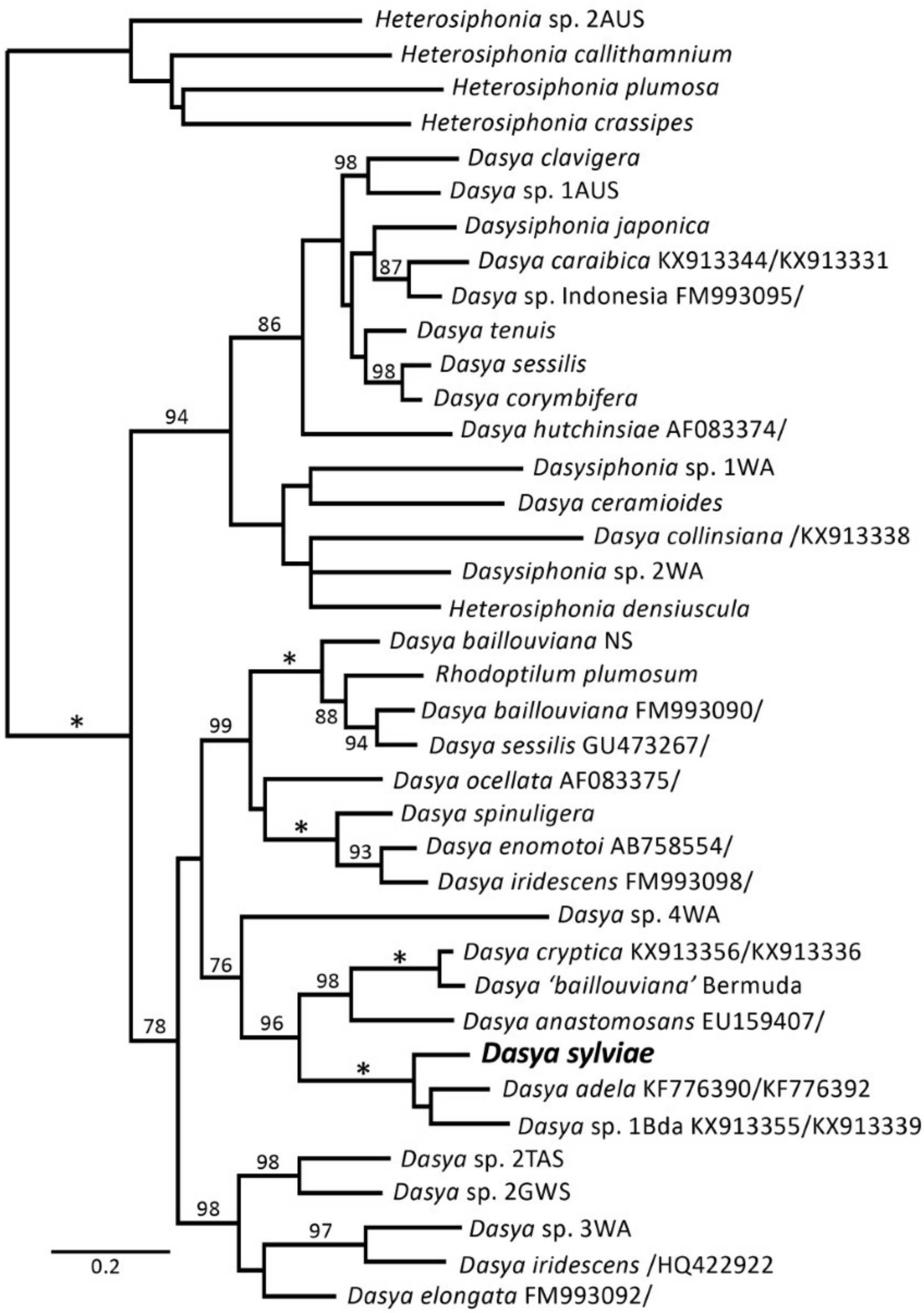

Fig. 1. Concatenated COI-5P and *rbc*L RAxML tree, partitioned by gene and codon, GTR+I+G with 1000 bootstrap replications (only bootstrap values >75% shown). Asterisks (*) denote 100% bootstrap support. Sequences taken from GenBank are indicated by including their accession numbers in parentheses (*rbc*L/COI-5P). The novel genetic group, *Dasya sylviae* sp. nov., is presented in bold type.

Material examined

Type

BERMUDA • Spittal, south of Cooper's I. off Castle Harbour; 31°19.23333′ N, 64°39.53333′ W; depth 63.8 m; on rhodoliths; 11 Aug. 2016; *Schneider & Popolizio* 16-21-14; GenBank nos: MW698721 (holotype), MW699769 (isotype); holotype (Fig. 2A): MICH [BDA2031]; isotypes (Fig. 2B–C): Bermuda Natural History Museum, MICH, NY, UNB, US, Herb. CWS [BDA2030].

Additional material

BERMUDA • Ledge north northeast of St. George's I.; 32°28.79600′ N, 64°35.68833′ W; depth 90 m; 28 Jul. 2016; *Schneider & Popolizio* 16-11-1, ⊕ [BDA1969] • *loc. cit.*; depth 60 m; 28 Jul. 2016; *Schneider & Popolizio* 16-11-10 [BDA1982] • *loc. cit.*; 32°28.96200′ N, 64°35.25183′ W; depth 90 m; 29 Jul. 2016, *Schneider & Popolizio* 16-12-2 [BDA1992] • Spittal, offshore of Midocean Point; 32°19.20000′ N, 64°39.48333′ W; depth 62.7 m; 3 Aug. 2016; *Schneider & Popolizio* 16-17-2 [BDA2011].

Description

Plants epilithic, erect to 17 cm tall, carmine red, arising from small discoidal holdfasts; indeterminate axes sympodially branched, appearing pseudodichotomously branched throughout, only slightly tapering from base to apex (Fig. 2A–C), 0.3–0.8 mm diam. in median to lower portions and completely corticated by rhizoidal downgrowth (Fig. 2D); indeterminate axes densely covered throughout with determinate, lightly pigmented, monosiphonous dichotomously branched axes (pseudolaterals; Fig. 2E), except in some older plants in the most basal portions; pseudolaterals 1.7–5.5 mm in length, 25–91 cells from base to apex, irregularly dichotomously branched from the first to the seventh cell of the pseudolateral, upper portions unbranched and slightly tapering (Fig. 2E); basal cells of pseudolaterals initially globose to ellipsoid (Fig. 2D), 21–37 µm diam. and 12–30 µm long, then slightly elongating; suprabasal cells 19–32 µm diam. and 8–32 µm long, elongating more centrally, 9–22 um diam. and 27–102 µm long, and reaching greatest lengths distally, 8–19 µm diam. and 32–127 µm long; tetrasporangial stichidia single, borne terminally on 3–7-celled unbranched pseudolaterals (Fig. 2F) or terminating basal dichotomies of pseudolaterals (Fig. 2G), lanceolate to narrowly elliptical in outline (Fig. 2F–G), 73–80 µm diam. and 269–305 µm in length at maturity, composed of 10–12 fertile segments, acropetally producing then releasing sporangia (Fig. 2F–G); sporangia globose, 21–29 µm diam., tetrahedrally divided, 3–5 per fertile segment, sporangia borne on 2-celled whorled branches, post-sporangial cover cells lacking (Fig. 2F); one to two spermatangial stichidia terminating a basal dichotomy on 4–10-celled pedicels (pseudolaterals), narrowly elliptical to lanceolate in outline (Fig. 2H), 46–69 µm diam. and 192–258 µm in length at maturity; carpogonial branches and cystocarps unknown.

Distribution and habitat

At present, endemic to mesophotic reefs off Bermuda, western Atlantic Ocean.

Discussion

The genus *Dasya* is characterized by the development of 2–4 pre- and post-sporangial cover cells that partially cover tetrasporangia in their stichidium (Parsons 1975). *Dasya sylviae* sp. nov. appears to be unique among its congeners as it completely lacks these cover cells, thus tetrasporangia sit naked on their whorl branches (Table 2, Fig. 2G). Among the presently accepted 90 species of *Dasya* (Guiry & Guiry 2020), only eight corticated species of *Dasya* that reach at least 3 cm tall at maturity, including three from Bermuda (*D. collinsiana*, *D. cryptica* and *D. punicea*), appear to share an overall axial pattern of pseudodichotomous branching with *D. sylviae* sp. nov. (Table 2, Fig. 2A–C). However, key morphological characteristics easily distinguish them from the new species presented here. Among the few species with longer pseudolaterals approaching the length of those in the new species (to 5.5 mm

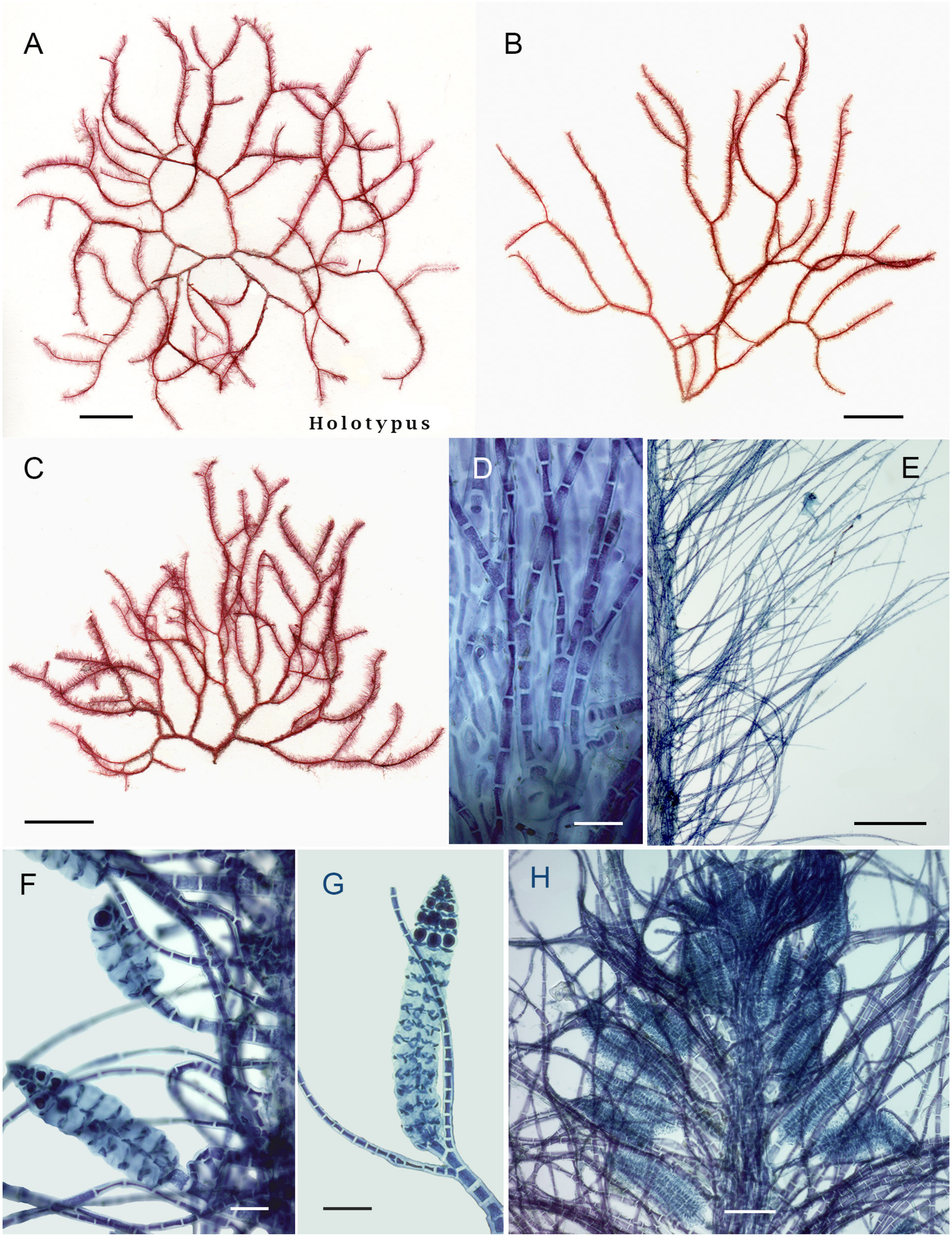

Fig. 2. *Dasya sylviae* C.W.Schneid., M.M.Cassidy & G.W.Saunders sp. nov. **A**. Holotype specimen, *CWS/TRP* 16-21-14 (BDA2031); MICH. **B–C**. Isotype specimens. **D**. Whole mount near apex with rhizoidal cortication and pseudolateral branches, *CWS/TRP* 16-17-2. **E**. Whole mount of axis with emerging pseudolaterals, *CWS/TRP* 16-21-14. **F**. Tetrasporangial stichidia on long pedicels, *CWS/TRP* 16-11-1 (BDA1969). **G**. Acropetal development in a tetrasporangial stichidium at base of pseudolateral branch with whorled two-celled branches bearing sporangia that lack post-sporangial cover cells, *CWS/TRP* 16-11-1 (BDA1969). **H**. Spermatangial stichidia at axis apex, *CWS/TRP* 16-21-14. Scale bars: A–C = 2 cm; D, F = 50 µm; E = 500 µm; G–H = 100 µm.

long), *D. anastomosans* (Weber Bosse) M.J.Wynne and *D. cryptica* demonstrate a short bushy habit with more dense pseudolateral growth, larger tetrasporangia and longer stichidia (Table 2).

The species most similar to *Dasya sylviae* sp. nov. in overall habit is *D. crouaniana* (type locality West Indies), but the latter species is characterized by its striking loss of deciduous pseudolaterals in the lower half of its main axes contrasted by densely enveloped distal portions as illustrated in Taylor (1928: pl. 35 fig. 5; 1960: pl. 71 fig 1). These pseudolaterals are shorter in length (1–2 µm) but more densely packed than the longer ones of *D. sylviae* sp. nov. (1.7–5.5 µm). Furthermore, the tetrasporangial stichidia of *D. crouaniana* are both longer and broader (to 1 mm × 80–120 µm) than in the new species (269–305 µm × 73–80 µm). Unfortunately, we do not have genetic information for this species, but its morphological differences distinguish it from *D. sylviae* sp. nov.

While *Dasya punicea* (type locality Venice) appears to be somewhat similar to *D. sylviae* sp. nov. in habit, the Mediterranean species can be differentiated by its subverticillate pseudolaterals, slightly longer tetrasporangial stichidia (300–400 µm vs 269–305 µm) and slightly larger tetrasporangia (30–40 µm vs 21–29 µm). Its long pseudolaterals (to 4.4 mm) are reminiscent of the new species. *Dasya punicea* was reported from Bermuda by Collins & Hervey (1917) who stated that their specimens had a tendency to issue ramelli [pseudolaterals] "in more or less distinct whorls," a condition dissimilar to that in specimens from the eastern Atlantic where the pseudolaterals were spirally arranged (Maggs & Hommersand 1993). Ballantine & Aponte (2004) argued that the entity first reported in the western Atlantic from Bermuda by Collins & Hervey (1917) as *D. punicea* was different from eastern Atlantic and Mediterranean isolates. Three archival specimens left by A. Hervey as *D. punicea* (Collins & Hervey 1917; NY 2178604) are an admixture of two species on a single sheet, one representing a young *Dasya spinuligera* Collins & Herv., the remaining representative of *Wrangelia* C.Agardh (Wrangeliaceae J.Agardh), not *Dasya*.

The mesophotic specimens described here as a new taxon were collected along with two other species of *Dasya* at these depths, *D.* cf. *baillouviana* (S.G.Gmel.) Mont. (58–77 m) and *D. spinuligera* (60 m). Unlike *D. sylviae* sp. nov., both of these species with different and distinctive morphologies are also known on shallow subtidal reefs in Bermuda. Including *D. collinsiana*, *D. cryptica* and *D. spinuligera*, *D. sylviae* sp. nov. represents the fourth species of the genus with its type locality in Bermuda (Collins & Hervey 1917; Howe 1918; Schneider *et al.* 2017).

Genetically, *Dasya sylviae* sp. nov. falls in a clade with the recently described *D. adela*, a species discovered in a landlocked fjord in Norway (Sjøtun *et al.* 2016), and the alternately to irregularly branched *Dasya* sp. 1Bda from the shallow subtidal of Bermuda (Schneider *et al.* 2017) (Fig. 1). *Dasya adela* is significantly smaller (to 3 cm) than *D. sylviae* sp. nov., and develops "radially to irregularly set side [indeterminate] branches" (Sjøtun *et al.* 2016) and cover cells for tetrasporangia in stichidia. These two species are morphologically easy to differentiate even if their habitats weren't also disparate.

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References

Ballantine D.L. & Aponte N.E. 2004. *Dasya abbottiana* sp. nov. (Dasyaceae, Rhodophyta) from Puerto Rico, Caribbean Sea. *Cryptogamie, Algologie* 25: 409–417.

Choi H.-G., Kraft G.T., Lee I.K. & Saunders G.W. 2002. Phylogenetic analyses of anatomical and nuclear SSU rDNA sequence data indicate that the Dasyaceae and Delesseriaceae (Ceramiales, Rhodophyta) are polyphyletic. *European Journal of Phycology* 37 (4): 551–569. https://doi.org/10.1017/S0967026202003967

Collins F.S. & Hervey A.B. 1917. The algae of Bermuda. *Proceedings of the American Academy of Arts & Sciences* 53: 1–195. https://doi.org/10.2307/20025740

Dawes C.J. & Mathieson A.C. 2008. *The Seaweeds of Florida*. University Press of Florida, Gainesville.

Earle S.A. 1972a. Introduction. *In*: Collette B.B. & Earle S.A. (eds) *Results of the Tektite Program: Ecology of Coral Reef Fishes*: 1–11. Natural History Museum, Los Angeles County Science Bulletin 14.

Earle S.A. 1972b. The influence of herbivores on the marine plants of Great Lameshur Bay, with an annotated list of plants. *In*: Collette B.B. & Earle S.A. (eds) *Results of the Tektite Program: Ecology of Coral Reef Fishes*: 17–44. Natural History Museum, Los Angeles County Science Bulletin 14.

Fredericq S. & Norris J.N. 1986. The structure and reproduction of *Dasya haitiana* sp. nov. (Dasyaceae, Rhodophyta) from the Caribbean Sea. *Phycologia.* 25: 185–196. https://doi.org/10.2216/i0031-8884-25-2-185.1

Guiry M.D. & Guiry G.M. 2020. AlgaeBase. Available from http://www.algaebase.org [accessed 15 Apr. 2020].

Howe M.A. 1918. Class 3. Algae. *In*: Britton N.L. (ed.) *Flora of Bermuda*: 489–540. Charles Scribner's Sons, New York.

Huisman J.M. 2018. *Algae of Australia. Marine Benthic Algae of North-Western Australia. 2. Red Algae*. ABRS & CSIRO Publishing, Canberra and Melbourne.

Kearse M., Moir R., Wilson A., Stones-Havas S., Cheung M., Sturrock S., Buxton S., Cooper A., Markowitz S., Duran C., Thierer T., Ashton B., Meintjes P. & Drummond A. 2012. Geneious Basic: an integrated and extendable desktop software platform for the organization and analysis of sequence data. *Bioinformatics* 28 (12): 1647–1649. https://doi.org/10.1093/bioinformatics/bts199

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.

López-Piñero I.Y. & Ballantine D.L. 2001. *Dasya puertoricensis* sp. nov. (Dasyaceae, Rhodophyta) from Puerto Rico, Caribbean Sea. *Botanica Marina* 44 (4): 337–344. https://doi.org/10.1515/BOT.2001.043

Maggs C.A. & Hommersand M.H. 1993. *Seaweeds of the British Isles. Vol. 1 Rhodophyta. Part 3A Ceramiales*. The Natural History Museum. HMSO Publications, London.

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. https://doi.org/10.1111/j.0022-3646.1996.00145.x

Parsons M.J. 1975. Morphology and taxonomy of the Dasyaceae and the Lophothalieae (Rhodomelaceae) of the Rhodophyta. *Australian Journal of Botany* 23 (4): 549–713. https://doi.org/10.1071/BT9750549

Richards J.L., Gabrielson P.W. & Schneider C.W. 2018. *Sporolithon mesophoticum* sp. nov. (Sporolithales, Rhodophyta) from Plantagenet Bank off Bermuda at a depth of 178 m. *Phytotaxa* 385 (2): 67–76. https://doi.org/10.11646/phytotaxa.385.2.2

Saunders G.W. & McDevit D.C. 2012. Methods for DNA barcoding photosynthetic protists emphasizing the macroalgae and diatoms. *Methods in Molecular Biology* 858: 207–222. https://doi.org/10.1007/978-1-61779-591-6_10

Saunders G.W. & Moore T.E. 2013. Refinements for the amplification and sequencing of red algal DNA barcode and RedToL phylogenetic markers: a summary of current primers, profiles and strategies. *Algae* 28: 31–43. https://doi.org/10.4490/algae.2013.28.1.031

Schneider C.W. 2003. An annotated checklist and bibliography of the marine macroalgae of the Bermuda islands. *Nova Hedwigia* 76: 275–361. https://doi.org/10.1127/0029-5035/2003/0076-0275

Schneider C.W., Quach P.K. & Lane C.E. 2017. A case for true morphological crypsis: Pacific *Dasya anastomosans* and Atlantic *D. cryptica* sp. nov. (Dasyaceae, Rhodophyta). *Phycologia* 56: 359–368. https://doi.org/10.2216/16-79.1

Schneider C.W., Lane C.E. & Saunders G.W. 2018. A revision of the genus *Cryptonemia* (Halymeniales, Rhodophyta) in Bermuda, western Atlantic Ocean, including five new species and *C. bermudensis* (Collins *et* M. Howe) comb. nov. *European Journal of Phycology* 53: 350–368. https://doi.org/10.1080/09670262.2018.1452297

Schneider C.W., Popolizio T.R., Kraft L.G.K. & Saunders G.W. 2019a. New species of *Galene* and *Howella* gen. nov. (Halymeniaceae, Rhodophyta) from the mesophotic zone off Bermuda. *Phycologia* 58: 690–697. https://doi.org/10.1080/00318884.2019.1661158

Schneider C.W., Popolizio T.R. & Saunders G.W. 2019b. Collections from the mesophotic zone off Bermuda reveal three species of Kallymeniaceae (Gigartinales, Rhodophyta) in genera with transoceanic distributions. *Journal of Phycology* 54: 415–424. https://doi.org/10.1111/jpy.12828

Schneider C.W., Peterson E.S. & Saunders G.W. 2020. Two new species of Solieriaceae (Rhodophyta, Gigartinales) from the euphotic and mesophotic zones off Bermuda, *Meristotheca odontoloma* and *Tepoztequiella muriamans*. *Phycologia* 59: 177–185. https://doi.org/10.1080/00318884.2020.1719326

Sjøtun K., Heggøy E., Gabrielsen T.M. & Rueness J. 2016. *Dasya adela* sp. nov. (Rhodophyta, Ceramiales), an enigmatic new *Dasya* from a landlocked fjord in southwest Norway. *Phycological Research* 64: 79–94. https://doi.org/10.1111/pre.12121

Stamatakis A. 2014. RAxML version 8: a tool for phylogenetic analyses and post-analysis of large phylogenies. *Bioinformatics* 30 (9): 1312–1313. https://doi.org/10.1093/bioinformatics/btu033

Stefanoudis P.V., Smith S.R., Schneider C., Wagner D., Goodbody-Gringley G., Xavier J., Rivers M., Woodall L.C. & Rogers A.D. 2018. *Deep Reef Benthos of Bermuda: Field Identification Guide*. Nekton, Oxford, England. https://doi.org/10.6084/m9.figshare.7333838

Taylor W.R. 1928. *The Marine Algae of Florida, with Special Reference to the Dry Tortugas.* Publication 379, Carnegie Institution of Washington.

Taylor W.R. 1960. *Marine Algae of the Eastern Tropical and Subtropical Coasts of the Americas*. University of Michigan Press, Ann Arbor.

Thiers B. continuously updated. Index Herbariorum: A Global Directory of Public Herbaria and Associated Staff. New York Botanical Garden's Virtual Herbarium.
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