Research article

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

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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, rbcL) 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. Schneider, 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 *rbcL* 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 *rbcL* 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 *rbcL* 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 *rbcL* 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 \textit{rbc}L-3P sequence generated here was linked to \textit{rbc}L-5P data available in GenBank (KX913353) for \textit{Dasya spinuligera} Collins & Herv.

| Species | Voucher no. | BOLD no. | Collectors | Coll. date | Country | Province/State | Locality | \(\degree\)Latitude | \(\degree\)Longitude | COI-5P | rbcL |
|---------|-------------|----------|------------|------------|---------|----------------|----------|-------------------|-------------------|--------|------|
| \textit{Dasya baillouviana} (S.G.Gmel.) Mont. | GWS012466 | ABMMC14293-10 | K. Dixon | 21 Aug. 2010 | Canada | Nova Scotia | South Harbour, Cape Breton Island | 46.867237 | -60.447124 | HQ919472 | MW698713 |
| \textit{Dasya baillouviana} | CWS/TRP 16-17-4 (BDA2013) | ABMMC22695-16 | C. Schneider, T. Popolizio | 3 Aug. 2016 | Bermuda | | Spittal, offshore of Midoccean Point | 32.320000 | -64.658056 | — | MW698701 |
| \textit{Dasya cenomiodes} Harv. | GWS014838 | ABMMC7112-10 | G. Kraft, G. Saunders | 14 Jan. 2010 | Australia | Victoria | Queenscliff Jetty, Port Phillip Heads | -38.2669 | 144.6678 | HM917437 | MW698711 |
| \textit{Dasya clavigera} (Womersley) M.J.Parsons | GWS014853 | ABMMC7125-10 | G. Kraft, G. Saunders | 14 Jan. 2010 | Australia | Victoria | Queenscliff Jetty, Port Phillip Heads | -38.2669 | 144.6678 | HM917445 | MW698723 |
| \textit{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 |
| \textit{Dasya sessilis} Yamada | GWS011955 | ABMMC7065-10 | G. Saunders, T. Abe, N. Yotsukura | 2 Dec. 2008 | Japan | | Kikoni (site of old marine station) | 41.70075 | 140.52399 | HM917402 | MW698700 |
| \textit{Dasya} sp. 1AUS | GWS002588 | ABMMC5285-09 | G. Saunders | 22 Jan. 2005 | Australia | Tasmania | Snug Park | -43.06615 | 147.2645 | HM916129 | MW698700 |
| \textit{Dasya} sp. 2GWS | GWS014969 | ABMMC7219-10 | G. Saunders, K. Dixon | 18 Jan. 2010 | Australia | Tasmania | Windmill Point, George Town | -41.1097 | 146.81699 | HM917514 | MW698716 |
| \textit{Dasya} sp. 2TAS | GWS025124 | OZSEA508-10 | G. Saunders, K. Dixon | 11 Nov. 2010 | Australia | Western Australia | Canal Rocks | -33.66935 | 114.99531 | MW699759 | MW698705 |
| \textit{Dasya} sp. 3WA | GWS024888 | OZSEA514-10 | G. Saunders, K. Dixon | 10 Nov. 2010 | Australia | Western Australia | Cozy Corner (Knobby Pt.) | -34.25595 | 115.02777 | MW699763 | MW698708 |
| \textit{Dasya} sp. 4WA | GWS024893 | OZSEA443-10 | G. Saunders, K. Dixon | 10 Nov. 2010 | Australia | Western Australia | Cozy Corner (Knobby Pt.) | -34.25595 | 115.02777 | MW699763 | MW698708 |
| \textit{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 |
| \textit{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. | 32.479933 | -64.594805 | MW699758 | MW698704 |
| \textit{Dasya sylviae} | CWS/TRP 16-11-10 (BDA1982) | ABMMC22692-16 | C. Schneider, T. Popolizio | 28 Jul. 2016 | Bermuda | | Ledge North northeast of St. George’s I. | 32.479933 | -64.594805 | MW699758 | MW698704 |
| \textit{Dasya sylviae} | 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 | MW698761 |
| \textit{Dasya sylviae} | CWS/TRP 16-17-2 (BDA2011) | ABMMC22694-16 | C. Schneider, T. Popolizio | 3 Aug. 2016 | Bermuda | | Spittal, offshore of Midoccean Point | 32.320000 | -64.658056 | MW699766 | MW698766 |
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     | rbcL       |
|-------------------------------|-------------|-----------|---------------------|------------|---------------|----------------|-----------------------------------------------|-----------|------------|------------|------------|
| Dasya sylviae                 | CWS/TRP 16-21-14 (BDA2030) Isootype | ABMMC22698-16 | C. Schneider, T. Popolizio | 11 Aug. 2016 | Bermuda       |                | Spittal, offshore of Midocean Point           | 31.3205555 | -64.658889 | MW09769    | —          |
|                               | 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 | MW097721   | MW698720   |
| Dasya tenuis                  | GWS025517   | OZSEA485-10 | G. Saunders, K. Dixon | 14 Nov. 2010 | Australia     | Western Australia | Blackwall Reach, Swan River                  | -32.02101 | 115.78316  | MW09764    | MW698709   |
| Dasyssiphonia japonica (Yendo) | GWS030121   | ABMMC16707-12 | A. Savie             | 18 Apr. 2012 | USA           | Massachusetts  | Garbage Beach, Breakwater, Woods Hole        | 41.52518  | -70.67256  | KC158582   | MW698722   |
| Dasyssiphonia sp. 1WA         | GWS024416   | OZSEA529-10 | G. Saunders, K. Dixon | 7 Nov. 2010  | Australia     | Western Australia | Little Beach                                  | -34.97163 | 118.19599  | MW09762    | MW698707   |
| Dasyssiphonia sp. 2WA         | GWS024798   | OZSEA536-10 | G. Saunders, K. Dixon | 9 Nov. 2010  | Australia     | Western Australia | Cape Leeuwin Lighthouse                      | -34.37167 | 115.1363   | MW09760    | MW698706   |
| Heterosiphonia callithamniunm (Sond.) Falkenh. | GWS024726   | OZSEA533-10 | G. Saunders, K. Dixon | 9 Nov. 2010  | Australia     | Western Australia | Cape Leeuwin Lighthouse                      | -34.37167 | 115.1363   | MW09772    | —          |
| Heterosiphonia crassipes (Harv.) Falkenh. | GWS024727   | OZSEA534-10 | G. Saunders, K. Dixon | 9 Nov. 2010  | Australia     | Western Australia | Cape Leeuwin Lighthouse                      | -34.37167 | 115.1363   | MW09771    | MW698720   |
| Heterosiphonia plumosa (J.Ellis) Batters | GWS025690   | ABMMC21928-16 | G. Saunders, T. Bringloe | 9 Jun. 2016  | Norway        |                | Kleppesjøen                                    | 60.18474  | 5.14936    | MN184231   | MN184525   |
| Heterosiphonia densiuscula Kylin | GWS028128   | ABMMC15502-11 | G. Saunders, K. Dixon | 7 Jul. 2011  | Canada        | British Columbia | Murchison L, east end, Gwaii Haanas           | 52.60585  | -131.43289 | MW09770    | MW698719   |
| Heterosiphonia sp. 2AUS        | GWS016476   | ABMMC8255-10 | G. Saunders, K. Dixon | 29 Jan. 2010 | Australia     | Tasmania       | Stanley Breakwater                            | -40.76731 | 145.30583  | MW09756    | MW698702   |
| Rhodoptilum plumosum (Harv. & Bailey) Kylin | GWS036815   | ABMMC21032-15 | G. Saunders, M. Bruce, T. Bringloe | 11 Jul. 2015 | Canada        | British Columbia | Smythe Passage East (Macrocystis bed), Haida Gwai | 54.06791  | -132.51958 | MW09768    | MW698718   |
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, Ruennes & Sjøtun that demonstrated a 6% divergence. Similarly, we generated an *rbcL* 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.

| Plant height (cm) | D. anastomosans | D. carteri | D. collinsiana | D. crouaniana | D. cryptica | D. haitiana | D. punicea | D. rosyliae | D. sylviae sp. nov. |
|------------------|-----------------|------------|---------------|---------------|-------------|-------------|------------|-------------|-------------------|
| 3–6(–20)         | to 11           | 1–3(–5+)   | to 7          | 4–5           | 5–9         | 5–10        | to 10      | 4–17          |

**Branching pattern**

- Pseudodichotomous
- Irregularly pseudodichotomous
- Alternate, irregular to somewhat pseudodichotomous
- Widely pseudodichotomous to irregular
- Pseudodichotomous
- Pseudodichotomous to irregular
- Alternate to pseudodichotomous and irregular
- Pseudodichotomous

| 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 | tapering slightly to tips |
| Pseudolaterals    | monosiphonous | monosiphonous | monosiphonous | monosiphonous | monosiphonous | monosiphonous | monosiphonous | 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 pseudodichotomously branched near base | 5–8 times divaricately pseudodichotomous | 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.

| Metric                                | *D. anastomosans* | *D. carteri* | *D. collinsiana* | *D. crouaniana* | *D. cryptica* | *D. haitiana* | *D. punctea* | *D. rosylniae* | *D. sylviae* | *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        | 5–12          | 8–12         | –              | –             | 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        |
| Tetrasporangium stichidium            |                   |              |                  |                |             |               |              |                |              |
| 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/stichidum        | 10–13             | 15           | –                | –              | 10–27       | –             | –             | –              | –             | 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              | –                 | –            | –                | –              | –           | –             | –             | –              | –             | –                   |
| Diameter (μm)                         | –                 | –            | 24–36            | 60–70          | –           | –             | –             | –              | –             | 50–60              |
| Length (μm)                           | –                 | –            | 60–100           | 150–225        | –           | –             | –             | –              | –             | 46–69              |
| 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 & Mathiesson 2008 | Schneider *et al.* 2017 | Fredericq & Norris 1986 | Taylor 1960; Littler & Littler 2000; Lope & Piñero & Ballantine 2001 | Millar 1996 | present study |
Fig. 1. Concatenated COI-5P and \textit{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 (\textit{rbc}L/COI-5P). The novel genetic group, \textit{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 60 m; 29 Jul. 2016, Schneider & Popolizio 16-12-2 [BDA1992] • Spittal, offshore of Mid Ocean 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 (pseudolaters; Fig. 2E), except in some older plants in the most basal portions; pseudolaters 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 pseudolater, upper portions unbranched and slightly tapering (Fig. 2E); basal cells of pseudolaters 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 µm 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 pseudolaters (Fig. 2F) or terminating basal dichotomies of pseudolaters (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 (pseudolaters), 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 pseudolaters 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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