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Article

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Sporolithon mesophoticum sp. nov. (Sporolithales, Rhodophyta) from Plantagenet Bank off Bermuda at a depth of 178 m

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Abstract

A coralline rhodolith was collected from a depth of 178 m, the lower end of the mesophotic zone, on Plantagenet Bank offshore of Bermuda by the submersible *Nomad* using a mechanical armature. DNA sequence comparisons of the plastid encoded *psb*A and *rbc*L loci of this specimen to Sporolithales from the tropical western Atlantic and worldwide revealed it to be an unnamed species of *Sporolithon*. *Sporolithon mesophoticum sp. nov.* possesses tetrasporangial sori flush to slightly raised above the thallus surface and has uniquely flattened perithallial and meristematic cells. Thus far, the new species is the deepest known living marine macroalga that has been sequenced and placed into a phylogenetic context.

Keywords: biogeography, coralline algae, marine algae, seaweeds

Introduction

There has been renewed interest in mesophotic macroalgae with our ability to not only observe these organisms (Kahng & Kelly 2007, Rooney *et al.* 2010), but also to collect them for scientific study, including biodiversity and taxonomy (e.g. McDermid & Abbott 2006, Ballantine *et al.* 2016, Spalding *et al.* 2016). Recently, Richards and Fredericq (2018) described a new mesophotic coralline species from the Gulf of Mexico, *Sporolithon sinusmexicanum* J.Richards & Fredericq based on DNA sequences. This followed the foundational study of Richards *et al.* (2017) that sequenced the type specimens of four other *Sporolithon* species previously reported from the western Atlantic: the generitype *S. ptychoides* Heydrich (type locality, El Tor, Egypt), *S. molle* (Heydrich) Heydrich (type locality: El Tor, Egypt), *S. dimotum* (Foslie & M.Howe) Yamaguishi-Tomita ex M.J.Wynne (type locality: Lemon Bay, near Guánica, Puerto Rico), and *S. episporum* (M.Howe) E.Y.Dawson (type locality: Point Toro, near Colon, Panama). *Sporolithon ptychoides* and *S. molle* were shown not to be present in the western Atlantic, whereas *S. dimotum* and *S. episporum* were confirmed as distinct species. Herein, we report a new mesophotic species of *Sporolithon* from a seamount offshore of Bermuda.

Materials & Methods

Using the mechanical armature of the ABS +1 Manned Triton submersible *Nomad* off the R/V *Baseline Explorer*, we collected a large (9.3 cm x 7.2 cm), nodular, coralline rhodolith from 178 m on Plantagenet Bank, a seamount offshore of the emerged islands of Bermuda. The rhodolith was quickly air dried with a fan. Specimen preparation, DNA extraction, and sequencing was performed following the protocol of Gabrielson *et al.* (2011); amplification of the 3' end of *rbc*L (694 bp) was performed as in Gabrielson *et al.* (2011) and *psb*A (899 bp) was amplified following Adey *et al.* (2015). Maximum Likelihood (ML) analyses were conducted according to the protocol of Richards *et al.* (2017). Table 1 provides a list of specimens and voucher information for taxa included in the analyses. Scanning electron microscopy was performed according to the protocol of Richards *et al.* (2017) with a Hitachi S-3000N Scanning

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Electron Microscope (SEM) and with a JEOL 6300F field emission SEM at an accelerating voltage of 25 kV. Cell dimensions were measured as described in Richards *et al.* (2017) with ten cells measured for each cell type except where otherwise noted. Herbarium abbreviations follow Thiers (2018, continuously updated).

TABLE 1. List of GenBank numbers and reference information for sequences of taxa included in phylogenetic analyses.

Taxa	Id. No.	Locality	Reference	GenBank Accession No.	
				*psb*A	*rbc*L
Clathromorphum compactum	US 170929	Labrador, Canada	Adey *et al.* 2015	KP142730	KP142774
Heydrichia cerasina	NCU 617165	Western Cape Province, South Africa	Richards *et al.* 2017	MF034551	KY994128
Heydrichia homalopasta	NZC0748	New Zealand	Broom *et al.* 2008	DQ167931	-
Heydrichia woelkerlingii	NCU 597127	South Africa	Mateo-Cid *et al.* 2014, Adey *et al.* 2015	JQ917415	KP142788
Heydrichia woelkerlingii	NZC2014	New Zealand	Nelson *et al.* 2015	FJ361382	KM369120
Lithophyllum incrustans	GALW 15746 (E137)	France	Hernández-Kantun *et al.* 2015	JQ896238	KR708543
Lithophyllum neocongestum	US 223011	Caribbean Panama	Hernández-Kantún *et al.* 2016	KX020466	KX020484
Membranoptera platyphylla	UC 1856248	Washington, U.S.A.	Hughey *et al.* 2017	KT266849	KT266849
Membranoptera tenuis	UC 266439	Washington, U.S.A.	Hughey *et al.* 2017	KP675983	KP675983
Membranoptera weeksiae	UC 264804	California, U.S.A.	Hughey *et al.* 2017	KJ513670	KJ513670
Neopolyporolithon reclinatum	UBC A88609	British Columbia, Canada	Adey *et al.* 2015	KP142762	KP142806
Renouxia sp.	HV508A	Jamaica	West *et al.* 2016	-	KC134345
Rhodogorgon carriebowensis	WELT TBA	Panama, Caribbean Sea	Nelson *et al.* 2015	KM369059	KM369119
Sporolithon cf. *ptychoides*	GM AF6	Brazil	Adey *et al.* 2015	KP142753	KP142787
Sporolithon dimotum	NY 900043 (Howe 2667)	Lemon Bay, near Guanica, Puerto Rico	Richards *et al.* 2017	-	KY994131
Sporolithon durum	NZC2375	New Zealand	Nelson *et al.* 2015	FJ361583	KM369122
Sporolithon durum	Aus	Australia	Nelson *et al.* 2015	DQ168023	KM369121
Sporolithon eltorensis	NCU 606659 (LAF 5850)	El Tor, Egypt, Gulf of Suez	Richards *et al.* 2017	MF034543	MG051269
Sporolithon eltorensis	LAF 5767 (NCU 649164)	Dahab, Egypt, Gulf of Aqaba	Richards *et al.* 2017	MF034544	-
Sporolithon episporum	NCU 598843 (PHYKOS 5467)	Bocas del Toro, Panama, Caribbean Sea	Richards *et al.* 2017	MF034547	KY994124
Sporolithon indopacificum	L 3964509	Tanzania	Maneveldt *et al.* 2017	MG051270	MG051266
Sporolithon mesophoticum	NCU 658543 (BDA 2048)	Plantagenet (Argus) Bank, SSW of Bermuda	Present study	MK159180	MK159181
Sporolithon molle	NCU 606657 (LAF 5848)	El Tor, Egypt, Gulf of Suez	Maneveldt *et al.* 2017, Richards *et al.* 2017	MG051272	KY994120

.....continued on the next page

TABLE 1. (Continued)

Taxa	Id. No.	Locality	Reference	GenBank Accession No.	
				*psb*A	*rbc*L
Sporolithon ptychoides	NCU 606660 (LAF 5875)	El Tor, Egypt, Gulf of Suez	Richards *et al.* 2017	MF034541	KY994117
Sporolithon sinusmexicanum	LAF 6956A	Sackett Bank, northwestern Gulf of Mexico	Richards *et al.* 2017	MF034549	KY994126
Sporolithon sp.	PHYKOS 4623	Gulf of Chiriquí, near Mono Feliz, Panama, Pacific Ocean	Richards *et al.* 2017	MF034548	-
Sporolithon sp.	LBC0695	Fiji	Bittner *et al.* 2011	GQ917501	-
Sporolithon sp. epilithic	NZC2175	New Zealand	Nelson *et al.* 2015	FJ361509	KM369123
Sporolithon sp.	GM AF5	Brazil	Adey *et al.* 2015	KP142752	KP142786
Sporolithon tenue	US 170943	Brazil	Adey *et al.* 2015	KP142751	KP142785
Sporolithon yoneshigueae	RB 600359	Brazil	Richards *et al.* 2017	MF034545	KY994122

Results

Results of the ML analyses showed that the specimen from Plantagenet Bank joined a clade with full support along with *Sporolithon yoneshigueae* Bahia, Amado-Filho, Maneveldt & W.H.Adey (Fig. 1) and was also sister to *S. sinusmexicanum* J.Richards & Fredericq. Sequence divergence values for *psb*A and *rbc*L sequences are presented in Tables 2–3.

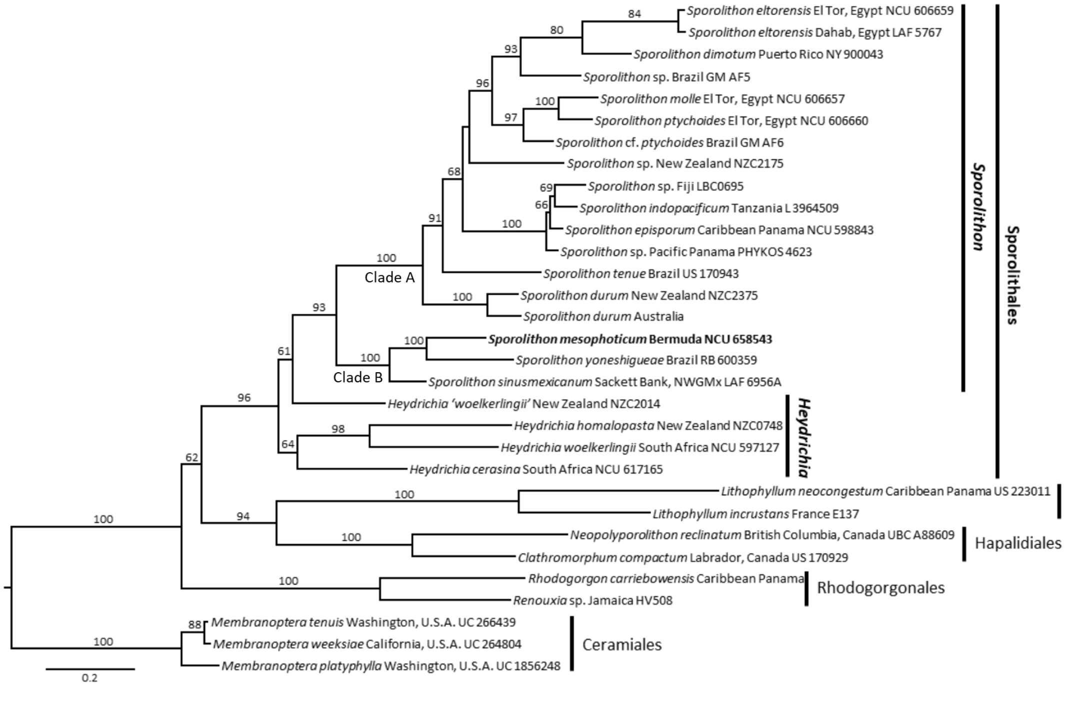


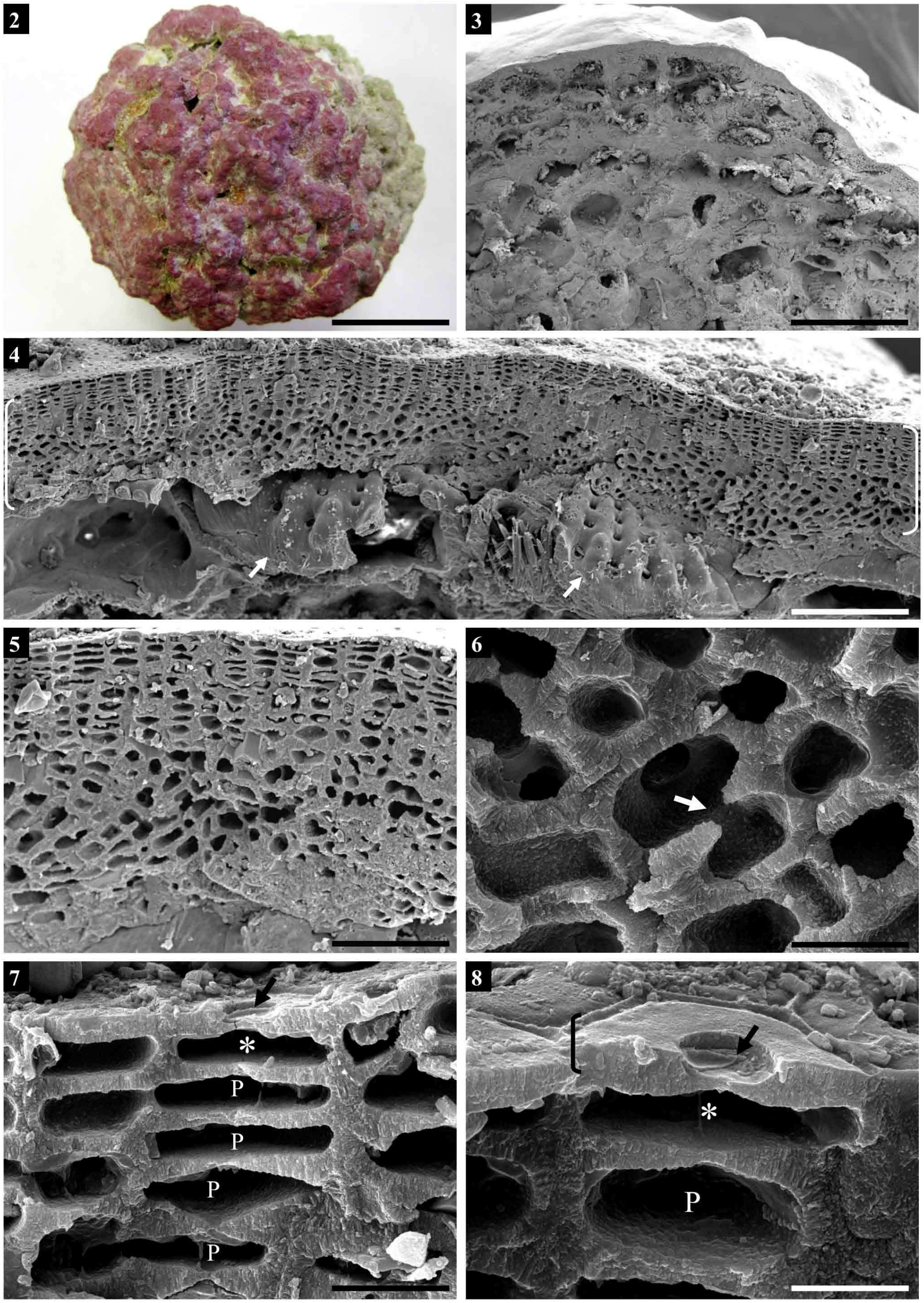
FIGURE 1. Phylogeny of Sporolithales based on Maximum Likelihood analyses of concatenated *psb*A and *rbc*L (2,247 bp) sequences, with *Membranoptera* spp. (Ceramiales) as outgroup. Numbers above nodes are bootstrap values (1,000 replicates).

TABLE 2. Pairwise sequence divergences (%) for *psb*A sequences (796 bp) reported in this study: *Sindo* = *Sporolithon indopacificum*; *Spty* = *S. ptychoides*; *Smol* = *S. molle*; *Selt* = *S. eltorensis*; *Sepi* = *S. episporum*; *S*sp. = *S.* species; *Sdur* = *S. durum*; *Sten* = *S. tenue*; *Syon* = *S. yoneshigueae*; *Ssin* = *S. sinusmexicanum*; *Smes* = *S. mesophoticum*; *Hhom* = *Heydrichia homalopasta*; *Hwoe* = *H. woelkerlingii* (South African Topotype); *H'woe'* = *H. 'woelkerlingii'* (New Zealand specimen); *Hcer* = *H. cerasina*.

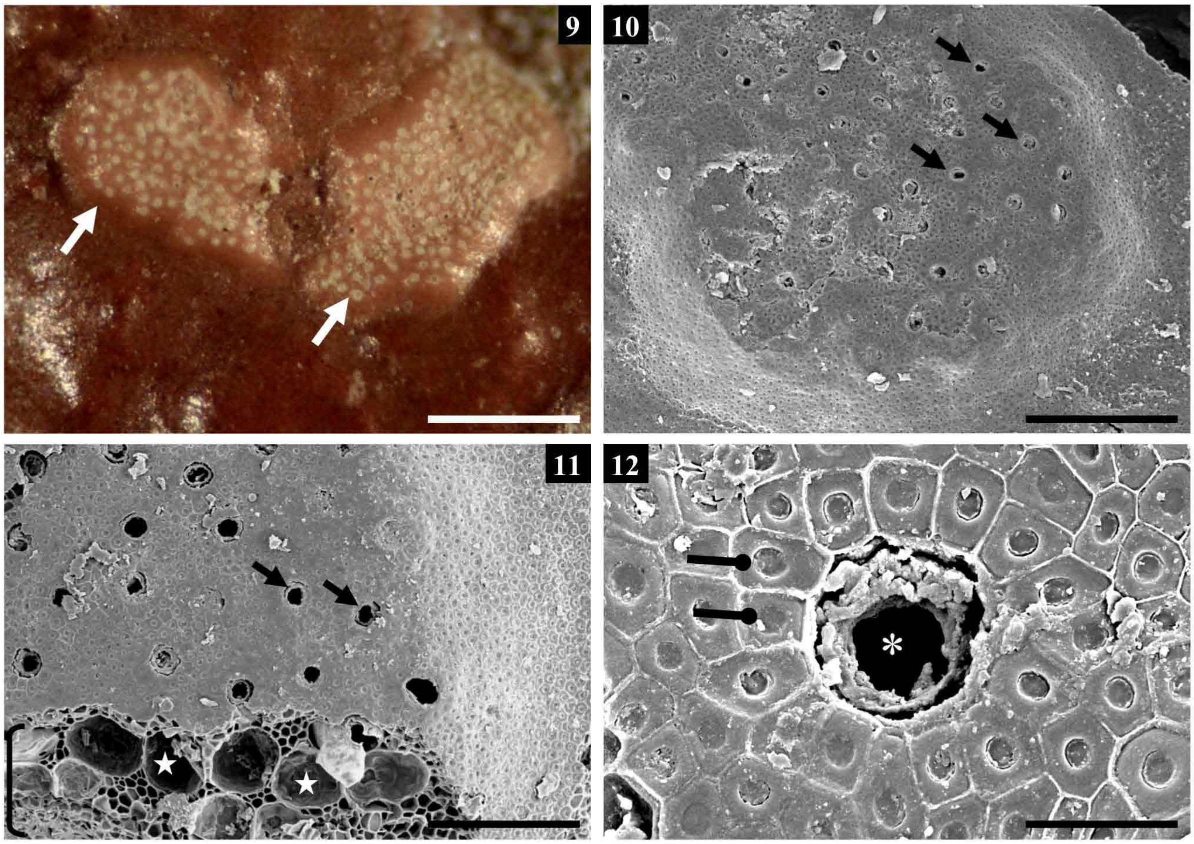
1. *Sindo* L 3964509	9.9																				
2. *Spty* NCU 606660	10.2	5.2																			
3. *Smol* NCU 606657	9.7	9.2	9.9																		
4. *Selt* LAF 5767	9.7	8.7	9.5	1																	
5. *Selt* NCU 606659	3.1	8.9	9.4	9.2	9																
6. *Sepi* NCU 598843	2.9	8.8	8.9	9	9.2	1.8															
7. *S*sp. PHYKOS 4623	8.2	5.8	6.2	6.9	6.7	7.3	7														
8. *S*cf.*pty* GM AF6	3.4	9.9	10.6	10.4	10.4	2.9	3	8.2													
9. *S*sp. LBC0695	9.3	8.5	9	6	5.8	8.4	8	6.5	8.9												
10. *S*sp. GM AF5	7.9	8	8.9	6.9	6.9	7	6.4	6	7.9	6											
11. *S*sp. NZC2175	8.3	9.7	10.6	8	8.3	7.8	8.2	8.8	8.8	7.7	7										
12. *Sdur* Aus	8.7	9.6	9.9	8.2	8.4	8.1	8.4	8.4	8.2	8.4	7.4	3.3									
13. *Sdur* NZCD375	8.9	7.2	8.8	8.7	8.7	8.3	8.2	7.4	8.5	7.2	6.5	7.8	7.2								
14. *Sten* US 170943	10.4	10.4	10.9	10.4	10.7	10.3	10.2	10.4	10.8	10.8	9.9	9	8.8	10.1							
15. *Syon* RB 600359	9.8	10.6	10.7	9.9	10.2	10.1	9.3	9.8	10.7	10.3	8.9	8	8.6	8	7.8						
16. *Ssin* LAF 6956A	11.3	10.7	10.6	10.3	10.1	11.3	10.9	10.3	11.6	10.6	9.4	9.4	9.2	10.3	5.9	8					
17. *Smes* NCU658543	11.9	11.4	12.4	11.1	10.9	10.8	10.9	10.6	11.6	10.9	10.3	11.2	11.5	11.1	12.3	11.7	12.8				
18. *Hhom* NZC0748	11.3	11.1	11.6	10.7	10.6	10.4	10.3	10.9	11.4	9.9	9.7	9.8	9.7	9.3	11.9	9.9	11.7	9.7			
19. *Hwoe* NCU 597127	11.4	11.2	12.3	11.7	12.1	10.8	10.7	10.6	11.1	10.8	9.5	9.7	9.6	9.9	10.2	8.4	10.6	10.7	9.5		
20. *H'woe'* NZC2014	9.2	10.8	11.7	10.4	10.6	8.9	8.8	9.3	10.3	9.7	7.9	8.9	9.4	8.7	11.3	9.4	11.6	10.2	9.4	7.8	
21. *Hcer* NCU 617165	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.	13.	14.	15.	16.	17.	18.	19.	20.	21.

TABLE 3. Pairwise sequence divergences (%) for *rbc*L sequences (657 bp) reported in this study: *Sindo* = *Sporolithon indopacificum*; *Spty* = *S. ptychoides*; *Smol* = *S. molle*; *Selt* = *S. eltorensis*; *Sepi* = *S. episporum*; *S*cf*pty* = *S.* cf. *ptychoides S*sp. = *S.* species; *Sdur* = *S. durum*; *Sten* = *S. tenue*; *Syon* = *S. yoneshigueae*; *Ssin* = *S. sinusmexicanum*; *Smes* = *S. mesophoticum*; *Hwoe* = *Heydrichia woelkerlingii* (South African Topotype); *H'woe'* = *H. 'woelkerlingii'* (New Zealand specimen); *Hcer* = *H. cerasina.*

1. *Sindo* L 3964509	9.4															
2. *Spty* NCU 606660	8.8	3.5														
3. *Smol* NCU 606657	10	8.7	9.4													
4. *Selt* NCU 606659	3.2	9.1	8.4	9.1												
5. *Sepi* NCU 598843	9.1	4.9	5.9	8.8	8.8											
6. *S*cf*pty* GM AF6	9.7	7.9	8.4	6.2	9	8.2										
7. *S*sp. GM AF5	9.3	10.2	9.9	11.9	9.3	9.9	10.7									
8. *S*sp. NZC2175	10.7	9.7	10.4	11.6	9.6	11	9.7	10.2								
9. *Sdur* NZCD375	9.6	10	10.4	11	9.1	10	9.9	10.7	9.6							
10. *Sten* US 170943	14.1	13.9	14.1	15.6	13.6	14.5	14.4	15.5	13.5	12.3						
11. *Syon* RB 600359	12	10.4	11.4	12.3	10.7	11.4	11.9	12.5	11.4	10.8	9.8					
12. *Ssin* LAF 6956A	14	11.3	12.9	14.6	12.8	11.4	13.7	14.6	12.3	13.1	11.2	6.7				
13. *Smes* NCU 658543	15.1	14.9	15.4	16.6	14.5	15.5	15.5	14.8	14.2	14.3	16.2	13.1	14.6			
14. *Hwoe* NCU 597127	12.9	13.7	13.7	15.1	12.5	13.9	13.9	12.5	11.7	13.5	13.6	9.1	10.8	12		
15. *H'woe'* NZC2014	13.2	13.9	14	14.8	12.6	14.2	14.8	14.3	12.3	13.1	15.3	11.9	14.2	13.1	11.3	
16. *Hcer*	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.	13.	14.	15.	16.



FIGURES 2–8. *Sporolithon mesophoticum* Holotype, NCU 658543. 2. Habit of holotype. Scale bar = 3 cm. 3. Fracture of rhodolith showing sedimentary composition of nodule below *S. mesophoticum* crust. Scale bar = 0.8 mm. 4. Partial surface and section view of thallus (brackets) over substratum consisting of sedimentary material including remains of invertebrate organisms (arrows). Scale bar = 138 µm. 5. Vertical fracture of thallus showing monomerous construction. Scale bar = 60 µm. 6. Cell fusion (arrow). Scale bar = 13.8 µm. 7. Section and partial surface view showing epithallial cell (arrow), meristematic cell (*), and layers of short, flattened perithallial cells (P). Scale bar = 9.2 µm. 8. Surface and section view of epithallial cell (bracket, arrow), and section views of putative meristematic cell (*) and perithallial cell (P). Scale bar = 6.3 µm.



FIGURES 9–12. *Sporolithon mesophoticum* Holotype, NCU 658543. 9. Surface view of tetrasporangial sori (arrows). Scale bar = 0.1 cm. 10. Surface view of tetrasprangial sorus with pores (arrows). Scale bar = 258 µm. 11. Surface view of tetrasprangial sorus with pores (arrows) including portion where upper cell layers were removed (bracket) showing top-down view of tetrasporangial compartments (stars). Scale bar = 164 µm. 12. Surface view of a tetrasporangial pore (*) with rosette cells (circle pointers). Scale bar = 27 µm.

Sporolithon mesophoticum J.Richards, P.W.Gabrielson & C.W.Schneider, *sp. nov.* (Figures 2–12)

Holotype (designated here): NCU 658543 (BDA silica gel no. 2048): Plantagenet (Argus) Bank, ca. 30 mi. south-southwest of Bermuda (31˚56'31.86"N, 65˚09'25.22"W), western Atlantic Ocean, 26.ix.2016, depth 178 m by submersible, leg. C.W. Schneider coll. no. 16–23–13.

Isotype: MICH 1210812. Fragment removed from holotype (see ICN Art. 8.3 Ex. 8).

Etymology: The specific epithet refers to the depth zone where the holotype specimen was collected.

Description: Thallus non-geniculate, forming a nucleated rhodolith with a thin crust (120–150 µm) growing over a core of consolidated sedimentary material and fragments of invertebrate organisms, putatively identified as bryozoans (Figs 2–4), found growing in a mesophotic benthic habitat. Thallus construction monomerous, with a weakly developed hypothallium (Figs 4–5). Hypothallial cells rectangular in shape, 14–19 µm long x 5–8 µm wide (n=4). In some locations two superimposed layers of thalli were observed, though extensive layering was not observed. Adjacent hypothallial and perithallial cells linked by cell fusions (Fig. 6); secondary pit connections not observed. The upper perithallium was comprised of layers of wide, flattened cells, 3.1–5.1 µm long x 10.6–16.4 µm wide (Figs 7–8). Meristematic cells also appeared wide and flattened, 2.5–6.1 µm long x 10.5–17.8 µm wide (Figs 7–8). Epithallium (Figs 7–8) a single layer of armored epithallial cells that are and very flattened, with thick, heavily calcified cell walls and a small round or slightly trapezoidal shaped lumen, 1.2–2.0 µm long x 4.8–7.0 µm wide (n=7) (Fig.8). Tetrasporangial sori observed from surface view were flush to slightly raised above the thallus surface and showed tetrasporangial pores surrounded by 10–14 rosette cells (Figs 9–12). No evidence of sloughing of tetrasporangial sori was shown, though no buried tetrasporangial compartments were observed in section views. Surface views of a sorus where upper cell layers were removed show compactly arranged tetrasporangial compartments (Fig. 11).

DNA sequences: Holotype–*rbc*L (GB accession = MK159181); *psb*A (GB accession = MK159180).

Distribution: Presently known only from the type locality on Plantagenet Bank, Bermuda.

Discussion

Sequence divergence values (Tables 2, 3) support the recognition of *S. mesophoticum* as a distinct species. For example, the *rbc*L sequence of *S. mesophoticum* is 11.2% divergent from *S. yoneshigueae* and 6.7% divergent from *S. sinusmexicanum*, which is greater than the *rbc*L divergence between other closely related species in the Sporolithales (e.g. *S. episporum* and *S. indopacificum* Maneveldt & P.W.Gabrielson, 2.7%). Taken from its collection site at 178 m, *S. mesophoticum* is the deepest growing marine alga identified by DNA sequencing, deeper than the sequenced Hawaiian chlorophyte *Umbraulva kaloakulau* H.LSpalding & A.R.Sherwood reported from 125 m (Spalding *et al.* (2016).

The rhodolith structure formed by *S. mesophoticum* is unique, although it fits the description of a nucleated rhodolith (Freiwald, A. & Henrich, R. 1994). The *S. mesophoticum* rhodolith has a core of loosely consolidated sedimentary material, including remains of invertebrate organisms putatively identified as bryozoans, that is brittle and easily fragmented when portions of the *S. mesophoticum* crust are removed. The *S. mesophoticum* crust appears to maintain the nodular rhodolith structure in its calm growth environment; without the alga protecting and consolidating the sedimentary material within, the nodule may erode away over time. Bastos *et al.* (2018) reported that bryozoans are a major component of tropical reefs in the South Atlantic. The findings in this study show that bryozoans, together with coralline algae, may also play a role in the formation of tropical reefs in the tropical western Atlantic.

Littler *et al.* (1985) documented the deepest growing marine alga (268 m depth), an undescribed non-geniculate coralline, from a seamount near San Salvadore Island, Bahamas. They illustrated but did not describe this non-geniculate coralline. Littler *et al.* (1985, fig. 1) showed cells with heavily calcified walls and adjacent perithallial cells linked by cell fusions, but no evidence of secondary pit connections. Based on these observable features, this alga could belong to any of the three, currently recognized, coralline orders, Corallinales, Hapalidiales or Sporolithales. Because this mesophotic specimen is on display at the United States Museum of Natural History (Smithsonian Institution), it could not be sampled for DNA sequencing. Other material from the original collection was examined, but did not appear to contain any coralline crusts. Morpho-anatomically, the Bahamian specimen appears to be distinct from *S. mesophoticum*, lacking the conspicuously flattened perithallial cells of the new species (Figs 5, 7, 8). The wide, flattened perithallial and meristematic cells of *S. mesophoticum* are unique, though it is uncertain if these cells are characteristic of this species, or a growth form resulting from the extreme depth. It is possible that these flattened cells are the result of exceptionally low light conditions and or higher pressure at 178 m depth at the collection site.

The ML analysis shows two fully supported clades of *Sporolithon* spp. (Fig. 1, clades A and B). The new Bermuda species resides in clade B with two other western Atlantic mesophotic species (depth range 27–68 m), *S. yonishigueae* and *S. sinusmexicanum*, the former from the Abrolhos continental shelf off Brazil (Bahia *et al.* 2015) and the latter from mesophotic rhodolith beds in the Gulf of Mexico (Richards & Fredericq 2018). Clade A, however, also contains species from the western Atlantic, as well as the Indo-Pacific Ocean and from both shallow waters, including intertidal species, and species restricted to the mesophotic zone. This is similar to another speciose genus of tropical-subtropical non-geniculate corallines, *Porolithon*, that also has well supported clades with species from both the western Atlantic and the Indo-Pacific, as well as different habitats, ranging from the intertidal to the shallow (<10 m depth) subtidal (Gabrielson *et al.* 2018). For the most part, in both of these genera, many more species are present than was hypothesized based on morpho-anatomy. Biogeographic patterns are complex with strongly supported clades of mixed tropical and subtropical western Atlantic and Indo-Pacific species rather than western Atlantic and Indo-Pacific species segregated into separate clades, and sister species are not clustered by habitat (Richards *et al.* 2017, Gabrielson *et al.* 2018). The exception is clade B of *Sporolithon* species, which thus far is found only in the western Atlantic from mesophotic depths (Fig. 1). The patterns revealed by phylogenetic analyses of coralline DNA sequences provide an evolutionary context for future biogeographic, ecophysiological and paleontological studies.

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