Phytotaxa 423 (2): 049–067
https://www.mapress.com/j/pt/

Article

ISSN 1179-3155 (print edition)
PHYTOTAXA
ISSN 1179-3163 (online edition)

https://doi.org/10.11646/phytotaxa.423.2.1

Sporolithon amadoi sp. nov. (Sporolithales, Rhodophyta), a new rhodolith-forming non-geniculate coralline alga from offshore the northwestern Gulf of Mexico and Brazil

JOSEPH L. RICHARDS[1,*], RICARDO G. BAHIA[2], MICHEL B. JESIONEK[2] & SUZANNE FREDERICQ[1]

[1]*University of Louisiana at Lafayette, Biology Department, Lafayette, LA 70504-3602, U.S.A.*

[2]*Instituto de Pesquisas Jardim Botânico do Rio de Janeiro, Diretoria de Pesquisa Científica, Rua Pacheco Leão 915, Rio de Janeiro, RJ 22460-030, Brazil*

[*]*Corresponding author (Joer207@gmail.com)*

This article is dedicated in loving memory to Dr. Gilberto M. Amado-Filho (October 6, 1959–March 15, 2019).

Abstract

DNA sequence analysis of plastid-encoded *psb*A and *rbc*L loci, and nuclear-encoded LSU rDNA of rhodolith-forming specimens of Sporolithales from Brazil and the northwestern Gulf of Mexico reveal that they belong to an unnamed species of *Sporolithon* (Sporolithaceae). *Sporolithon amadoi sp. nov.* is morpho-anatomically characterized by a vegetative thallus reaching more than 20 cell layers, a tetrasporophyte with tetrasporangial sori slightly raised above the thallus surface that become overgrown and buried after spore release, and by cruciately divided tetrasporangia with pores surrounded by 9–13 rosette cells. Since these morpho-anatomical features are shared with some other *Sporolithon* species, identification of this species can only be confirmed by DNA sequences.

Keywords: Abrolhos bank, biogeography, CCA, coralline algae, marine algae, marine biodiversity, mesophotic, reefs, rhodoliths, seaweeds

Abbreviations: CCA = crustose coralline algae; GB = GenBank; ML = Maximum Likelihood; NWGMx = northwestern Gulf of Mexico; SEGMx = southeastern Gulf of Mexico; SEM = Scanning Electron Microscope

Introduction

The name *Sporolithon ptychoides* Heydrich has previously been assigned to crustose (non-geniculate) coralline algal (CCA) specimens from Brazil exhibiting the following features: 1) raised tetrasporangial sori, 2) a layer of elongate cells at the base of tetrasporangia, 3) tetrasporangial compartments that are not sloughed off after spore release, 4) paraphyses between tetrasporangial compartments comprised of 3–5 cells (Bahia *et al*. 2011, Bahia *et al*. 2015), and 5) 8–11 rosette cells surrounding the pores of tetrasporangial compartments. Recent studies, however, have shown that performing comparative analyses of DNA sequences based on sequences of type specimens is the only way to unequivocally identify non-geniculate coralline algae and that morpho-anatomical characters alone can be misleading (Hind *et al*. 2016, Gabrielson *et al*. 2018, Richards *et al*. 2017, Richards *et al*. 2018a). Richards *et al.* (2017) showed that DNA sequences (*psb*A and *rbc*L) of Brazilian specimens identified as *Sporolithon ptychoides* based on morpho-anatomy did not form a clade with sequences of the type and topotype specimens of *S. ptychoides* from El Tor, Egypt. Other species that do not slough off their tetrasporangial sori, i.e. *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. yoneshigueae* Bahia, Amado-Filho, Maneveldt & W.H.Adey (type locality: Bahia, Brazil), were also shown to be different species than the Brazilian specimens identified previously as *S. ptychoides* (Richards *et al*. 2017, Bahia *et al*. 2015). Additionally, the sequences from the Brazilian specimens were identical to the taxon referred to as *Sporolithon sp. nov.* (LAF 7260) from the northwestern Gulf of Mexico (Fredericq *et al*. 2019). Herein, we describe this taxon as a new species of *Sporolithon* from Brazil and the Gulf of Mexico.

Accepted by Jeffery Hughey: 2 Oct. 2019; published: 4 Nov. 2019

TABLE 1. List of GenBank numbers and reference information for sequences of taxa included in phylogenetic analyses. Sequences in concatenated tree (Fig. 1) shown in italics. Type specimens and specimens of species whose identifications are confirmed by comparison to type or topotype material are shown in bold. *Not analyzed in present study.

Taxa	Id. No. & type designation where applicable.	Locality	Reference	GenBank Accession No.		
				*psb*A	*rbc*L	LSU
Clathromorphum compactum	US 170929	Labrador, Canada	Adey *et al*. 2015	*KP142730*	*KP142774*	-
Heydrichia cerasina	NCU 617165 isotype	Western Cape Province, South Africa	Richards *et al*. 2017	*MF034551*	*KY994128*	KY980439
Heydrichia homalopasta	NZC0748	New Zealand	Broom *et al*. 2008	*DQ167931*	-	-
Heydrichia woelkerlingii	NCU 597127 topotype	South Africa	Mateo-Cid *et al*. 2014, Adey *et al*. 2015	*JQ917415*	*KP142788*	-
Lithophyllum incrustans	GALW 15746 (E137) [species identity confirmed by comparison of *rbc*L to holotype]	France	Hernández-Kantun *et al*. 2015	*JQ896238*	*KR708543*	-
Lithophyllum neocongestum	US 223011 holotype	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 neotype	Washington, U.S.A.	Hughey *et al*. 2017	*KP675983*	*KP675983*	-
Membranoptera weeksiae	UC 264804 holotype	California, U.S.A.	Hughey *et al*. 2017	*KJ513670*	*KJ513670*	-
Mesophyllum lichenoides	LBC0031	France	Bittner *et al*. 2011	*GQ917439	-	GQ917312
Neopolyporolithon reclinatum	UBC A88609	British Columbia, Canada	Adey *et al*. 2015	*KP142762*	*KP142806*	-
Phymatolithon calcareum	LBC0001 [*psb*A and COI is identical to neotype of this species]	France	Bittner *et al*. 2011	*GQ917436	-	GQ917309
Renouxia sp.	LAF 6170	Egypt	Lee *et al*. 2018	*MH281629*	*MH281629*	MK091141
Rhodogorgon carriebowensis	WELT TBA	Panama, Caribbean Sea	Nelson *et al*. 2015	*KM369059*	*KM369119*	-
Rhodogorgon sp.	N.A.	N.A.	Harper & Saunders 2001	-	-	AF419142
Rhodogorgon sp.	SGAD1304047	Indonesia	Lee *et al*. 2018	*MH281630	*MH281630	MK091143
Sporolithales sp. A (as *H. woelkerlingii*)	NZC2014	New Zealand	Nelson *et al*. 2015	*FJ361382*	*KM369120*	-

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TABLE 1 (Continued)

Taxa	Id. No. & type designation where applicable.	Locality	Reference	GenBank Accession No.		
				*psb*A	*rbc*L	LSU
Sporolithon amadoi	RB 779739 paratype	Amazon Reefs, Itaubal, Amapá, Brazil (01°19'08'' N; 46°50'09'' W), 55 m deep, *leg*. GM Amado-Filho, 17.vii.2017	Present study	*MN434067*	-	-
Sporolithon amadoi	RB 779740 paratype	Amazon Reefs, Itaubal, Amapá, Brazil (01°19'08'' N; 46°50'09'' W), 55 m deep, *leg*. GM Amado-Filho, 17.vii.2017	Present study	*MN434068*	-	-
Sporolithon amadoi	RB 779736 holotype	Recifes Esquecidos, São Mateus (18°52'32" S; 39°26'13" W), Espírito Santo, Brazil, 30 m deep, *leg*. RG Bahia, 14.iii.2018	Present study	*MN434069*	-	-
Sporolithon amadoi	RB 779737 isotype	Recifes Esquecidos, São Mateus (18°52'32" S; 39°26'13" W), Espírito Santo, Brazil, 30 m deep, *leg*. RG Bahia, 14.iii.2018	Present study	*MN434070*	-	-
Sporolithon amadoi	RB 779738 isotype	Recifes Esquecidos, São Mateus (18°52'32" S; 39°26'13" W), Espírito Santo, Brazil, 30 m deep, *leg*. RG Bahia, 14.iii.2018	Present study	*MN434071*	-	-
Sporolithon amadoi (as *Sporolithon ptychoides*)	Amado-Filho Brazil 8	Fernando de Noronha Archipelago, Brazil	Bahia *et al*. 2014	*KC870926*	-	-
Sporolithon amadoi (as *Sporolithon ptychoides*)	Amado-Filho Brazil 7	Fernando de Noronha Archipelago, Brazil	Bahia *et al*. 2014	*KC870927*	-	-
Sporolithon amadoi (as *Sporolithon* cf. *ptychoides*)	GM AF6	Fernando de Noronha Archipelago, Brazil	Adey *et al*. 2015	*KP142753*	*KP142787*	-
Sporolithon amadoi	LAF 7256 (5-4-18-4-2) paratype	Ewing Bank (28° 05.937' N; 91°; 01.349' W), NWGMx, offshore Louisiana, U.S.A., 70 meters deep, *leg.* J. Richards & S. Fredericq, 4.v.2018	Present Study	*MN266235*	*MN258542*	MN266234
Sporolithon amadoi	LAF 7260 (5-7-18-3-4) paratype	Bright Bank (27° 53.353' N; 93°; 17.964' W), NWGMx, offshore Louisiana-Texas border, U.S.A., 50-58 meters deep, *leg.* J. Richards & S. Fredericq, 7.v.2018	Present Study	*MN266236*	-	-
Sporolithon amadoi	LAF 7261 (5-7-18-3-4) paratype	Bright Bank (27° 53.353' N; 93°; 17.964' W), NWGMx, offshore Louisiana-Texas Border, U.S.A., 50-58 meters deep, *leg.* J. Richards & S. Fredericq, 7.v.2018	Present Study	*MN266237*	-	-
Sporolithon dimotum	NY 900043 (Howe 2667) holotype	Lemon Bay, near Guanica, Puerto Rico	Richards *et al*. 2017	-	*KY994131*	-

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TABLE 1 (Continued)

Taxa	Id. No. & type designation where applicable.	Locality	Reference	GenBank Accession No.		
				*psb*A	*rbc*L	LSU
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) holotype	El Tor, Egypt, Gulf of Suez	Richards *et al*. 2017	*MF034543*	*MG051269*	KY980433
Sporolithon eltorensis	LAF 5767 (NCU 649164)	Dahab, Egypt, Gulf of Aqaba	Richards *et al*. 2017	*MF034544*	-	KY980434
Sporolithon episporum	NCU 598843 (PHYKOS 5467) [*rbc*L is identical to holotype of this species]	Bocas del Toro, Panama, Caribbean Sea	Richards *et al*. 2017	*MF034547*	*KY994124*	-
Sporolithon indopacificum	L 3964509 holotype	Tanzania	Maneveldt *et al*. 2017	*MG051270*	*MG051266*	-
Sporolithon mesophoticum	NCU 658543 (BDA 2048) holotype	Plantagenet (Argus) Bank, SSW of Bermuda	Richards *et al*. 2018b	*MK159180*	*MK159181*	-
Sporolithon molle	NCU 606657 (LAF 5848) topotype [*rbc*L is identical to isolectotype of this species]	El Tor, Egypt, Gulf of Suez	Maneveldt *et al*. 2017, Richards *et al*. 2017	*MG051272*	*KY994120*	KY980432
Sporolithon ptychoides	NCU 606660 (LAF 5875) topotype [*rbc*L is identical to lectotype of this species]	El Tor, Egypt, Gulf of Suez	Richards *et al*. 2017	*MF034541*	*KY994117*	KY980430
Sporolithon ptychoides	NCU606663 (LAF5846) topotype [*rbc*L is identical to lectotype of this species]	El Tor, Egypt, Gulf of Suez	Richards *et al*. 2017	*MF034542	*KY994118	KY980431
Sporolithon 'ptychoides'	ARS02349	Hawaii	Sherwood *et al*. 2010	-	-	HQ421906
Sporolithon 'ptychoides'	ARS02819	Hawaii	Sherwood *et al*. 2010	-	-	HQ421797
Sporolithales	ARS02572	Hawaii	Sherwood *et al*. 2010	-	-	HQ421744
Sporolithon sinusmexicanum	LAF 6956A holotype	Sackett Bank, NWGMx	Richards *et al*. 2017	*MF034549*	*KY994126*	KY980437
Sporolithon sinusmexicanum	LAF 6970B	Dry Tortugas Vicinity, SEGMx	Richards *et al*. 2017	*MF034550*	*KY994127*	KY980438
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*	-	GQ917344
Sporolithon sp.	ARS02833	Hawaii	Sherwood *et al*. 2010	-	-	HQ421810

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TABLE 1 (Continued)

Taxa	Id. No. & type designation where applicable.	Locality	Reference	GenBank Accession No.		
				*psb*A	*rbc*L	LSU
Sporolithon sp.	GM AF5	Brazil	Adey *et al*. 2015	*KP142752*	*KP142786*	-
Sporolithon sp.	NTOU001470	Taiwan	Liu *et al*. 2018	*MH377024*	-	-
Sporolithon sp. 1	1WA	Western Australia	Unpublished	*KY682926*	*KY682902*	KY682886
Sporolithon tenue	US 170943	Brazil	Adey *et al*. 2015	*KP142751*	*KP142785*	-
Sporolithon yoneshigueae	RB 600359 paratype	Brazil	Bahia *et al*. 2015, Richards *et al*. 2017	*MF034545*	*KY994122*	KY980435
Sporolithon yoneshigueae	RB 600360 paratype	Brazil	Bahia *et al*. 2015, Richards *et al*. 2017	*MF034546	*KY994123	KY980436

Materials & Methods

Specimen collection. Mesophotic specimens were collected aboard the R/V *Pelican*, the UNOLS (University National Oceanographic Laboratory System) research vessel stationed at LUMCON (Louisiana Universities Marine Consortium), using an hourglass design box dredge (Joyce & Williams 1969) with minimum tows (usually 10 minutes or less) from offshore Louisiana and offshore the Texas-Louisiana border in the Gulf of Mexico in the vicinity of Ewing Bank (28˚ 05.937' N; 91˚; 01.349' W) and Bright Bank (27˚ 53.353' N; 93˚; 17.964' W) at depths of 45–90 m. Collection dates were from May 3–11, 2018. Gulf of Mexico specimens are housed at the University of Louisiana at Lafayette Herbarium (LAF). Brazilian specimens were collected using metal dredges at 55 m depth from the Amazon Reef (Moura *et al*. 2016) and by SCUBA diving in the following locations: Fernando de Noronha Archipelago (55 m depth) (Bahia *et al*. 2014), shallow reefs (2–7 m depth) in the Abrolhos bank continental shelf (Jesionek *et al*. 2016), and from a rhodolith bed at 30 m depth in Espírito Santo State (present study). Brazilian specimens are housed at the Rio de Janeiro Botanical Garden Herbarium (RB). Herbarium abbreviations follow Thiers (2019, continuously updated). Table 1 provides a list of specimens and voucher information for taxa included in the analyses.

DNA extraction and sequencing. DNA was extracted from the NWGMx specimens following the protocol of Richards *et al*. (2014) and from Brazilian specimens following the protocol of Jesionek *et al*. (2016). Markers chosen for PCR and sequencing included the plastid-encoded genes *psb*A (encodes photosystem II reaction center protein D1 gene) and *rbc*L (encodes the large subunit of the enzyme ribulose-1,5-bisphosphate carboxylase/oxygenase), and the nuclear-encoded LSU (partial 28S rDNA). PCR and sequencing followed the protocols and primers described in Richards *et al*. (2014, 2016) and Jesionek *et al*. (2016).

Alignment and phylogenetic analysis. A concatenated alignment (2,247 bp) of *psb*A (863 bp) and *rbc*L (1,384 bp) was constructed using MacClade 4.08 (Maddison & Maddison 2000) and Sequence Matrix (Vaidya *et al*. 2011). A single-gene alignment of LSU (549 bp) was constructed and aligned using MUSCLE (Edgar 2004) in MEGA 5.2.2 (Tamura *et al*. 2011) with ambiguous regions cropped to the nearest conserved regions. Maximum Likelihood (ML) analyses with 1,000 bootstrap replicates were conducted according to the protocol of Richards *et al.* (2017). Sequence divergence analyses for *psb*A and *rbc*L were performed in MEGA 5.2.2 (Tamura *et al*. 2011). Alignments were cropped at the 5' and 3' ends prior to divergence analyses to remove missing data.

Microscopy. Scanning electron microscopy was performed with a Hitachi S-3000N Scanning Electron Microscope (SEM) and a JEOL 6300F field emission SEM according to the protocol of Richards *et al.* (2017, 2018b) and with a Zeiss EVO 40 SEM according to the protocol of Bahia *et al*. (2010) at an accelerating voltage of 14–15 kV. Decalcification and light microscopy protocols followed Jesionek *et al*. (2016). Cell dimensions were measured from all available images for eight specimens as described in Maneveldt *et al.* (2017). Conceptacles were not measured due to the small samples size.

Results

Results of the ML analyses of concatenated *psb*A and *rbc*L sequences (Fig. 1) show that the specimens of *Sporolithon amadoi* from Brazil and the NWGMx belong to clade A within *Sporolithon* and form a clade with full support that is sister to the true *S. ptychoides* and *S. molle*. *Psb*A sequences of *S. amadoi* were 6.4% and 6.2% diverged from *S. ptychoides* and *S. molle*, respectively and *rbc*L sequences of *S. amadoi* were 7.6% and 8% diverged from *S. ptychoides* and *S. molle*, respectively (Tables 2–3). ML analyses of LSU (Fig. 2) show that *S. amadoi*, specimen LAF 7256, is in a clade separate from the true *S. ptychoides* and also separate from Hawaiian species of *Sporolithon*.

Sporolithon amadoi J.Richards & Bahia *sp. nov.* (Figures 3–37)

Holotype (designated here): RB 779736: Recifes Esquecidos, São Mateus, Espírito Santo, Brazil (18°52'32" S; 39°26'13" W), western Atlantic Ocean, 14.iii.2018, depth 30m, collected by SCUBA, *leg.* R.G. Bahia.

Isotypes: RB 779737, RB 779738.

Additional material examined (Paratypes): RB 779739, RB 779740, LAF 7256, LAF 7260, LAF 7261. See Table 1 for specimen details.

Etymology: The specific epithet is in honor of Dr. Gilberto M. Amado-Filho, for his excellent contributions to the ecology and systematics of coralline algae from Brazil.

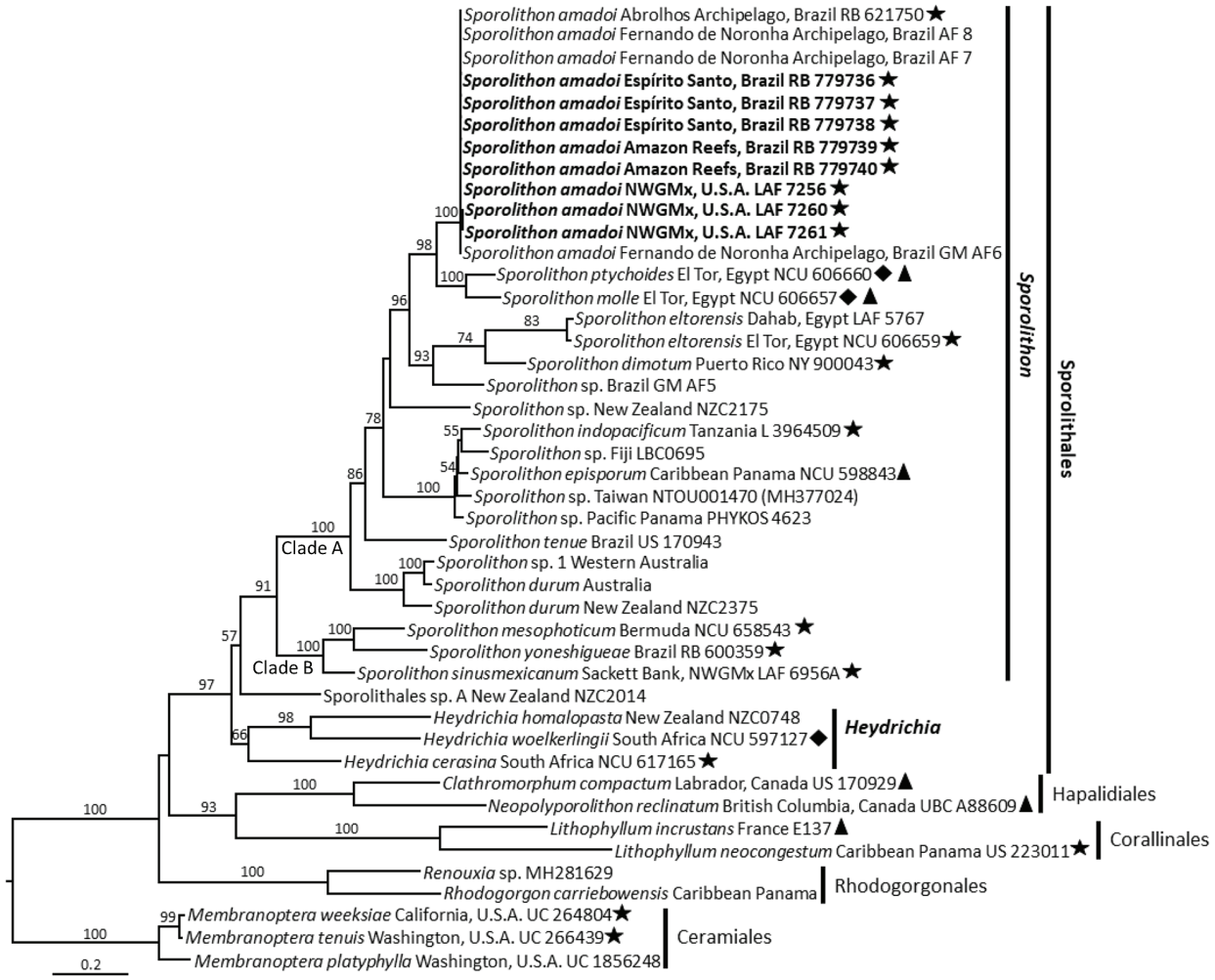


FIGURE 1. Phylogeny of Sporolithales based on ML analyses of concatenated *psb*A and *rbc*L (2,247 bp) sequences, with *Membranoptera* spp. (Ceramiales) as outgroup. Numbers at nodes are bootstrap values (1,000 replicates). Newly generated sequences shown in boldface. Stars represent holotype, isotype, neotype, or paratype specimens; diamonds represent topotype specimens; triangles represent species whose identification is confirmed by comparison of DNA sequences with type material. See Table 1 for GenBank numbers corresponding to specimen voucher numbers and details of type specimen designations.

Description

DNA sequences: Holotype –*psb*A (GB accession = MN434069); Isotypes –*psb*A (GB accessions = MN434070, MN434071). See Table 1 for GB accessions for *psb*A, *rbc*L, and LSU sequences of additional material examined (Paratypes).

Habit and vegetative anatomy: Thallus non-geniculate, thallus thickness reaching more than 20 cell layers (occasionally 12–15 cell layers), primarily forming rhodoliths (Figs. 3, 11, 13, 18, 30) or occasionally growing attached to coral reef substrata, found growing in mesophotic benthic habitats (30–90 m deep) and in shaded environments in shallow (2–7 m deep) reefs. Thallus construction monomerous, with a multi-layered, plumose hypothallium (Figs. 4, 28, 29). Hypothallial cells rectangular in shape, 10.7–42 µm long × 5.6–12 µm wide. In some locations two superimposed layers of thalli were observed, though in other locations growth appeared continuous without layering. Adjacent hypothallial and perithallial cells linked by cell fusions and secondary pit connections (Figs. 5, 19). Perithallial cells 5.2–19.5 µm long × 3–13.6 µm wide (Figs. 5, 6, 12, 19, 20, 21, 31, 32, 33). Pseudodichotomous branching of perithallial cells was occasionally observed (Figs. 31, 32). Intercalary meristematic cells appeared wide and flattened or approximately isodiametric, 3–8 µm long × 6–14.4 µm wide (Figs. 6, 12, 20, 21, 33). Epithallium a single layer of cells with thick, heavily calcified cell walls (armored) and a small round or trapezoidal shaped lumen, 1.2–3.6 µm long × 3.1–7.2 µm wide (Fig. 6, 12, 21, 33).

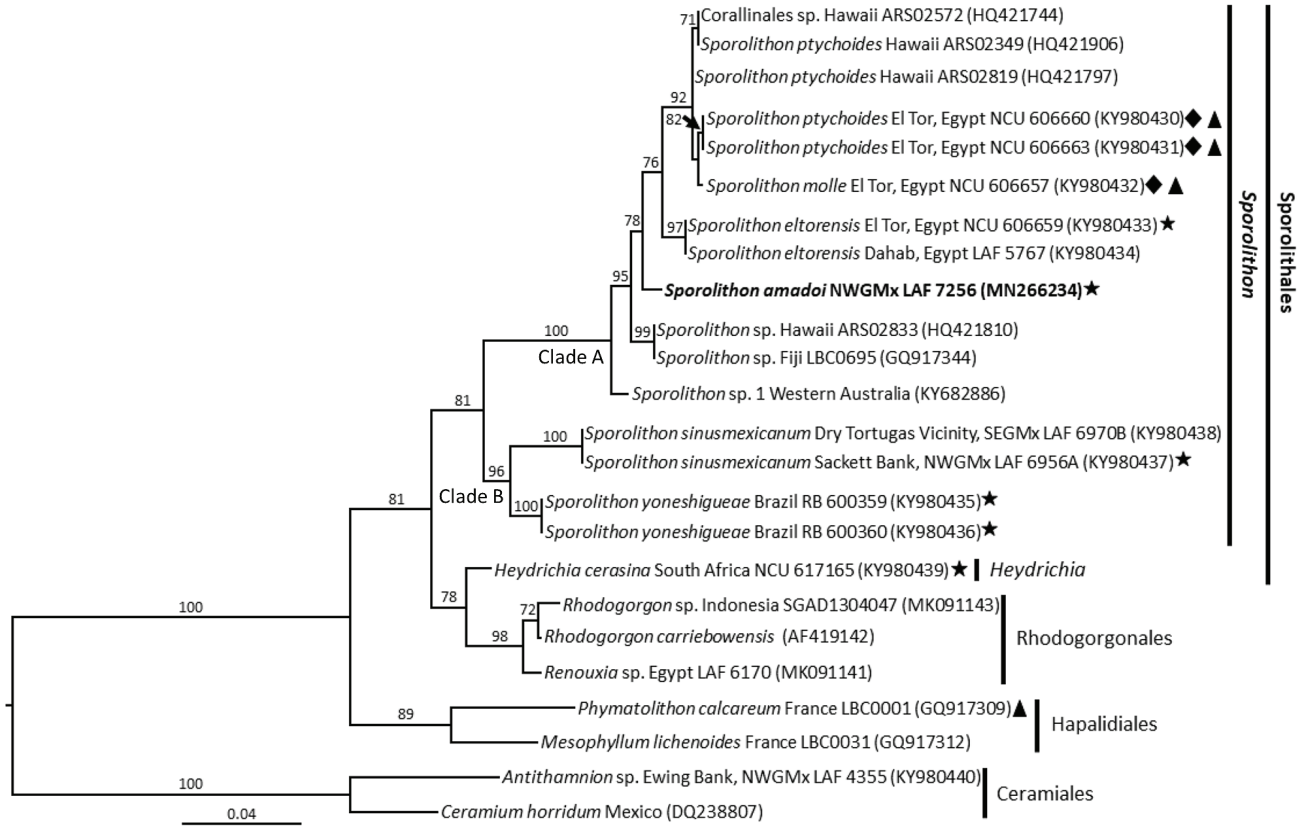


FIGURE 2. Phylogeny of Sporolithales based on Maximum Likelihood analyses of LSU (549 bp) sequences with *Antithamnion* and *Ceramium* (Ceramiales) as outgroup. Numbers at nodes are bootstrap values (1,000 replicates). Newly generated sequence shown in boldface. Stars represent holotype, isotype, neotype, or paratype specimens; diamonds represent topotype specimens; triangles represent species whose identification is confirmed by comparison of DNA sequences with type material. See Table 1 for details of type specimen designations.

Reproduction: Tetrasporangial sori observed from surface view were raised above the surrounding thallus surface (Figs. 14, 15, 22) and showed tetrasporangial pores, 8.5–16.5 in diameter, surrounded by 9–13 rosette cells (Figs. 7, 8, 23, 24). Section views showed tetrasporangial compartments borne among a basal layer of slightly elongated cells. Tetrasporangial compartments not sloughed off, and become buried after spore release (Figs 9, 10, 25, 26), that are 65–108 µm long × 41–64 µm wide subtended by a triangular stalk cell 8–16 µm long × 20–32 µm wide (Figs. 10, 16, 27). Paraphyses 3–4 celled. Tetrasporocytes (Fig. 16) develop into cruciately divided tetrasporangia (Fig. 17). A gametophytic specimen (Figs. 30–37) was observed with uniporate conceptacles. However, examination with SEM (Fig. 35) and light microscopy of decalcified sections (Figs. 36, 37) showed empty conceptacles; thus it was not determined if they were male or female conceptacles. Conceptacles become overgrown after gamete or spore release (Fig. 37).

Distribution: Presently known from mesophotic rhodolith beds offshore the NWGMx, and from shallow reefs and mesophotic rhodolith beds in Brazil (see Table 1 for locality details).

Discussion

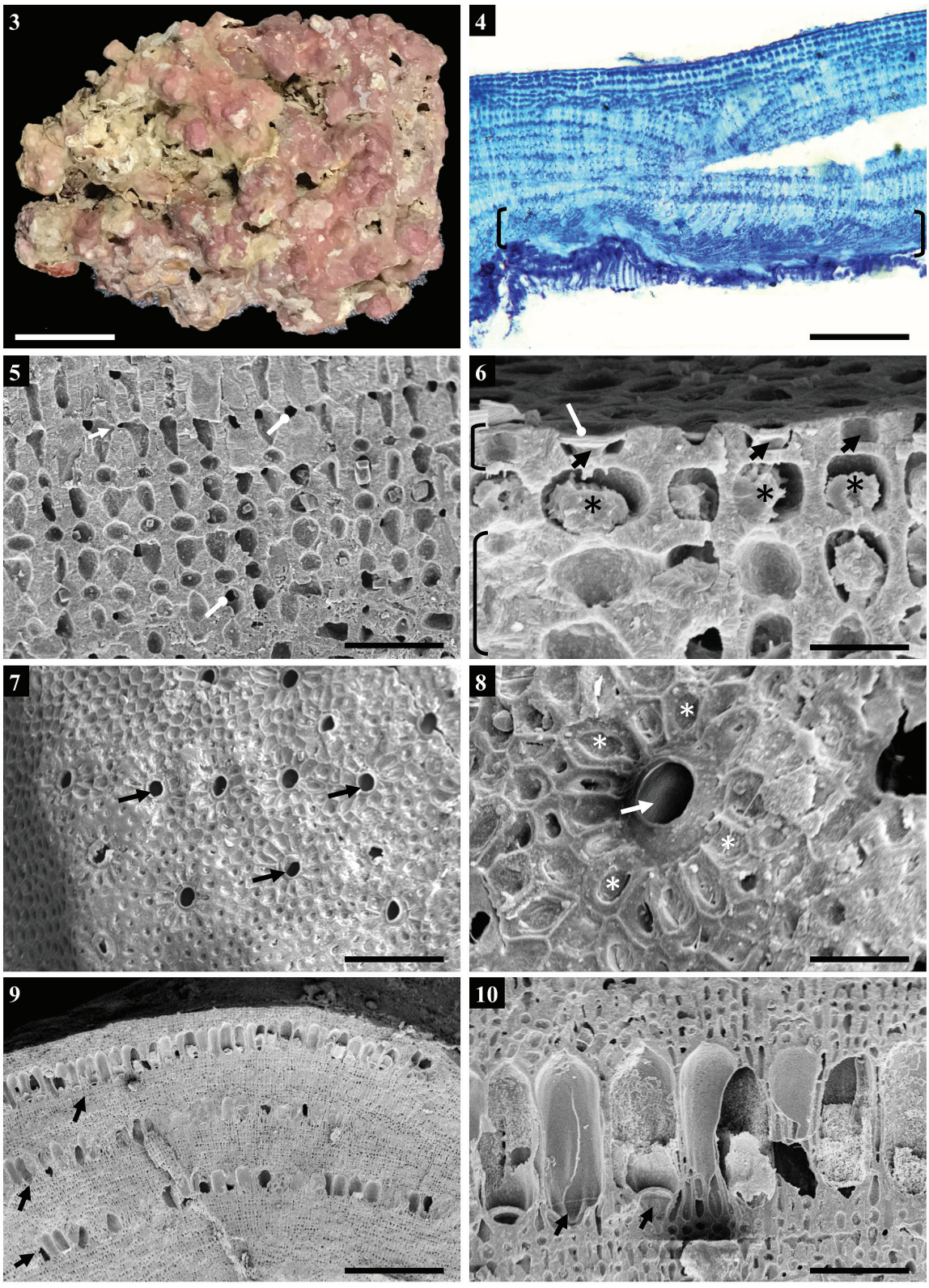
Sequence divergence values (Tables 2, 3) support the recognition of *S. amadoi* as a distinct species. For example, the *rbc*L sequence of *S. amadoi* is 7.6% divergent from *S. ptychoides* and 8% divergent from *S. molle*, which is greater than the *rbc*L divergence between other closely related species in the Sporolithales (e.g. 3.2% between *S. episporum* (M.Howe) E.Y.Dawson and *S. indopacificum* Maneveldt & P.W.Gabrielson).

TABLE 2. Pairwise sequence divergences (%) for *psb*A sequences (850 bp) reported in this study: *Sindo* = *Sporolithon indopacificum*; *Spty* = *S. ptychoides*; *Smol* = *S. molle*; *Selt* = *S. eltorensis*; *Sepi* = *S. episporum*; *Samad* = *S. amadoi; S*sp. = *S.* species; *Sdur* = *S. durum*; *Sten* = *S. tenue*; *Syon* = *S. yoneshigueae*; *Smes* = *S. mesophoticum*; *Ssin* = *S. sinusmexicanum*; *Hwo* = *Heydrichia woelkerlingii*; Ssp.A. = Sporolithales sp. A; *Hcer* = *H. cerasina*.

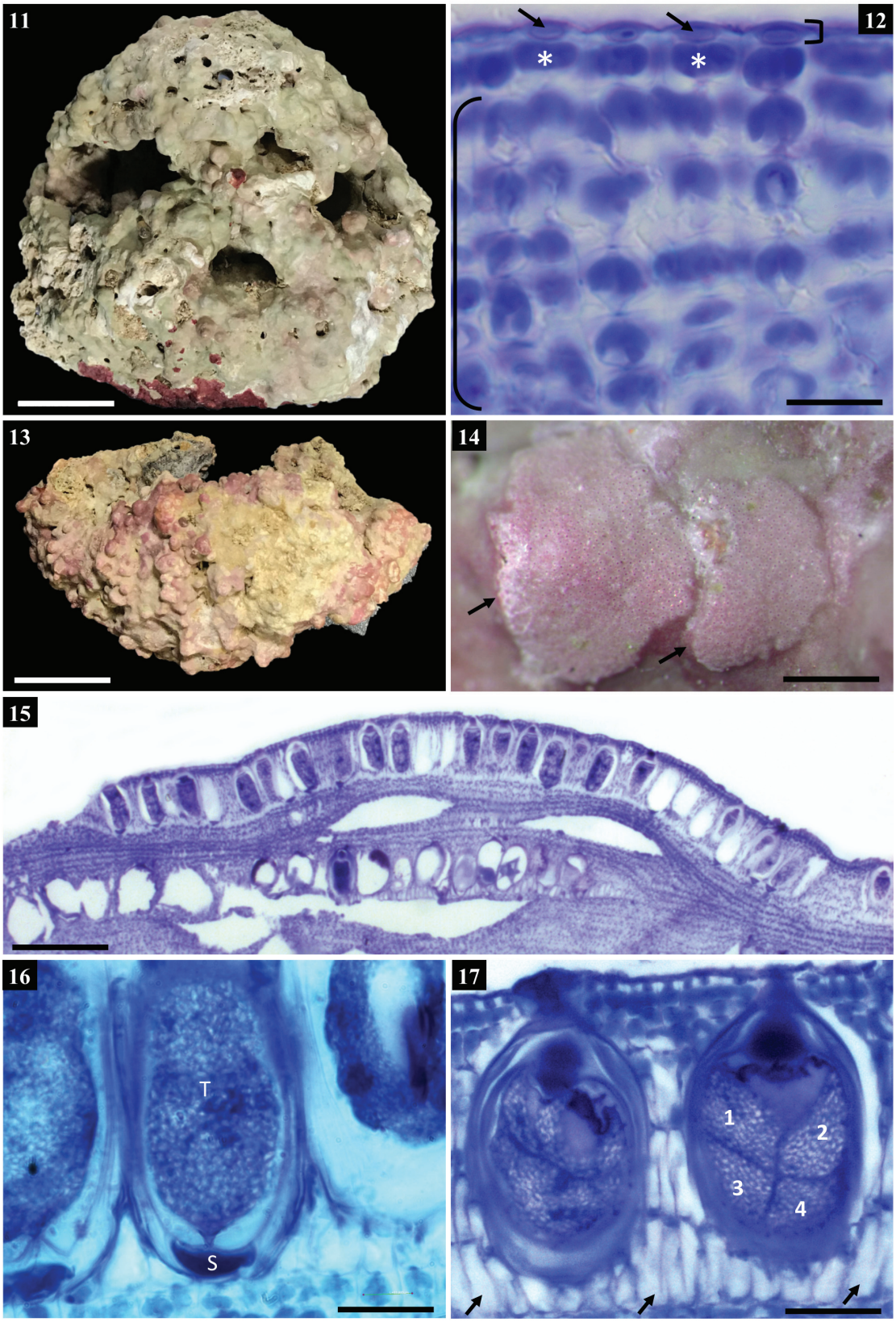
1. *Sindo* L3964509																					
2. *Spty* NCU 606660	10.4																				
3. *Smol* NCU 606657	10.4	5.4																			
4. *Selt* NCU 606659	9.7	8.8	9.4																		
5. *Selt* LAF 5767	9.7	9.3	9.8	0.9																	
6. *Sepi* NCU 598843	3.1	9.3	9.5	8.9	9.1																
7. *Samad* LAF 7256	8.5	6.4	6.2	6.7	6.9	7.5															
8. *Samad* LAF 7260	8.5	6.4	6.2	6.5	6.7	7.8	0.2														
9. *Samad* Holotype	8.5	6.4	6.2	6.7	6.9	7.5	0	0.2													
10. *Samad* GM AF6	8.5	6.4	6.2	6.7	6.9	7.5	0	0.2	0												
11. *S*sp. GM AF5	9.4	8.8	9.1	6	6.2	8.5	6.7	6.5	6.7	6.7											
12. *S*sp. NZC2175	8.6	8.4	9.3	7.5	7.5	7.7	6.5	6.5	6.5	6.5	6.1										
13. *S*sp. 1WA	9.1	10.4	11.1	8.6	8.4	8.5	8.8	8.6	8.8	8.8	8.7	8									
14. *Sdur* NZCD375	9.2	10.3	10.3	8.8	8.6	8.5	8.5	8.5	8.5	8.5	8.4	7.4	4.1								
15. *Sten* US170943	9.4	8	9.3	9.1	9.1	8.7	7.7	7.4	7.7	7.7	7.8	6.8	8.5	7.6							
16. *Syon* RB 6000359	10.8	10.8	11.4	10.9	10.7	10.6	10.9	10.9	10.9	10.9	11.2	10.4	9.8	9.3	10.1						
17. *Smes* NCU658543	11.3	11.4	11.4	10.5	10.7	11.4	10.9	10.7	10.9	10.9	11.1	10	10.5	9.8	10.5	5.9					
18. *Ssin* LAF 6956A	10.4	11.3	11.5	10.8	10.6	10.7	10.5	10.2	10.5	10.5	10.6	9.3	9.2	9.1	8.4	7.9	8				
19. *Hwo* NCU 597127	11.5	11.5	11.6	10.5	10.6	10.6	11.1	10.9	11.1	11.1	10.2	10.5	10.1	10.4	10	12.5	12.1	10.5			
20. *S*sp.A NZC2014	11.8	11.9	12.5	12	11.6	11.1	10.5	10.7	10.5	10.5	10.7	9.5	9.8	9.2	9.9	10.4	10.8	8.8	10		
21. *Hcer* NCU 617165	9.2	11.2	11.9	10.8	10.7	8.82	9.7	9.7	9.7	9.7	9.9	8.2	9.1	9.8	8.8	11.3	11.4	9.7	9.7	8.2	
Taxa	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 (251 bp) reported in this study: *Sindo* = *Sporolithon indopacificum*; *Spty* = *S. ptychoides*; *Smol* = *S. molle*; *Selt* = *S. eltorensis*; *Sepi* = *S. episporum*; *Samad* = *S. amadoi;* *S*sp. = *S.* species; *Sdur* = *S. durum*; *Sten* = *S. tenue*; *Syon* = *S. yoneshigueae*; *Smes* = *S. mesophoticum*; *Ssin* = *S. sinusmexicanum*; *Hwo* = *Heydrichia woelkerlingii*; Ssp.A. = Sporolithales sp. A; *Hcer* = *H. cerasina*.

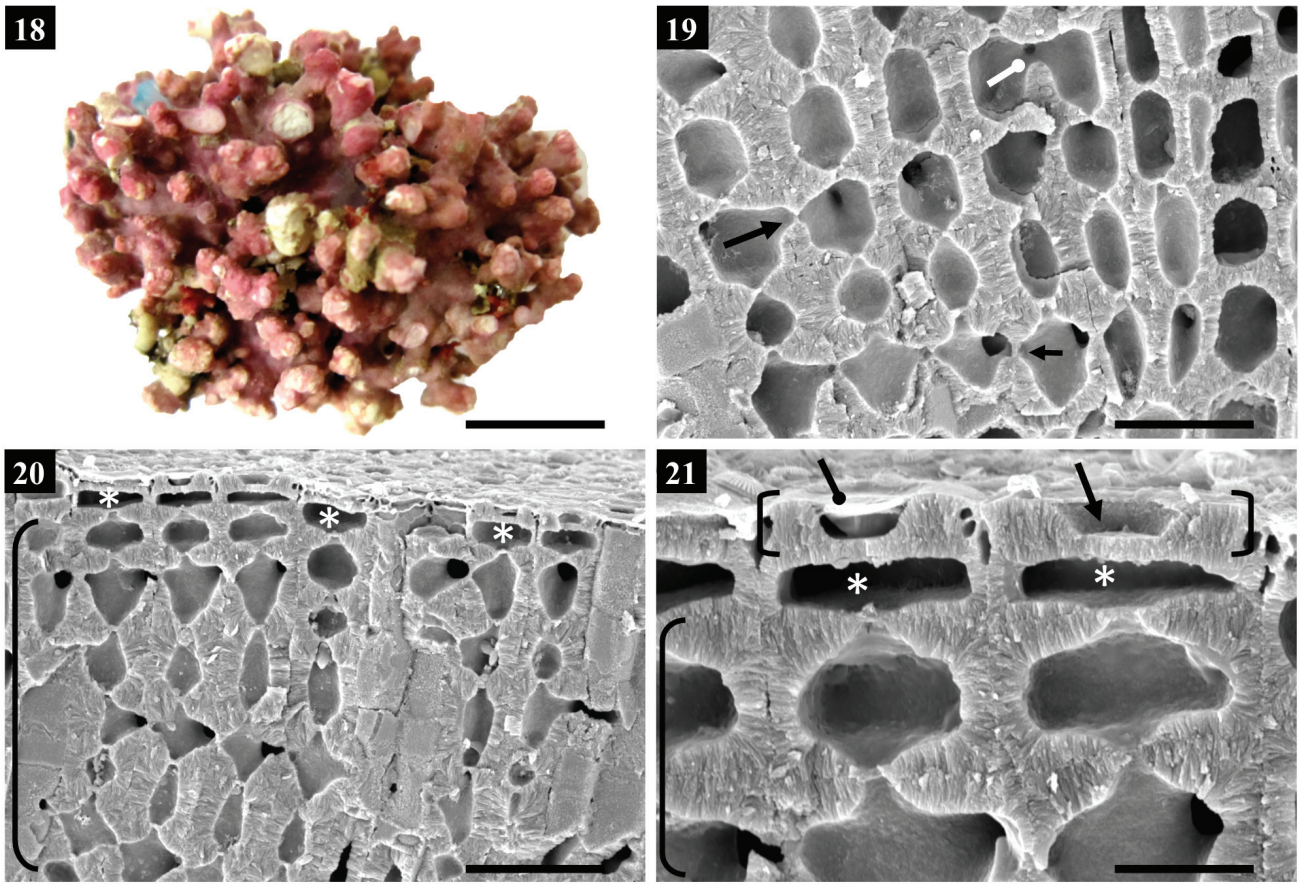
1. *Sindo* L3964509																			
2. *Spty* NCU 606660	10.0																		
3. *Smol* NCU 606657	7.2	4.4																	
4. *Selt* NCU 606659	10.8	8.4	8.4																
5. *Sepi* NCU 598843	3.2	10.0	7.2	10.8															
6. *Samad* GM AF6	9.6	7.6	8.0	9.2	9.6														
7. *Samad* LAF 7256	9.6	7.6	8.0	9.2	9.6	0.0													
8. *S*sp. GM AF5	9.6	8.8	7.6	4.4	9.2	8.8	8.8												
9. *S*sp. NZC2175	7.6	11.6	9.6	12.0	8.4	12.0	12.0	10.4											
10. *S*sp. 1WA	10.0	10.4	9.6	10.8	10.4	12.7	12.7	11.2	10.4										
11. *Sdur* NZCD375	10.8	11.6	11.2	13.1	10.8	14.3	14.3	12.0	11.2	5.2									
12. *Sten* US 170943	8.0	11.2	10.0	12.4	8.8	12.0	12.0	9.6	9.6	10.0	10.4								
13. *Sdim* NY 900043	11.2	11.2	10.0	6.8	11.6	8.8	8.8	7.2	10.8	12.7	14.3	12.0							
14. *Syon* RB 6000359	15.8	15.0	13.8	17.8	14.2	16.6	16.6	16.2	16.6	15.0	15.4	14.6	17.0						
15. *Smes* NCU 658543	16.7	11.6	13.5	15.9	15.5	13.1	13.1	15.5	16.7	16.3	15.5	16.3	16.3	13.8					
16. *Ssin* LAF 6956A	13.5	10.0	10.4	13.1	12.0	13.5	13.5	12.0	13.9	13.5	14.3	12.0	13.9	10.9	7.6				
17. *Hwo* NCU 597127	15.5	16.7	16.7	17.1	15.1	17.5	17.5	15.9	14.7	17.1	16.3	14.3	15.5	19.4	17.5	14.3			
18. *S*sp.A NZC2014	12.4	13.9	12.0	16.3	12.4	14.7	14.7	14.7	11.6	13.9	13.9	14.3	15.9	15.0	12.4	8.8	12.4		
19. *Hcer* NCU 617165	13.9	14.7	13.5	16.3	13.9	15.5	15.5	15.9	14.3	14.3	15.9	12.7	15.9	17.4	16.3	12.4	12.4	11.2	
Taxa	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.	13.	14.	15.	16.	17.	18.	19.



FIGURES 3–10. *Sporolithon amadoi* Holotype, RB 779736. FIG. 3. Habit of holotype. Scale bar = 1.5 cm. FIG. 4. Section of thalllus showing monomerous construction and multilayered hypothallium (brackets). Scale bar = 120 µm. FIG. 5. Perithallium with secondary pit connection (arrow) in x-axis and cell fusions shown as black holes in z axis (circle pointers). Scale bar = 33 µm. FIG. 6. Vertical fracture showing epithallial cells (arrows), some with intact epithallial cell roofs (circle pointer), intercalary meristematic cells (*) and portion of perithallium (bracket). Scale bar = 9 µm. FIG. 7. Surface view of tetrasporangial sorus with tetrasporangial pores (arrows) and rosette cells. Scale bar = 48 µm. FIG. 8. Detail of tetrasporangial pore (arrow) surrounded by rosette cells (*). Scale bar = 18 µm. FIG. 9. Vertical fracture showing layers of unshed tetrasporangial compartments (arrows). Scale bar = 300 µm. FIG. 10. Detail of tetrasporangial compartments with stalk cells (arrows). Scale bar = 57 µm.



FIGURES 11–17. *Sporolithon amadoi*. FIGS. 11–12, Isotype, RB 779737. FIG. 11. Habit of isotype. Scale bar = 2.1 cm. FIG. 12. Epithallium (arrows, upper bracket), intercalary meristematic cells (*), and perithallium (lower bracket). Scale bar = 10 µm. FIG. 13. Isotype, RB 779738. Habit of isotype. Scale bar = 2.7 cm. FIG. 14. RB 779740. Surface view of two adjacent tetrasporangial sori (arrows). Scale bar = 0.7 mm. FIG. 15. RB621750. Section of thallus showing layers of tetrasporangial compartments, many with intact tetrasporangia. Scale bar = 200 µm. FIG. 16. RB621750. Tetrasporocyte (T) with stalk cell (S). Scale bar = 20 µm. FIG. 17. RB779739. Detail of cruciately divided tetrasporangia (1–4) born among basal layer of slightly elongated cells (arrows). Scale bar = 30 µm.

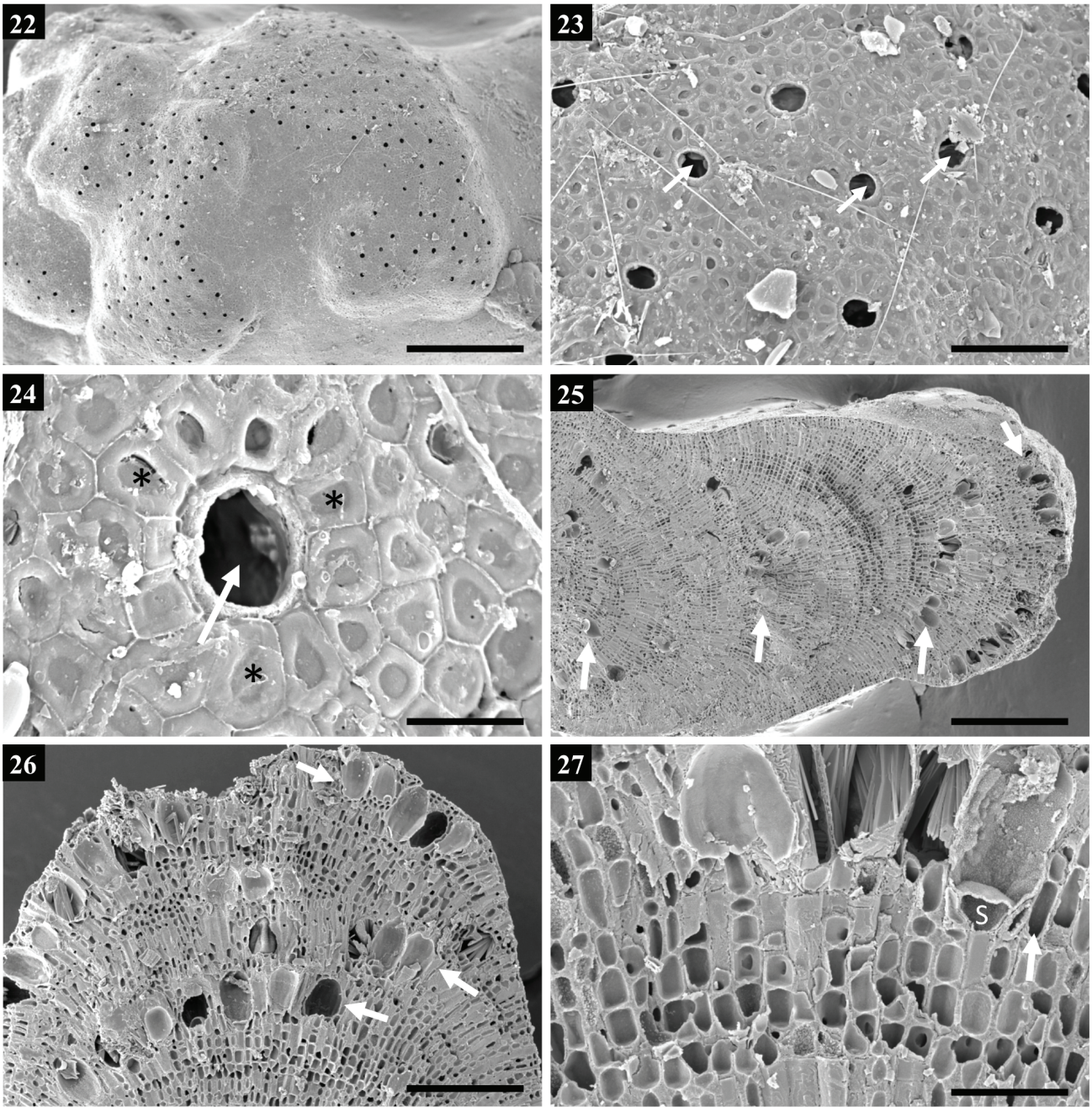


FIGURES 18–21. *Sporolithon amadoi,* LAF 7260. FIG. 18. Thallus habit showing abundant protuberances. Scale bar = 1 cm. FIG. 19. Perithallium with secondary pit connection (arrows) and cell fusion (circle pointer). Scale bar = 23 µm. FIG. 20. Vertical fracture showing perithallium (bracket) intercalary meristem (*) and epithallium. Scale bar = 30 µm. FIG. 21. Vertical fracture showing epithallial cells, one with intact epithallial cell roof (circle pointer) and one with the roof missing (arrow), intercalary meristematic cells (*) and portion of perithallium (bracket). Scale bar = 9 µm.

The ML analysis shows two fully supported clades of *Sporolithon* spp. (Fig. 1, clades A and B), with *S. amadoi* in clade A along with other species from the tropical western Atlantic, the Red Sea, and the Indo-Pacific Ocean. The LSU tree (Fig. 2) shows that *S. amadoi* is in a clade separate from Hawaiian species of *Sporolithon*, thus not conspecific with Hawaiian species. Previously Brazilian species of *Sporolithon* could not be compared to the Hawaiian specimens due to a lack of corresponding markers (Richards *et al*. 2017). This is noteworthy because other coralline species, eg. *Mesophyllum erubescens*, are present in both Brazil and Hawaii (Sissini *et al*. 2014). It is interesting that *S. amadoi* is associated with salt domes (diapirs) that are rich in oil deposits in both the northwestern Gulf of Mexico (Felder *et al*. 2014) and the Abrolhos bank continental shelf off the coast of Bahia in northeastern Brazil (Fainstein & Summerhayes 1982, Amado Filho *et al*. 2012, Jesionek *et al*. 2016). However, this species is not restricted to mesophotic habitats and was also found growing in shallow reefs in Brazil.

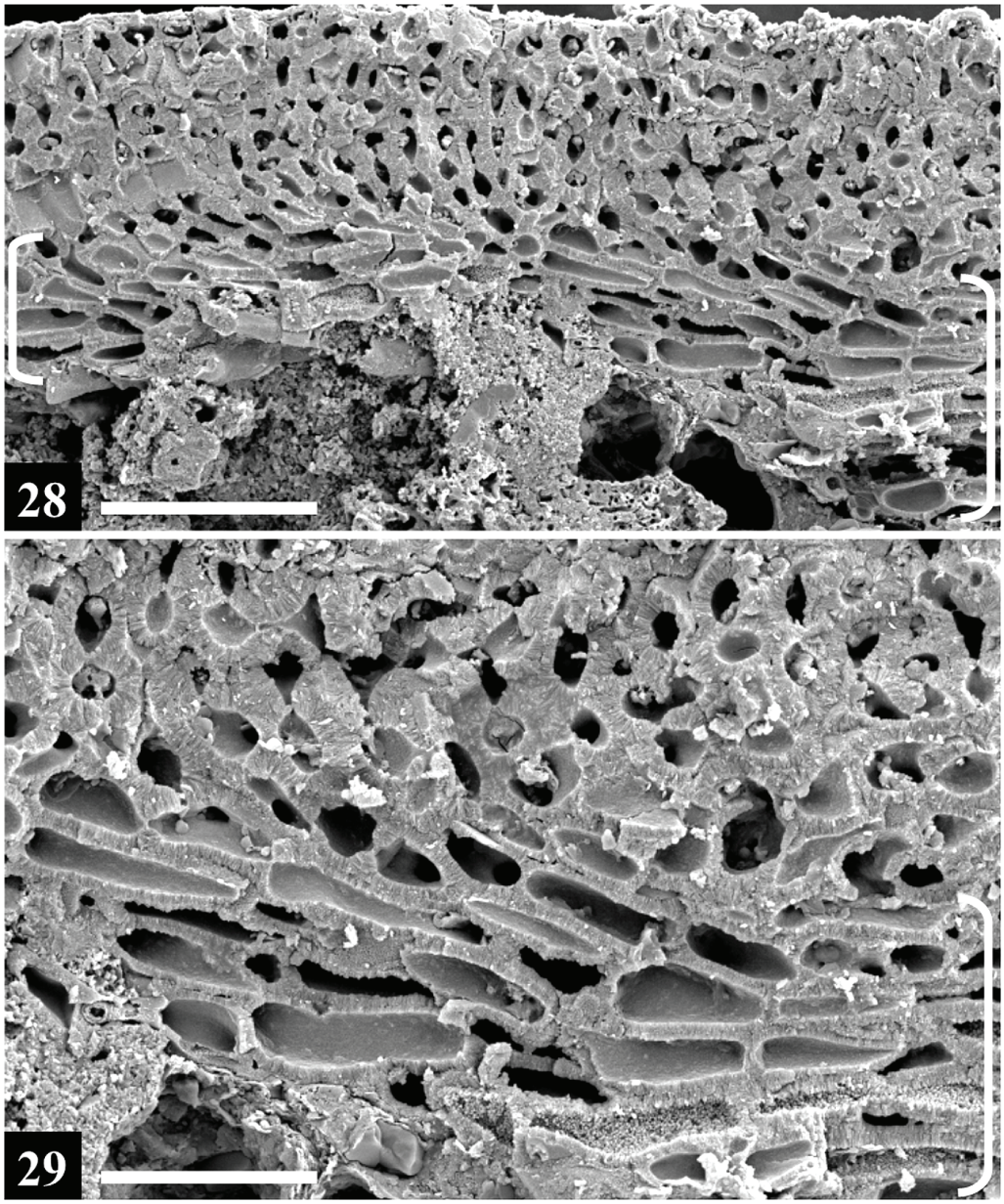
No exclusive diagnostic morpho-anatomical features or combination of features were found to distinguish *Sporolithon amadoi* from related species, such as *S. ptychoides, S. molle, S. eltorensis* and *S. dimotum* (Richards *et al.* 2017). However, the new species can be separated from other extant *Sporolithon* species from the Atlantic mainly by the following features: 1) thallus reaching more than 20 cell layers (differentiating from *S. tenue* which has less than 20 cell layers); 2) non-sloughed off tetrasporangial sori that become overgrown and buried after spore release (differentiating from *S. episporum*, *S. sinusmexicanum* and *S. tenue* which all slough off their sori); 3) tetrasporangial pores surrounded by 9–13 rosette cells (differentiating from *S. yoneshigueae* which has 19–24 rosette cells) (Bahia et *al.* 2014, 2015; Richards & Fredericq 2018).

Sporolithon amadoi belongs to the group of rhodoliths that are referred to as biogenic rhodoliths which are formed by the non-geniculate crustose coralline algae themselves, in contrast to autogenic rhodoliths which are a specific type of nucleated rhodoliths that are derived from already existing calcium carbonate rubble (Fredericq *et al*. 2014, 2019; Felder *et al*. 2014; Richards & Fredericq 2018; Richards *et al*. 2014, 2016, 2017, 2018a, b; Krayesky-Self *et al*. 2017). Fredericq *et al*. (2019) noted that *Sporolithon sinusmexicanum* and other biogenic rhodoliths that include putative cellular inclusions of microalgal life history stages within their perithallial cells, slough off their tetrasporangial sori and surface layers, and that species that do not slough off tetrasporangial sori layers, namely *S. amadoi,* do not show cellular inclusions. In future studies, larger sample sizes of rhodoliths are needed to shed light on whether similar phenomena occur in the gametophytic stages of *S. sinusmexicanum* and *S. amadoi* or in other species of rhodoliths.

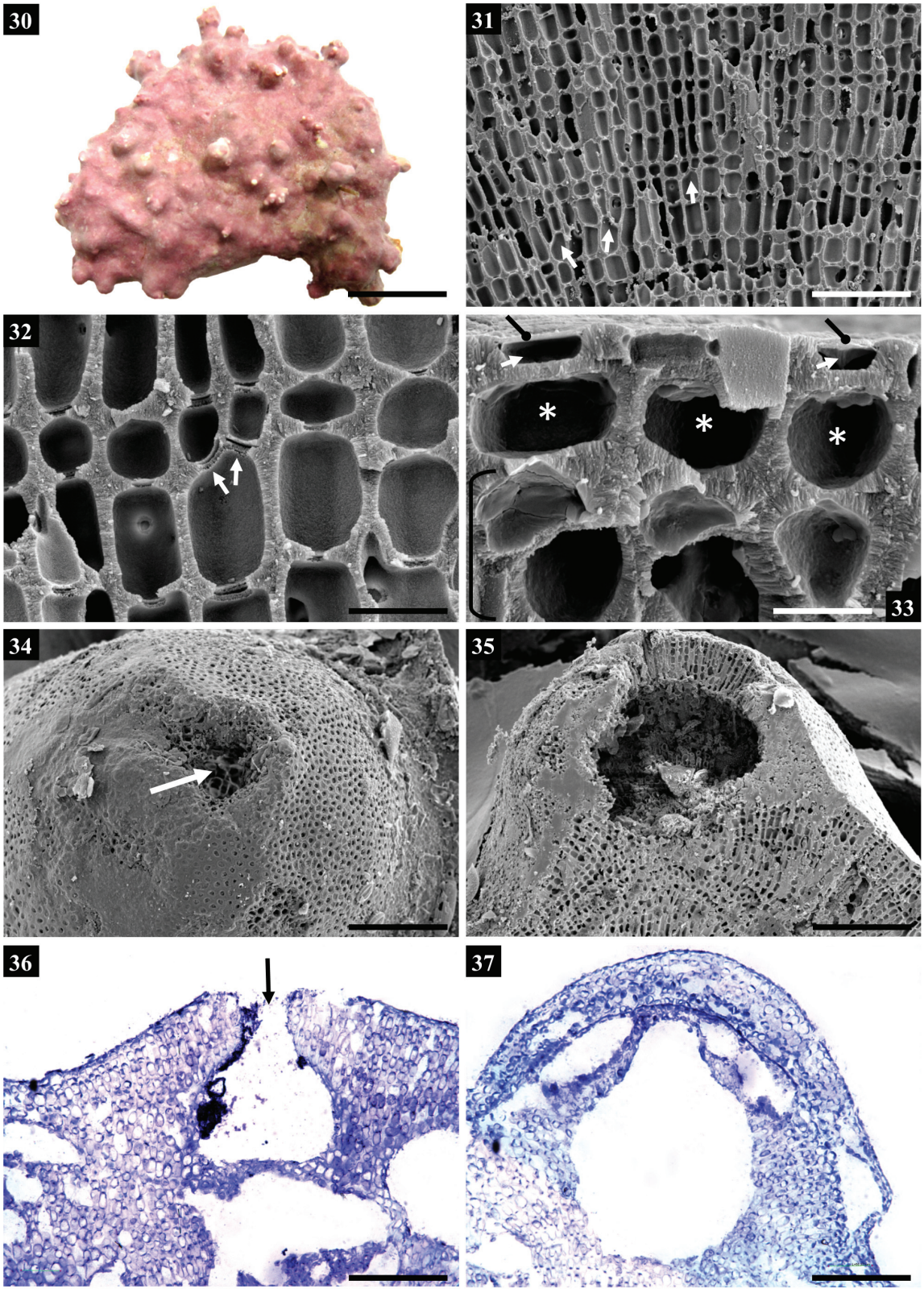


FIGURES 22–27. *Sporolithon amadoi,* LAF 7260. FIG. 22. Surface view showing adjacent tetrasporangial sori. Scale bar = 400 µm. FIG. 23. Tetrasporangial pores (arrows) and rosette cells. Scale bar = 60 µm. FIG. 24. Detail of tetrasporangial pore (arrow) surrounded by rosette cells (*). Scale bar = 18 µm. FIGS 25–26. Longitudinal fractures of protuberance showing layers of unshed and buried tetrasporangial compartments (arrows). Scale bars = 400, 180 µm. FIG. 27. Magnified view of tetrasporangial compartment with stalk cell (S) born among basal layer of somewhat elongated cells (arrow). Scale bar = 55 µm.

The findings in this study show that *S. amadoi* is a significant component of tropical reefs in the tropical western Atlantic. *Sporolithon amadoi* is the third species of *Sporolithon* described from Brazil, in addition to *S. tenue* Bahia, Amado-Filho, Maneveldt, & W.H.Adey and *S. yoneshigueae* recently described by Bahia *et al*. (2014, 2015) from NE and SE Brazil, and the second species described from the NWGMx, in addition to *S. sinusmexicanum* J.Richards & Fredericq (Richards *et al.* 2018). Future studies likely will reveal additional new species of *Sporolithon* from the tropical western Atlantic as specimen collection and ongoing DNA sequencing efforts continue.



FIGURES 28–29. *Sporolithon amadoi,* LAF 7261. Vertical fracture showing monomerous construction and multilayered, plumose (non-coaxial) hypothallium (brackets). Scale bars = 80, 40 µm.



FIGURES 30–37. *Sporolithon amadoi.* LAF 7256. FIG. 30. Thallus habit showing protuberances. Scale bar = 1 cm. FIGS. 31–32. Perithallium showing locations of pseudodichotomous branching (arrows). Scale bars = 70, 15 µm. FIG. 33. Vertical fracture showing part of perithallium (bracket), intercalary meristematic cells (*) and epithallial cells (arrows) with intact epithallial cell roofs (circle pointers). Scale bar = 8 µm. FIG. 34. Surface view of uniporate conceptacle showing pore opening (arrow). Scale bar = 110 µm. FIG. 35. Longitudinal section showing conceptacle chamber. Scale bar = 150 µm. FIG. 36. Decalcified longitudinal section showing conceptacle chamber and pore canal (arrow). Scale bar = 125 µm. FIG. 37. Decalcified longitudinal section showing conceptacle chamber overgrown by a vegetative layer. Scale bar = 125 µm.

Acknowledgements

This work was funded by NSF grant DEB–1754504 for rhodolith research to SF and by the Brazilian Science Support Agencies, CNPq and FAPERJ, and funds from P&D program ANP/BRASOIL. MJ acknowledges the Coordination for the Improvement of Higher Education Personnel (CAPES) for providing a PhD scholarship. RGB acknowledges FAPERJ for providing a postdoctoral fellowship grant (process PDR-10 202.375/2017) and research fellowship. JLR acknowledges Tom Pesacreta and Mike Purpera at the UL Lafayette Microscopy Center for help and advice using the SEM and William E. Schmidt for assistance with phylogenetic analyses. We also thank the crew of the R/V *Pelican* for help with sampling protocols.

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