



Three deep water species of *Sporolithon* (Sporolithales, Rhodophyta) from the Brazilian continental shelf, with the description of *Sporolithon elevatum* sp. nov.

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Abstract

Nongeniculate calcareous algae are bio-constructors of many marine habitats, some of which are considered biodiversity hotspots. The genus *Sporolithon* is widely distributed around the world. As part of a review of material from the Brazilian continental shelf we found *Sporolithon episoredion*, that extend its distribution range into the Atlantic Ocean, *Sporolithon ptychoides*, which is widely distributed across oceans, and a new species of this genus named *Sporolithon elevatum* sp. nov. This species presents sorus 2–3 cells elevated above the thallus that sloughs off when senescent, paraphyses with 2–3 cells and a basal layer of elongated cells in areas where sporangia develop. The new species was found at 133 m depth. This study contributes to the understanding of the diversity in this genus and indicates the importance of systematic studies in the framework of conservation programs and evaluation of impacts in an area under exploitation activities.

Key words: Rhodolith; Corallinophycidae; Sporolithaceae; *Sporolithon ptychoides*, *Sporolithon episoredium*

Introduction

Nongeniculate calcareous algae are bio-constructors of many marine habitats (Jones *et al.* 1994, 1997), some of which are considered biodiversity hotspots (BIOMAERL Team 1998). These algae can form reefs or free-living structures called rhodoliths, which can be grouped to form the extensive rhodolith beds that are found in all oceans (Foster 2001). They are subjected to human activity impacts such as fisheries, ore extraction, and oil and gas exploration (Hall-Spencer 1999; Gomes *et al.* 2000; Barberá *et al.* 2003; Bordehore *et al.* 2003; Riul *et al.* 2009). The Brazilian continental shelf is known for having the largest area covered by rhodolith beds in the world (Foster 2001; Amado-Filho *et al.* 2012). Despite the ecological importance of rhodolith beds and the impacts that they suffer, they are poorly known, especially in Brazil. The Brazilian government is establishing guidelines to regulate exploration, commercialization, and transportation of seaweeds (IN/IBAMA n.º 46/2004, Brazil, 2004). Thus, biodiversity studies of rhodolith beds and taxonomic information of their forming species are important to generate relevant information for environmental management programs.

Sporolithales Le Gall, Payri, Bittner & G.W.Saunders (2009:302) was recently elevated from the family status to become an order which exclusively produces cruciate tetrasporangia within calcified sporangial compartments (Le Gall *et al.* 2010). It has commonly been found growing epilithically or forming rhodoliths distributed at low latitudes and in deep waters (Verheij 1993; Lund *et al.* 2000; Aguirre *et al.* 2000; Braga & Bassi 2007; Basso *et al.* 2009; Villas-Boas *et al.* 2009). It has the oldest stratigraphic record within coralline algae (Aguirre *et al.* 2000). Despite its

older age, there are only a few modern recognized species and their distribution is poorly known. Sporolithales contains two genera, *Sporolithon* Heydrich (1897: 66) and *Heydrichia* R.A.Townsend, Y.M.Chamberlain & Keats (1994: 177), which are differentiated by the presence of an involucre surrounding the tetrasporangia compartments in *Heydrichia* and the absence of this involucre in *Sporolithon* (Harvey *et al.* 2002; Le Gall *et al.* 2009). Some *Sporolithon* species have been recently reported in various areas of the world including Brazil (Harvey *et al.* 2005; Farr *et al.* 2009; Basso *et al.* 2009; Bahia *et al.* 2011, 2013). There are no records of *Heydrichia* in Brazil.

In Brazilian waters, *Sporolithon* was studied by Yamaguishi-Tomita (1976). She reported eight species for this genus but only a few of them have been confirmed in the literature (Wynne 1986). Recently, Amado-Filho *et al.* (2007) stated that *Sporolithon* is one of the dominant genera in Espírito Santo state and Nunes *et al.* (2008) reported *Sporolithon episorum* (M.A.Howe) E.Y.Dawson (1960: 40) as a new record on the northeastern coast of Brazil. In addition, *Sporolithon durum* (Foslie) R.A.Townsend & Woelkerling in R.A.Townsend *et al.* (1995: 86) was reported as a new occurrence for the Atlantic Ocean (Wynne 2011), however, there was no detailed description of this record. Bahia *et al.* (2011) confirmed the presence of *Sporolithon ptychoides* Heydrich (1897: 67) as a new record for Espírito Santo, reviewed material described as *Sporolithon dimotum* (Foslie & M.A.Howe) Yamaguishi-Tomita ex M.J.Wynne (1986: 2258), and proposed the synonymy of *S. dimotum* as a heterotypic synonym of *S. ptychoides*. Bahia *et al.* (2013) described a new *Sporolithon* species from the eastern coast of Brazil named *Sporolithon tenue* Bahia, Amado-Filho, Maneveldt *et* W.H. Adey (2013). They also observed that specimens previously designated as *Sporolithon africanum* (Foslie) J. Afonso-Carillo (1984: 142) in Brazil from Tomita (1976) specimens correspond to *S. tenue*. The aim of this study is to identify species of *Sporolithon* that are present in rhodolith beds along the Brazilian continental shelf, describing new species and contributing with new records for the Atlantic Ocean.

Materials and Methods

Field work

In the framework of the REVIZEE program (Lavrado, 2006), rhodolith samples were collected offshore by dredge (50–133 meters depth) from October to November of 1997 in the Vitória-Trindade Sea Mountains, Espírito Santo State continental shelf, Brazil. At that time it was not possible to identify the coralline red algae because of lack of taxonomic expertise and support, so the samples were stored in the Botanical Garden of Rio de Janeiro. Some species of the genus *Spongites* Kützinger (1841: 30) and *Lithothamnion* Heydrich, (1897: 412) have been studied (Henriques *et al.* 2012) and the present work is focused in the genus *Sporolithon*. Two more similar collection were carried out along the Rio de Janeiro state outer shelf, in October of 2010 and November of 2011.

The region is influenced by the Brazilian Current that runs along the South Atlantic Ocean and is characterized by sea surface temperatures ranging from 21 to 27 °C (Lavrado 2006). From 50 to 100m depth the region is influenced by the South Atlantic Central Waters (SACW) and is characterized by temperatures from 6 to 20 °C (Silveira *et al.* 2000).

Laboratory work

Samples collected from different places of the Brazilian outer continental shelf had been preserved in 4% formalin seawater (Yoneshigue-Valentin *et al.* 2006), decalcified in 10% nitric acid, dehydrated in alcohol series and embedded in hystoresin (Moura *et al.* 1997). As a consequence of this long preservation time, specimens were degraded, and it was difficult finding intact reproductive structures. The material was exhaustively sectioned with a microtome and stained for Optical Microscopy analysis. Measurements were taken of vegetative and reproductive structures. Cellular secondary connections, thallus organization, epithallial cells, subepithallial cells, and reproductive structures (shape and type) were analyzed. Type specimens were not examined.

Thallus anatomical terminology and typification data follow Woelkerling (1988) and growth-form terminology follows Woelkerling *et al.* (1993). Moreover, diagnostic features used in many taxonomic reviews (Verheij 1993; Keats & Chamberlain 1993; Townsend *et al.* 1995; Alongi *et al.* 1996; Bahia *et al.* 2011; Bahia *et al.* 2013) were used: 1) diameter/length of the tetrasporangial compartment, 2) fate of old sporangial cases, 3) number of cells in the paraphyses, 4) Presence of a basal layer of elongated cells in areas where sporangia develop, (5) number of cells by which sorus is raised above surrounding thallus surface and (6) soral organization. Identified samples were incorporated into the herbarium collection of the Botanical Garden of Rio de Janeiro (RB) and Museu Nacional (R). The Herbarium codes follow the *Index Herbariorum* (Holmgren and Holmgren, 2014; continuously updated).

Results

Systematic treatment

Sporolithon episoredion (Adey, Townsend & Boykins) Verheij (1992: 501) (Figures 1 and 2; Table 1)

Basionym:—*Archaeolithothamnion episoredion* Adey, Townsend & Boykins (1982: 48) Holotype:—USNC 71–79–(35–47f), August 1971, D. Child.

Paratypes:—USNC 71–55–18, 71–67–9, 71–75–4, 71–50–77.

Type Locality:—HAWAII, St Rogatien Bank (Verheij 1993: 86).

Description:—Nongeniculate thalli, rhodolith with a lumpy growth form (Fig 1). Monomeric organization composed by a group of filaments running from the ventral part of the thallus to the surface forming three cell layers, central, peripheral and epithallial (Fig 2A). Cells in the core area were 14–17 μm long and 6–9 μm in diameter (Fig 2A); cells in the peripheral area were 9–12 μm long and 8–12 μm in diameter (Fig 2A); and epithallial cells were flared (Fig 2B), 3–4 μm long and 8–9 μm in diameter. Cells from adjacent filaments were linked by secondary pit connections and cell fusions (Fig 2C) in a 1:4 ratio, trichocytes absent.

Tetrasporangia formed in sori that are flush to raised in relation to the thallus surface becoming embedded in the thallus when senescent (Fig 2D, E) by thallus overgrowing. Presence of a basal layer of elongated cells in areas where sporangia develop (Fig 2F, arrow). Tetrasporangia compartments were sized 82–110 μm in diameter and 135–180 μm in length without differentiated stalk cells in the area where the spores will be formed, 2–5 paraphyses between tetrasporangia compartments, each row with 7–9 cells. Cruciate tetrasporangia (Fig 2G) are located at the base of the sporangial compartment (Fig. 2F) and are 40–60 μm in diameter and 30–40 μm in length.

Material examined:—BRAZIL, Espirito Santo, Vitória-Trindade sea mountains (20°08'46" S, 37°29'06" W) 50 m depth, tetrasporangial, RB 498396, RB 584551, RB 584552, RB 584553, collected x.1997

Geographic distribution:—Indonesia (Verheij 1993); French Polynesia (Payri, N'Yeurt & Orepuller 2000, N'Yeurt & Payri 2010), Hawaiian Islands (Verheij 1993).

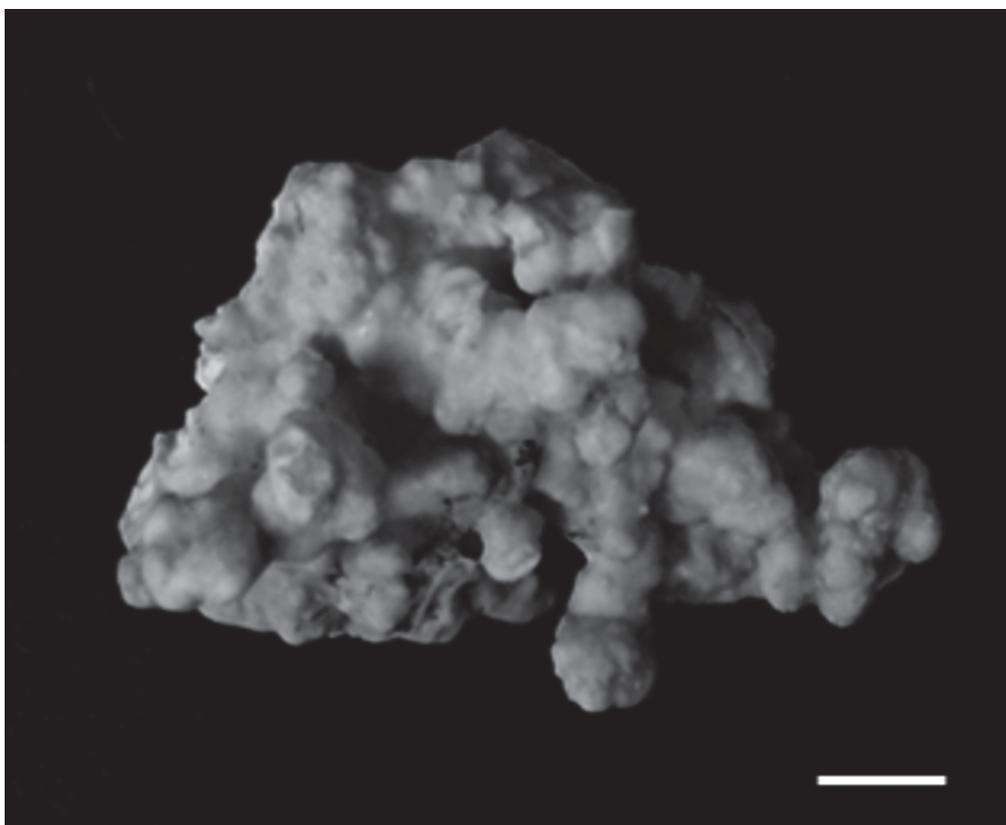


FIGURE 1 *Sporolithon episoredion*. Lumpy growth form. Scale bar 5 mm.

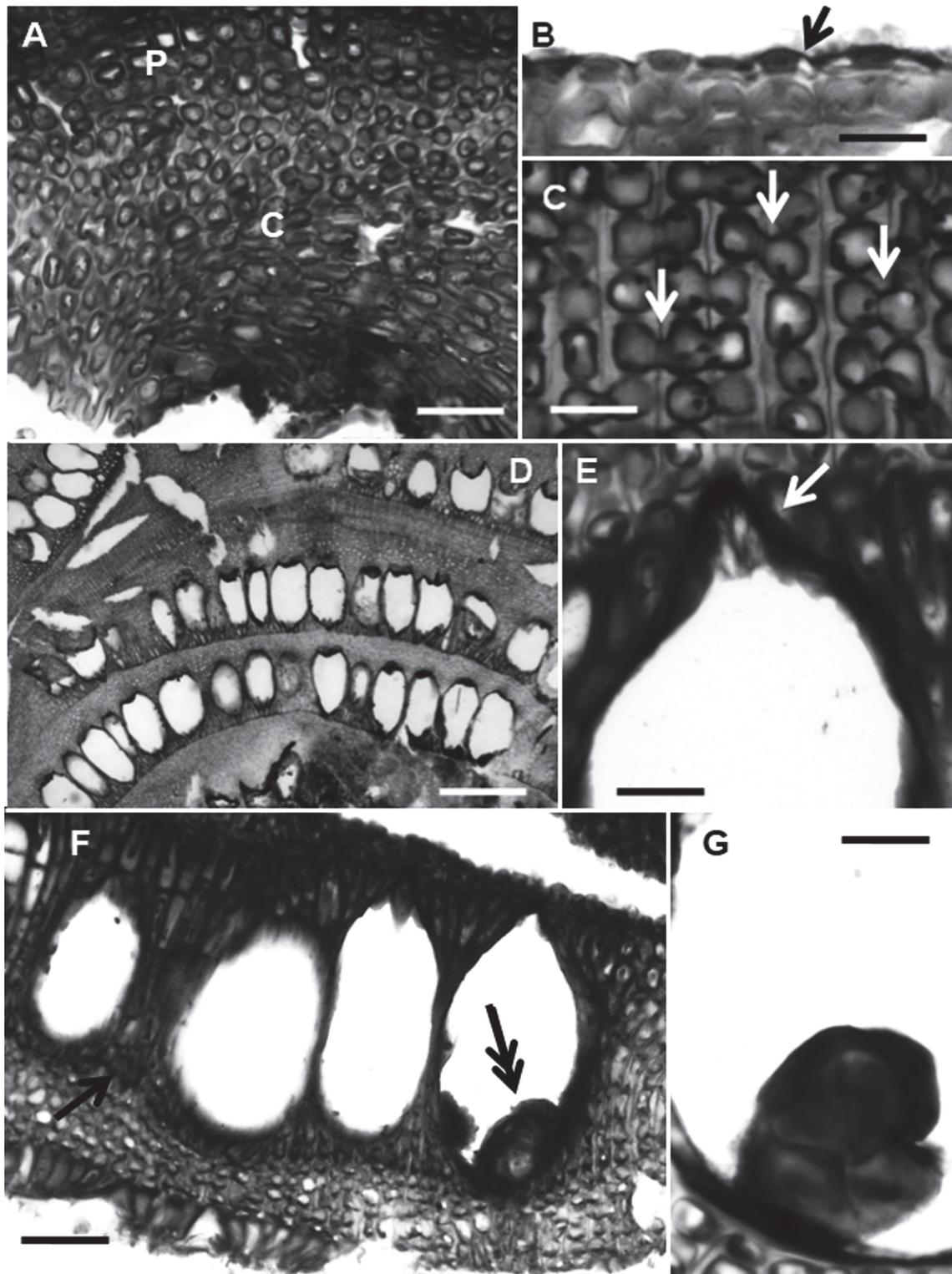


FIGURE 2 Longitudinal sections of *Sporolithon episorredion* showing: A: Monomeric arrangement with central (c) and peripheral (P) cell layers. Scale bar: 40 μ m; B: Flared epithallial cells (arrow). Scale bar: 10 μ m; C: Cell fusions (arrow). Scale bar: 20 μ m; D: Embedded sori. Scale: 200 μ m; E: Detail of sori (arrow). Scale bar: 20 μ m; F: Detail of sporangia compartments showing the presence of a basal layer of elongated cells in areas where sporangia develop (Arrow) and a tetrasporangium at the bottom (double arrow). Scale bar: 45 μ m; G: Cruciate tetrasporangia. Scale bar: 15 μ m.

Sporolithon ptychoides Heydrich (1897: 67) (Figures 3 and 4; Table 1)

Lectotype:—TRH (not shown, considering that Verheij 1993 has presented descriptions), El Tor, Red Sea, no number (as *Sporolithon ptychoides* f. *dura*) designated by Woelkerling & Townsend (in Woelkerling 1988:204).

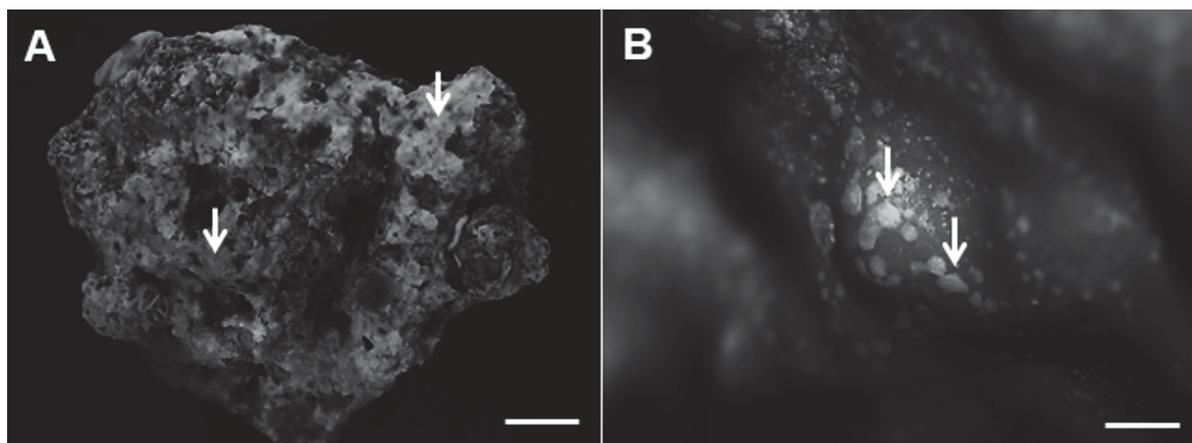


FIGURE 3 *Sporolithon ptychooides* showing: A: the encrusting growth form (arrow). Scale bar 20 mm; B: tetrasporangia compartments surface view (arrow). Scale 2 mm.

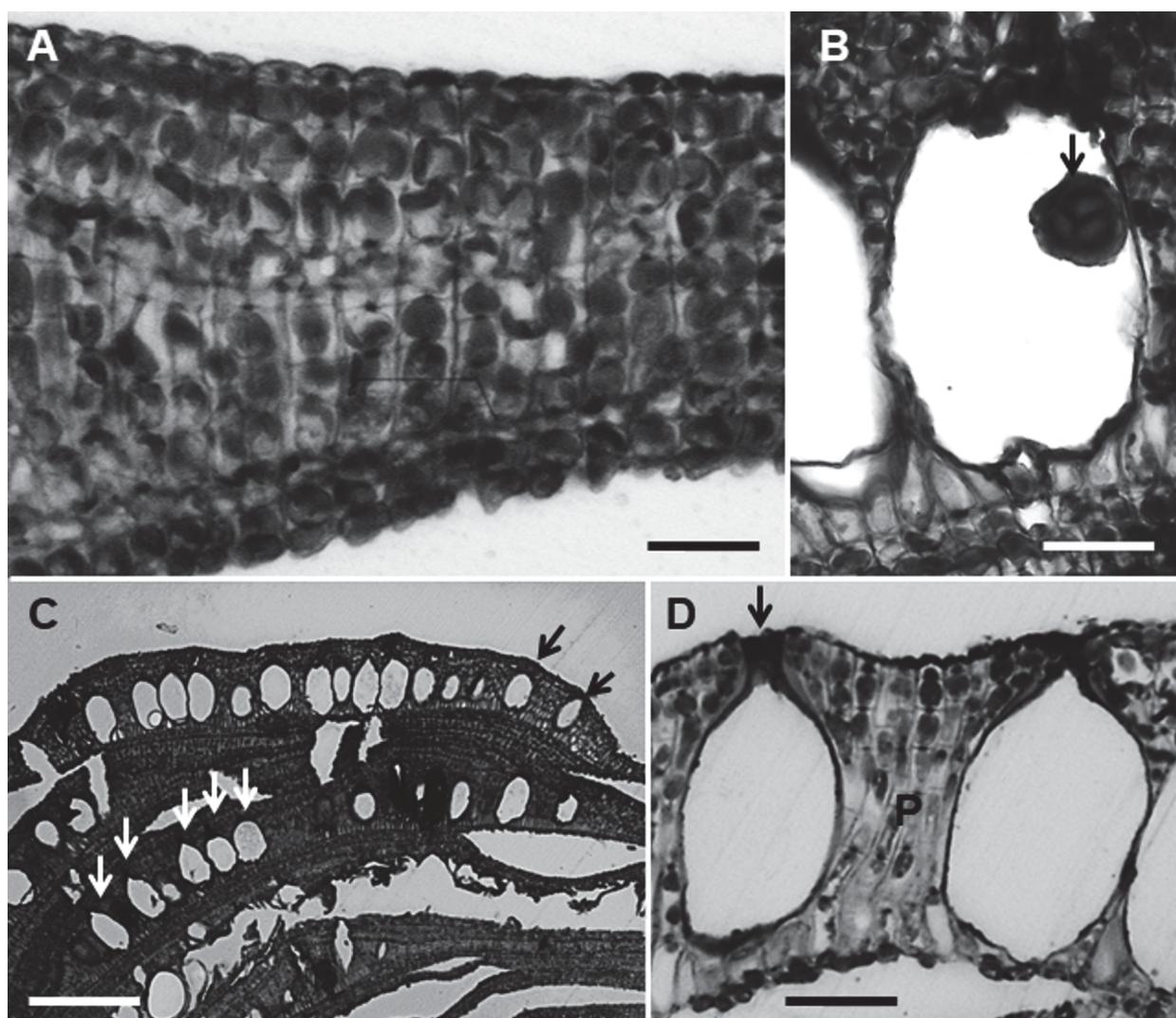


FIGURE 4 Longitudinal sections of *Sporolithon ptychooides* showing: A: Dimerous thallus arrangement. Scale bar: 20 µm; B: Sporangia compartments with a cruciate tetrasporangium (arrow). Scale bar: 30 µm; C: Embedded and raised (arrows) sori in relation to the thallus. Scale bar: 220 µm; D: Detail of pore sori (arrow) and paraphyses (P). Scale bar: 40 µm.

Description:—Nongeniculate thalli, rhodolith with a encrusting growth form (Fig 3A, B). Thalli with dimeric organisation (Fig 4A) that forms a core running more or less vertical to the substrate. Epithallial cells flared (Fig 4A). Cells from adjacent filaments were linked by secondary pit connections and cell fusions in a 2:1 ratio, and trichocytes were absent.

Cruciate tetrasporangia (Fig 4B, arrow) formed in sori that is raised in relation to the thallus (Fig 4C, D arrows) surface. Basal layer of elongated cells in areas where sporangia develop (Fig 4B). Sorus becoming embedded in the thallus when senescent (Fig 4C) by thallus overgrowing. Tetrasporangia compartments (Fig 4D) were 50–67 μm in diameter and 96–110 μm in length without differentiated stalk cells in the area where the spores are formed, 1–6 paraphyses between tetrasporangia compartments, each with 4–5 cells (Fig 4D).

Material examined:—BRAZIL, Rio de Janeiro, Continental shelf (22° 55' 07" S– 40° 54' 01" W) 107 m depth, tetrasporangial, RB 584554, RB 584555, RB 584556, collected 18.xi.2011

Geographic distribution:—Indonesia (Verheij 1993), South Africa (Keats & Chamberlain 1993), Mediterranean Sea (Alongi 1996), Brazil (Bahia *et al.* 2011), Thailand (Kaewsuralikhit *et al.* 2012).

***Sporolithon elevatum* sp. nov.** Henriques *et* Riosmena-Rodriguez (Figures 5 and 6; Table 1)

Holotype:—BRAZIL, Rio de Janeiro, continental shelf (22°14'36" S, 40°04'56" W) 133 m depth, tetrasporangial plant, Henriques, 10.x.2010; RB 584581.

Complementary collection (paratypes):—Brazil, Rio de Janeiro, continental shelf (22°14'36" S, 40°04'56" W) 133 m depth, tetrasporangial, Henriques, 10.x.2010, RB 584585, (22° 17' 24" S, 40° 15' 13" W) 109 m depth, tetrasporangial Henriques, 11.x.2010, RB 584582, (22° 23' 01" S, 40° 28' 06" W) 120 m depth, tetrasporangial RB 584583, RB 584584, Henriques, 20.x.2010.

Etymology:—*elevatum* referring to the tetrasporangia formed in sori that is above the thallus surface.

Description:—Nongeniculate thalli, rhodolith with incrusting growth form (Fig 5A, B). Thalli with dimeric organisation that forms a core running more or less vertical to the substrate (Fig 6A). Flared epithallial cells were 4.0–5.5 mm long and 7.5–12.5 mm in diameter (Fig 6B). Cells were 4.0–12.0 mm long and 7.0–13.0 mm in diameter (Figs 6A, B). Cells from adjacent filaments were linked by secondary pit connections and cell fusions (Fig 6C) in a 2:3 ratio and trichocytes were absent.

Tetrasporangia formed in sori that are totally above the thallus (Fig 6B) and are sloughed off of the thallus when senescent (Fig 6D). Presence of a basal layer of elongated cells in areas where sporangia develop (Fig 6E). Tetrasporangia compartments pore without plugs (Fig 6E). Tetrasporangia compartment is 34–45 μm in diameter and 60–76 μm in length without differentiated stalk cells in the area where the spores will be formed. 1–4 paraphyses between tetrasporangia compartments, each paraphyses with 2–3 elongated cells (Figs 6E, F). Cruciate tetrasporangia (Fig 6F) are located at the base of the sori and are 15–28 μm in diameter and 14–27 μm in length. Male, female and carposporangial conceptacles not observed.

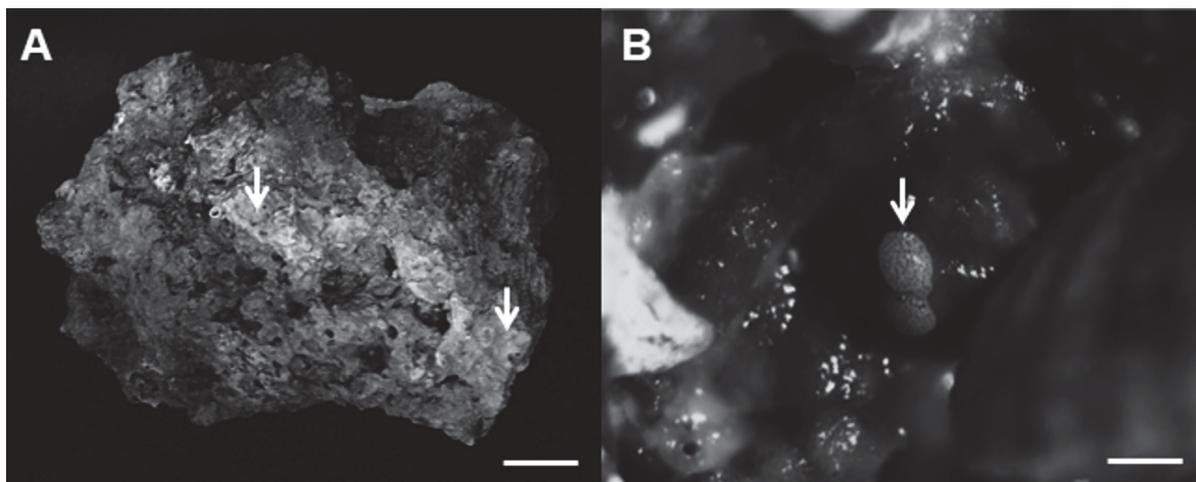


FIGURE 5 *Sporolithon elevatum* sp. nov. A: Encrusting growth form (arrows). Scale bar 20 mm; B: Tetrasporangia compartments surface view (arrow). Scale 2 mm.

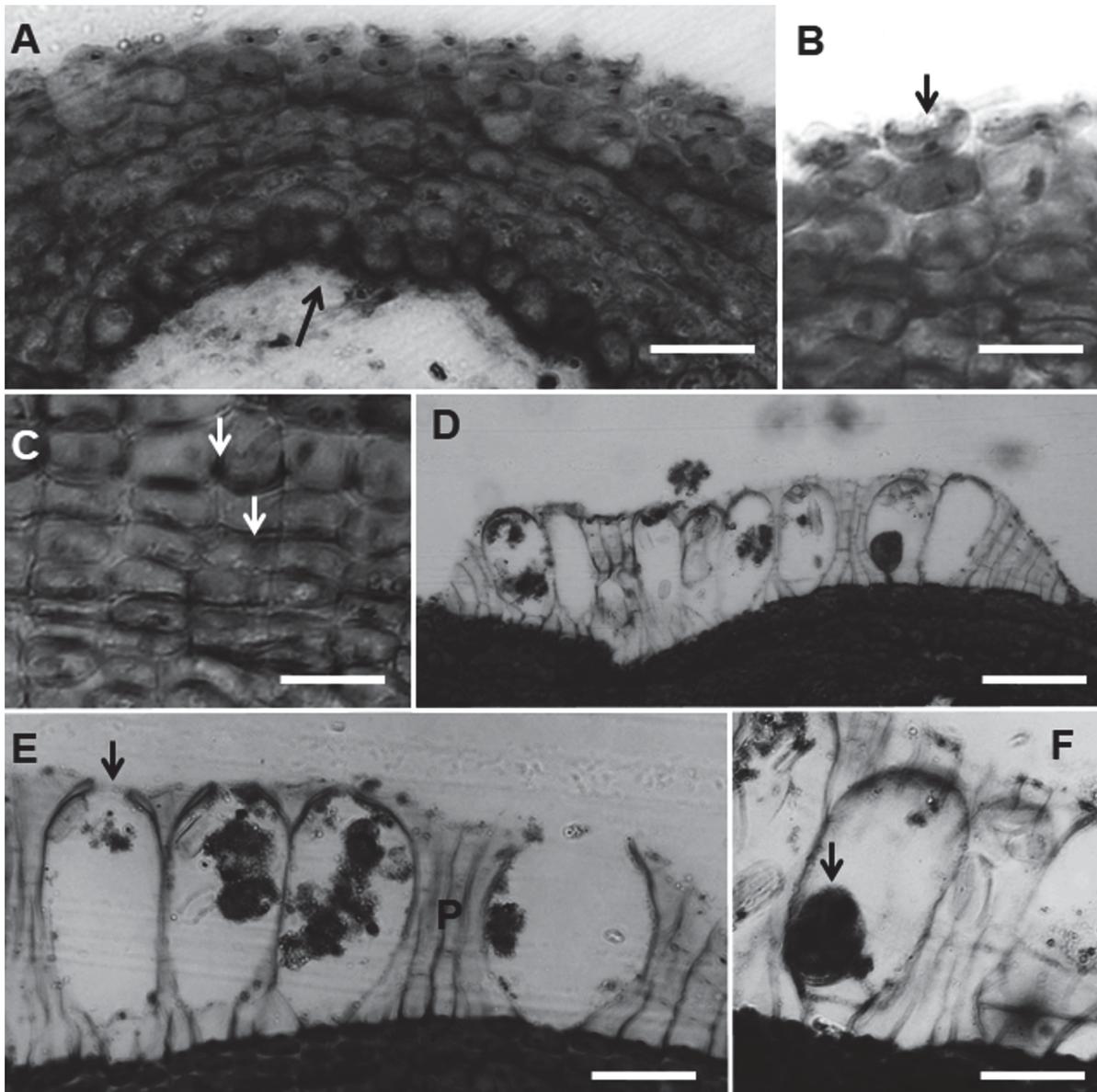


FIGURE 6 Longitudinal sections of *Sporolithon elevatum* sp. nov. showing: A: Dimeric arrangement. Scale bar: 20 μ m; B: Flared epithelial cells (arrow). Scale: 10 μ m; C: secondary pit connections (arrows). Scale bar: 10 μ m; D: Sori totally above the thallus. Scale bar: 60 μ m; E: Tetrasporangia compartments pore (arrow) with paraphyses (P) between compartments. Scale bar: 30 μ m; F: Detail of cruciate sporangium (arrow) into its compartment. Scale bar: 30 μ m.

Discussion

This study identified *Sporolithon* species that are present in rhodolith beds along the Brazilian continental outer shelf. Of the three identified species we found *Sporolithon episoredion*, a new record for the Atlantic Ocean, at 50 m deep in Espirito Santo state, *S. ptychoides* in Rio de Janeiro state at 107 m deep and a new species named *Sporolithon elevatum* sp. nov., found at 133 m deep in Rio de Janeiro state.

Only three species of *Sporolithon* have been consistently identified and described in Brazilian waters: *Sporolithon episporum* (Nunes *et al.* 2008), *Sporolithon ptychoides* (Bahia *et al.* 2011) and *Sporolithon tenue* (Bahia *et al.* 2013). Yamaguishi-Tomita (1976) identified eight species mainly based on old concepts of coralline red algal taxonomy such as tetrasporangial chamber size, tetrasporangial pore density, and thallus texture. According to modern concepts of coralline red algal taxonomy, these characters are no longer sufficient for precise identification because they are too variable (Verheij 1993; Bahia *et al.* 2011). The most important characters currently used in

Sporolithon taxonomy are: 1) diameter/length of the tetrasporangial compartment, 2) fate of old sporangial cases, 3) number of cells in the paraphyses, 4) Presence of a basal layer of elongated cells in areas where sporangia develop, (5) number of cells by which sorus is raised above surrounding thallus surface and (6) soral organization (Verheij 1993; Keats & Chamberlain 1993; Townsend *et al.* 1995; Alongi *et al.* 1996; Bahia *et al.* 2011; Bahia *et al.* 2013). In the present work we compared *Sporolithon* species for which recent (since 1990) detailed descriptions are available (Table 1).

The character that delimits *Sporolithon episoredion* from other species of *Sporolithon* is the size of tetrasporangia compartments and the number of cells in paraphyses. The Brazilian specimens of *Sporolithon episoredion* reported here possess the same features of the original description of *S. episoredion* (as *Archaeolithothamnion episoredion*, Adey *et al.* 1982) and of *S. episoredion* from Indonesia (Verheij 1993) (Table 1). *S. episoredion* from Indonesia differs from *S. episoredion* from Brazil by presenting more cell fusions than secondary pit connections (ratio 4:1 against 1:2–4) (Table 1). This character is not considered diagnostic to *Sporolithon* species. South-eastern Australia collections of *S. durum* support by molecular analyses (Harvey *et al.* 2002) showed great variability in kinds and ratios of cellular connections between species of *Sporolithon*. All collections, however, possessed cell fusion, with secondary pit connections varying from absent to common. *Sporolithon Episorum*, *S. durum* (Foslie) Townsend and Woelkerling and *S. tenue* differ from *S. episoredion* in their soral organization. In these species the sori are sloughed off instead of embedded when senescent, while in *S. episoredion* the sori become buried.

Sporolithon episoredion is closely related to *S. ptychoides* and *S. molle*, because they have a similar soral organization, becoming buried when senescent. *S. episoredion* is easily distinguished from *S. ptychoides* by the number of cells in paraphyses and the presence of a bigger sori (Table 1). It also differs from *S. molle* by having different number of cells in paraphyses. In addition, *S. molle* lacks elongated cells in the region where sporangia develop (Table 1).

Sporolithon ptychoides was described as the first report in the Atlantic Ocean by Bahia *et al.* (2011). The diagnostic features of this species are the number of cells in paraphyses, tetrasporangium size, and tetrasporangial compartments buried in the thallus. These characters observed in our material correspond to those observed in *S. ptychoides* described by Verheij (1993), Keats and Chamberlain (1993), Alongi *et al.* (1996), and Bahia *et al.* (2011) (Table 1).

Sporolithon elevatum sp. nov. present a distinctive set of features compared to the other known species in the genus. The sorus of *S. elevatum* are 2–3 cells elevated above the thallus, sloughs off when senescent and had a lower number of cells (2–3) in paraphyses (Table 1). The diagnostic features that determine the new species are the conjunction of the number of cells the sorus are elevated above the thallus and the number of cells in paraphyses. *Sporolithon elevatum* presents a similar soral organization to *S. tenue*, *S. episorum* and *Sporolithon durum*. They have different number of cells in paraphyses (2–3 in *S. elevatum* sp. nov., 4–6 in *S. tenue*, 3–8 in *S. episorum* and 6–7 in *S. durum*) and the sorus is 2–3 cells elevated above the thallus in *S. elevatum* sp. nov., while it is 5–7 cells in *S. tenue*, 1–4 in *S. episorum* and 2–3 in *S. durum*. *S. elevatum* also differs from *S. tenue* having a basal layer of elongated cells in areas where sporangia develop.

Sporolithon molle (Heydrich) Heydrich (1897: 416), *S. ptychoides*, and *S. episoredion* are different from *S. elevatum* especially because of their soral organization. In these species the sori become buried instead of sloughing off when senescent, while in *S. elevatum* the sori are always sloughed off.

The biodiversity of Sporolithales and Corallinales in Brazil seems to be higher than previously known. It is evidenced by the description of a new species and a new record in the Atlantic Ocean, increasing the recent reports for the genus *Sporolithon*. At the present five species in Brazil are well described, which are *S. episorum*, *S. ptychoides*, *S. episoredium*, *S. tenue* and *S. elevatum*. This study contributes to the understanding of the diversity in this genus and indicates that new systematic studies are necessary to complete taxonomic information and relevant data to include in conservation programs, exploitation activities, and evaluation of impacts.

TABLE 1. Comparison of *Sporolithon* species (vegetative and tetrasporangial features) for which detailed descriptions are available recently. Sources at the bottom.

Character	<i>S. episporum</i>	<i>S. durum</i> ^d	<i>S. tenue</i> ^e	<i>S. elevatum</i> ^f	<i>S. pychooides</i> ^{a,b,g,h}	<i>S. pychooides</i> ^d	<i>S. episorredion</i> ^{a,1}	<i>S. episorredion</i> ^f	<i>S. molle</i> ^a
Locality	Panama (Caribbean coast) and Indian Ocean	Southern Australia	Northeastern Brazil	Southeast Brazil	Red sea, Indian Ocean, Hawaii, Mediterranean Sea, Southeast Brazil	Southeast Brazil	Hawaii and Indonesia	Southeast Brazil	Red sea and Indian Ocean
Number of cells in paraphyses	3-5 ^a 4-8 ^b 4-8 ^c	6-7	4-6	2-3	3-5 ^a 7-9 ^b 4-6 ^g 3-5 ^h	4-5	6-9 ^a	7-9	3-4
Thallus organization	Monomerous	Monomerous	Monomerous	Dimerous	Dimerous	Dimerous	Monomerous	Monomerous	Monomerous
Ratio of secondary pit connections to cell fusions	4:1 ^a Secondary pit connections but rarely cell fusions ^b Secondary pits common, cell fusions in core ^c	Cell fusions common; secondary pit connections rare or apparently absent	Secondary pit connections, predominant	2:3 Secondary pit connections common; cell fusions rare	2-3: 1 ^a Secondary pit connections usually less common than cell fusions ^b 2:1 ^g Mainly secondary pit connections	2:1 Secondary pit connections usually less common than cell fusions	Secondary pit connections common; cell fusions rate 2-4:1 ^a	1: 4 Secondary pit connections usually much less common than cell fusions	2-3:1
Basal layer of elongated cells in areas where sporangia develop	Present	Present	Absent	Present	Present ^{g,h}	Present	Present ^d	Present	Absent
Tetrasporangia compartment length (µm)	70-90 ^a 95-112 ^b 50-70 ^c	92-105	50-75	60-76	85-105 ^a 77-108 ^b 85-130 ^g 75-105 ^h 35-45 ^a 29-53 ^b 40-60 ^g 40-55 ^h	96-110	180-200 ^a 70-200 ⁱ	135-180	70-85
Tetrasporangia compartment diameter (µm)	45-55 ^a 33-50 ^b 25-40 ^c	38-54	30-40	34-45		50-67	100-135 ^a	82-110	25-45
Fate of old sporangial cases	Sloughed off ^{a,b}	Sloughed off	Sloughed off	Sloughed off	Become buried ^{ab,g,h}	Become buried	Become buried ^a	Become buried	Become buried
Position of sori relative to surrounding vegetative surface (number of cells)	Raised 1-2 ^a 3-4 ^{b,c}	Raised (2-3)	Raised (5-7)	Raised (2-3)	Raised (1-2) ^a (2-8) ^b (2-4) ^h	Raised (2-4)	Raised ^d (3-5)	Flush to Raised (2-3)	Flush

^aVerheij (1993); ^bKeats and Chamberlain (1993); ^cType of *S. episporum* in Keats and Chamberlain (1993); ^dTownsend et al. (1995); ^eBahia et al. (2013); ^fPresent study; ^gAlongi et al. (1996); ^hBahia et al. (2011); ⁱAs *Archaeolithothamnion episorredion* in Adey et al. (1982)

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