

***Sporolithon molle* (Heydrich) Heydrich (Sporolithales, Corallinophycidae, Rhodophyta): an addition to the Atlantic flora found on a remote oceanic island**

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ABSTRACT – *Sporolithon molle* (Heydrich) Heydrich has previously only been reported from the Red Sea, Arabian Gulf, Indonesia, and eastern Australia. The species is reported for the first time from the Atlantic Ocean where it was found in the remote oceanic island of Trindade, Brazil. This study provides a comparative account of tetrasporic plants from the Atlantic Ocean against those from the other known locations and from other well-described species of the genus *Sporolithon*. The specimens reported here, presented all the features of the genus, namely: flared epithallial cells, cells of adjacent filaments joined by both cell fusions and secondary pit connections, cruciately divided tetrasporangia formed within sori; and tetrasporangia bearing apical pore plugs and formed on a single stalk cell. *Sporolithon molle* differs from other species of *Sporolithon* mainly by the absence of a layer of elongate cells at the base of tetrasporangial sori. Samples from Trindade differ slightly from the type collection and from specimens from other known locations by the tetrasporangial sori which can be flush to slightly raised (to 3 cells) above the surrounding vegetative thallus surface as opposed to being flush only in all material reported previously.

Coralline algae / Rhodolith / Taxonomy / Southwestern Atlantic / Brazil

INTRODUCTION

The crustose coralline red algae (CCA) constitute one of the most difficult taxonomic groups within the Rhodophyta in terms of identification process (see Woelkerling, 1988; Irvine & Chamberlain, 1994; Woelkerling & Lamy, 1998). This perception can be attributed to a legacy of poor quality taxonomic work (see Woelkerling & Lamy, 1998) and largely to the fact that, unlike most seaweeds, they require specific collection and laboratory methods for taxonomic study (Maneveldt *et al.*, 2008). What makes the study of CCA difficult is that organisms with same genotype display a wide range of external morphologies or contrary, similar external morphology shows a variable genotype (e.g. Broom *et al.*, 2008; Farr *et al.*, 2009). For these reasons, accurate and reliable

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identification of new records of CCA should be accompanied by detailed descriptions providing evidence of the main taxonomic features used to delineate taxa. Reproductive anatomy has been confirmed to be one of the most important features to distinguish CCA (Woelkerling, 1988; Le Gall *et al.*, 2010). Simply providing names, or less useful characterisations with only brief descriptions, in floristic inventories and checklists, should be treated with caution.

Sporolithon molle (Heydrich) Heydrich, along with *S. durum* (Foslie) Townsend *et Woelkerling*, *S. episoredion* (Adey, Townsend *et Boykins*) Verheij, *S. episporum* (M.A.Howe) E.Y.Dawson and *S. ptychoides* Heydrich, is one of five extant species of *Sporolithon* whose taxonomic circumscription has been clarified within a modern context (Verheij, 1993; Harvey & Woelkerling, 2007). *Sporolithon molle* can be distinguished from other species in the genus by the cells located at the base of the tetrasporangial compartments; these cells are similar in size and shape compared to those of the surrounding vegetative cells (Verheij, 1993; Townsend *et al.*, 1995). In other *Sporolithon* species, the cells at the base of the tetrasporangial compartments are elongated and form a distinct layer (Verheij, 1993; Townsend *et al.*, 1995).

Sporolithon molle has previously only been reported from the Red Sea (its type locality), Arabian Gulf, eastern Australia and Indonesia, where the species occurs epilithically, or unattached and free-living (as rhodoliths) from the shallow subtidal zone to depths of 117 m (Verheij, 1993; De Clerck & Coppejans, 1996; Lund *et al.*, 2000). In eastern Australia, the species plays an important ecological role in deep-water rhodolith formation as it is one of the most abundant coralline algae below 80 m depth (Lund *et al.*, 2000).

During surveys examining the diversity of rhodolith beds of Trindade Island (see Pereira-Filho *et al.*, 2012), which is a remote oceanic island at the easternmost extent of the Brazilian territory, numerous coralline red algae were collected. *Sporolithon molle* was identified among the coralline those collections. This study represents the first reporting of *S. molle* from the Atlantic Ocean and provides a comparative taxonomic account of tetrasporic plants from the Atlantic Ocean against those from other known locations and from other well-described species of the genus *Sporolithon*.

MATERIAL AND METHODS

Specimens were collected from a rhodolith bed at 65 m depth by SCUBA diving in the Trindade Island (20°30'13" S; 25°21'17" W) in February 2011. Samples for light microscopy examination were prepared using the histological methods described by Maneveldt and van der Merwe (2012). For scanning electron microscopy (SEM) the procedure followed Bahia *et al.* (2010). For species descriptions, growth-form terminology follows Woelkerling *et al.* (1993), and thallus anatomical terminology follows Adey and Adey (1973). For cell length measurements, the distance between primary pit connections was considered while for cell diameters, the maximum cell lumen at right angles to the length was considered. The tetrasporangial chamber height was measured from the base of the stalk cell to the pore opening. Specimens were deposited at Rio de Janeiro Botanical Garden Herbarium (RB) and are composed of slides and dry samples from formalin preserved material.

RESULTS

Sporolithon molle (Heydrich) Heydrich, 1897: 416-417

Figs 1-10

Basionym: *Sporolithon ptychoides* f. *molle* Heydrich

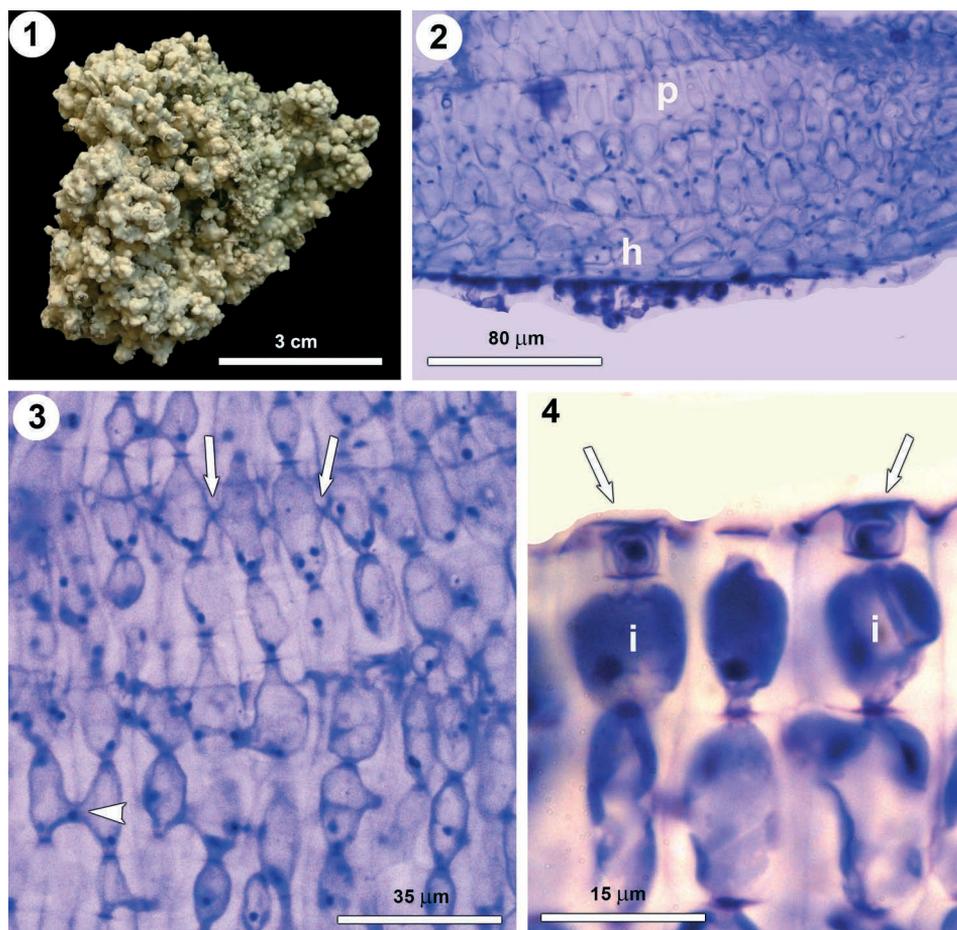
Lectotype: C, unnumbered, Heydrich (Verheij 1993: 189, figs. 13, 14), designated by Verheij (1993: 189).

Isolectotype: TRH, unnumbered, Heydrich.

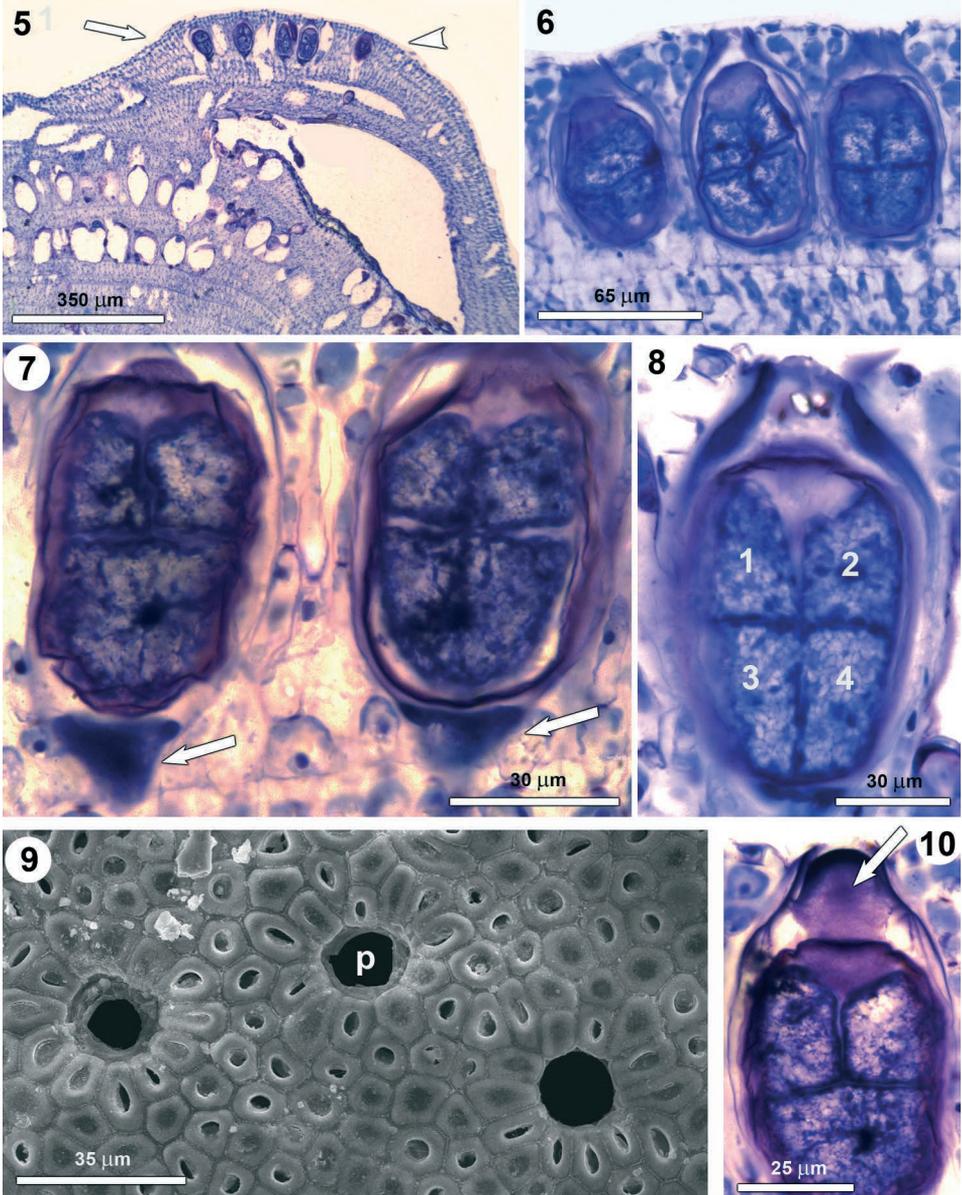
Type locality: El Tor, Red Sea.

Etymology: *molle* from Latin = soft, pliant.

Specimens examined: Espírito Santo, Ilha de Trindade (20°30'13" S; 25°21'17" W, 65 m, GM Amado Filho, 18.ii.2011, RB 564704, RB 568173, RB 568174).



Figs 1-4. Morphology and vegetative anatomy of *Sporolithon molle* (RB 564704). **1.** A rhodolith mainly composed of *Sporolithon molle*. **2.** Vertical section through the inner thallus showing a monomerous, plumose (non-coaxial) internal construction with hypothallial (h) and perithallial (p) filaments. **3.** Vertical section of the perithallium showing contiguous filaments connected by both secondary pit connections (arrows) and cell fusions (arrowhead). **4.** Vertical section of the outer thallus surface showing flared epithallial cells (arrows) subtended by subepithallial initials (i).



Figs 5-10. Tetrasporangial anatomy of *Sporolithon molle* (RB 564704). **5.** Vertical section through the thallus showing a tetrasporangial sorus slightly raised above the adjacent vegetative thallus surface to the left (arrow). Note that the same sorus is flush with the vegetative thallus surface to the right (arrowhead). Senescent, empty tetrasporangial sori are buried deep in the thallus. **6.** Vertical section of the outer thallus showing tetrasporangia with cruciately divided tetrasporangia. Note that each tetrasporangial chamber lacks a layer of elongated cells at its base. **7.** Detail of two tetrasporangia, each with incomplete cruciately dividing tetrasporangia and subtended by a single stalk cell (arrows). Note that each tetrasporangial chamber lacks a layer of elongated cells at its base. **8.** Detail of a tetrasporangium bearing complete cruciately divided tetrasporangia (1-4). **9.** SEM of the sori surface showing tetrasporangial chamber pores (p) surrounded by 10-12 rosette cells. **10.** Detail of an incomplete cruciately dividing tetrasporangium bearing an apical pore plug (arrow).

Habit: Plants encrusting, free living, warty to lumpy, forming rhodoliths up to 7 cm in diameter (Fig. 1). Crusts are firmly adherent and when freshly collected, living plants are pink to purplish pink in colour. Protuberances are nodular or more irregularly shaped measuring 0.2-0.6 cm in length and 0.1-0.4 cm in diameter. Individual thalli measure 500-800 μm thick.

Vegetative anatomy: The thallus is dorsiventrally organized and monomerous, and haustoria are absent (Fig. 2). The hypothallium is thin (1-4 layers) and plumose (non-coaxial) (Fig. 2). Cells of the hypothallium are elongate to square to rounded, and measure 10-30 μm in length and 8-15 μm in diameter (Fig. 2). Cells of the perithallium are elongate to rounded, and measure 9-23 μm in length and 5-14 μm in diameter (Fig. 3). Cells of contiguous (adjacent) filaments are joined by both cell fusions and secondary pit connections (Fig. 3). Secondary pit connections predominate at a ratio of 3-4:1. Subepithallial initials are square to rounded, measure 10-15 μm in length and 8-12 μm in diameter, and are typically as short as or shorter than their immediate inward derivatives (Fig. 4). Epithallial cells occur in a single layer, are thick-walled with flared upper margins (Fig. 4), and measure 5-6 μm in length and 4-6 μm in diameter.

Reproductive anatomy: Only tetrasporic plants were found. Tetrasporangial compartments are grouped into sori (Figs 5 and 6) that are flush to only slightly raised (up to 3 cells) above the adjacent vegetative thallus surface. Both flush and raised tetrasporangial compartments can occur on the same plant (Fig. 5). Tetrasporangial chambers are uniporate, elliptical to rounded, measure 70-95 μm in height and 38-50 μm in diameter, and are separated from one another by 1-3 paraphyses comprised of 3-4 elongate cells (Figs 5-8). Chamber pores are generally flush with the surrounding reproductive thallus surface to slightly sunken towards their inner surface, measure 10-17 μm in diameter and are surrounded by 10-12 rosette cells (Fig. 9). Within sori, each chamber bears only one tetrasporangium that is cruciately divided and measures 63-80 μm in length and 36-48 μm in diameter (Figs 6-8, 10). Tetrasporangia bear apical pore plugs (Fig. 10) and are subtended by a single triangular stalk cell measuring 11-17 μm in length and 19-28 μm in diameter (Fig. 7). Cells located at the base of tetrasporangial chambers are similar in size and shape to those of the surrounding vegetative cells (Figs. 6 and 7). Senescent and empty tetrasporangial sori become buried in distinct horizontal layers (Fig. 5) and sometimes are filled by vegetative growth.

DISCUSSION

The features observed in the specimens examined from Trindade Island correspond to *S. molle* as described by Verheij (1993) and De Clerck & Coppejans (1996). Notably there are some minor differences in our material compared against those described by Verheij (1993) and De Clerck & Coppejans (1996) (Table 1). The main difference pertains to the position of the tetrasporangial sori in relation to the adjacent vegetative thallus surface. In the Trindade Island material, the tetrasporangial sori can be flush to slightly raised above the surrounding vegetative thallus surface whereas in the samples described by Verheij (1993) (including the type collection) and De Clerck & Coppejans (1996), tetrasporangial sori have only been observed to occur flush with the thallus surface.

Table 1. Comparative analysis of *Sporolithon* species for which recent, detailed descriptions are available. ND = no data available.

Character	<i>S. molle</i> (this study)	<i>S. molle</i> ¹	<i>S. molle</i> ²	<i>S. episoredion</i> ^{1,3}	<i>S. episporum</i> ^{1,4}	<i>S. durum</i> ⁵	<i>S. ptychoides</i> ^{1,4,6,7,8}
Locality	Southwestern Atlantic (Trindade Island, Brazil)	Red Sea and Indian Ocean	Arabian Gulf	Hawaii and Indonesia	Panama (Caribbean coast), South Africa, and Indonesia	Southern Australia	Red Sea, Mediterranean Sea, Atlantic, Pacific, and Indian Ocean
Tetrasporangium length × diameter ⁹	63-80 × 36-48 µm	70-85 × 25-45 µm	75-85 × 30-40 µm	70-220 × 35-135 µm	70-96 × 30-55 µm	92-105 × 38-54 µm	55-130 × 25-60 µm
Tetrasporangial chamber pore diameter	10-17 µm	ND	ND	10-20 µm ¹⁰	16-30 µm	13- 21 µm	9-15 µm
Number of rosette cells surrounding tetrasporangial chamber pore	10-12	ND	ND	11-13 ⁸	8-16	14-15	8-11
Layer of elongate cells at the base of tetrasporangial sorus	Absent	Absent	Absent	Present	Present	Present	Present
Tetrasporangial chambers buried/shed	Buried	Buried	Buried	Buried	Shed	Shed	Buried
Position of sori relative to surrounding vegetative surface (number of cells including epithallials)	Flush to slightly raised (0-3)	Flush (0)	Flush (0)	Raised (3-5)	Raised (1-4)	Raised (2-3)	Raised (1-8)

¹ Verheij (1992, 1993); ² De Clerck & Coppejans (1996); ³ Adey et al. (1982); ⁴ Keats & Chamberlain (1993); ⁵ Townsend et al. (1995); ⁶ Alongi et al. (1996); ⁷ Bahia et al. 2011; ⁸ Kaewsuralikhit et al. (2012). ⁹ Tetrasporangium length × diameter might be confused with the tetrasporangial chamber length × diameter due to measurement method, as observed by Kaewsuralikhit et al. (2012). ¹⁰ Measurements taken directly from both the holotype (USNC 71-79-35-47f) and the paratypes (USNC 71-55-18, 71-67-9, 71-75-4 and 71-50-77) of *S. episoredion*.

Verheij (1993: 189) commented that *S. molle* is closely related to *S. ptychoides*. The two species can be distinguished from one another by the respective absence and presence of a conspicuous layer of elongated cells at the base of each tetrasporangial chamber (Table 1). This layer of elongated cells has been observed in all other currently known, well documented extant species of *Sporolithon*. In *S. molle* the cells located at the base of the tetrasporangial chambers are consistently similar in size and shape to the surrounding vegetative cells. Kaewsuralikhit et al. (2012: 274) noted in specimens of *S. ptychoides* from Thailand that the elongate cells at the base of the tetrasporangial chambers can be present or absent in the same sorus. Although they made no reference to the shape of the cells when elongate cells were absent, Kaewsuralikhit et al. (2012: see Table 1) did emphasize that the elongate cells were “mainly present”. They stated that “the position of tetrasporangia on the elongated cells may depend on the direction of cutting in regions where tetrasporangia and paraphyses developed or their natural variations, which need further confirmations”.

This study has expanded the known geographic distribution of *S. molle* and has contributed to the knowledge of the rhodolith-forming CCA diversity in the Atlantic Ocean. Nine species of *Sporolithon* are now reported for the Atlantic

Ocean. The previous eight reported species include: *S. africanum* (Foslie) J.Afonso-Carillo, *S. australasicum* (Foslie) N.Yamaguishi-Tomita ex M.J.Wynne, *S. durum* (Foslie) Townsend et Woelkerling, *S. erythraeum* (Rothpletz) Kylin, *S. howei* (Lemoine) N.Yamaguishi-Tomita ex M.J.Wynne, *S. pacificum* E.Y.Dawson, *S. episporum* (M.A.Howe) E.Y.Dawson and *S. ptychoides* Heydrich (Bahia et al., 2011; Wynne, 2011; Guiry & Guiry, 2013). Of these eight species, however, only the latter two have consistently been identified and described for the Atlantic Ocean (Nunes et al., 2008; Bahia et al., 2011) based on the modern understanding of the genus characterisation. *Sporolithon durum* was reported as a new occurrence for the Atlantic Ocean (Wynne, 2011), however, a detailed description of this record was not provided. This record should therefore be considered with caution until such time as a detailed description is provided. The remaining five *Sporolithon* species were reported in the doctoral dissertation of Tomita (1976), but have never been formally published. Based on the illustrations (all depicting layers of elongated cells at the base of tetrasporangial chambers) from Tomita's (1976) doctoral dissertation, we can confirm that *S. molle* was not reported by her, even under a synonym.

As noted by Bahia et al. (2011), a new review with extensive inventory of the genus *Sporolithon* in Brazil is needed to assess the real number of species belonging to this genus. Producing such an extensive review has in the past been hampered largely because *Sporolithon* is generally considered a deep-water (occurring at depths > 20 m) genus of CCA (Verheij, 1993; Lund et al., 2000; Braga & Bassi, 2007; Basso et al., 2009). However, modern sampling techniques have made deep-water collecting far easier and so should go a long way to adding value to the taxonomy and systematics of the CCA.

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