



Nongeniculate coralline red algae (Rhodophyta: Corallinales) in coral reefs from Northeastern Brazil and a description of *Neogoniolithon atlanticum* sp. nov.

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Abstract

A taxonomic reassessment of coralline algae (Corallinales, Rhodophyta) associated with reef environments in the Abrolhos Bank, northeastern Brazil, was developed based on extensive historical samples dating from 1999–2009 and a critical evaluation of type material. Our goal was to update the taxonomic status of the main nongeniculate coral reef-forming species. Our results show that four species are the main contributors to the living cover of coral reefs in the Abrolhos Bank: *Lithophyllum stictaeforme*, *Neogoniolithon atlanticum* sp. nov., *Porolithon pachydermum* and *Spongites fructiculosus*. Comparison of the type material to modern collections has shown that *Lithophyllum congestum* is a heterotypic synonym of *L. stictaeforme*. However, *L. stictaeforme* and *P. pachydermum* were the most abundant species at the studied sites, a finding consistent with other coral reefs in the region. This is the first record of *S. fructiculosus* in the southwestern Atlantic. This review provides the baseline data needed for the monitoring and management of the southernmost limits of coral reefs in the western Atlantic Ocean.

Key words: *Lithophyllum stictaeforme*, *Porolithon pachydermum*, *Spongites fructiculosus*

Introduction

Morphological features of nongeniculate coralline red algae (Corallinales, Rhodophyta) may indicate adaptations to various environmental factors that led to their classification into different functional groups (Littler & Littler 1980, 1984, Steneck 1986). These calcareous algae tend to dominate in habitats with high productivity and high exposure to disturbance (Steneck & Dethier 1994) as well as being associated with herbivores (Steneck 1990). Nongeniculate coralline red algae cover large areas of reef substrate and contribute to its framework (Macintyre 1997, Braga & Aguirre 2004). One region where coralline algae are important as reef-forming species is the western Atlantic (Kikuchi & Leão 1997, Gherardi & Bosence 1999, 2001). Morphological features of the thallus led to their classification as growth forms (Woelkerling *et al.* 1993a) however, these features may vary depending on environmental conditions, which may promote the convergent evolution of different genera and species (Irvine & Chamberlain 1994) and make the growth forms and vegetative anatomy poor taxonomic delimiters (Adey & Adey 1973). Therefore, evaluating the anatomic features of the tetrasporangial conceptacle is necessary to delimit genera and species in a modern context (Woelkerling 1988). Kato *et al.* (2011) and Bittner *et al.* (2011) have updated the taxonomy of this group, proposing several new subfamilies and the resurrection of the genus *Porolithon* Foslie (1909: 57). However, regional surveys are necessary to develop a complete picture of how the coralline species might be delimited in each region.

Due to the complexity of their taxonomy, surveys of regional flora have ignored this group of algae or have not taken a modern approach, as Harvey *et al.* (2005) did in the Pacific Ocean. Studies on the distribution of these algae

describe them in the temperate waters of the Atlantic Ocean, with the great majority being more conservative in their descriptions (Adey 1966, Adey & Adey 1973, Steneck & Paine 1986), except for Irvine & Chamberlain (1994), who considered the divisions of cells in the germination disks. The description of Brazilian reefs has not been updated. These crustose coralline algae occupy a wide variety of habitats, from the live coverage of hard substrates in the subtidal-to-intertidal region to waters more than 20 m deep off the northeastern Brazilian coast (Figueiredo 1997, 2000, Villaça & Pitombo 1997, Figueiredo & Steneck 2002, Figueiredo 2005, Tâmega & Figueiredo 2007).

In tropical and subtropical regions of the Atlantic, a few studies have described these algae, such as Steneck & Adey (1976), Littler & Littler (2000), Figueiredo & Steneck (2002), Tâmega & Figueiredo (2005, 2007), Nunes *et al.* (2008) and Villas Bôas *et al.* (2009). Two species are commonly described in Brazilian coral reef habitats: *Lithophyllum congestum* (Foslie 1898: 13) Foslie (1900: 20) and *Porolithon pachydermum* (Foslie 1904: 4) Foslie (1909: 57) neither species has been studied in a modern context based on the detailed anatomical analysis of the type with respect to modern collections. Our goal is thus to identify the species of crustose coralline algae that are common in the region of the Abrolhos archipelago.

Materials and methods

Material for this study was obtained from materials collected around the northeastern Brazilian coast, particularly from Abrolhos Marine National Park (Fig. 1), which includes an offshore archipelago. The archipelago is located between coordinates 17°57'–17°59' S and 38°41'–38°43' W, broadening the Brazilian continental shelf known as the Abrolhos Bank, to approximately 70 km from the continent. The archipelago consists of five islands: Santa Barbara, Redonda, Siriba, Sueste and Guarita. Additional material was provided by extensive sampling in Abrolhos Bank by Figueiredo (2005). In addition, we compared our data to data and materials collected from 1999 to 2009 that have been described in several regional publications (Figueiredo 1997, 2000, Villaça & Pitombo 1997, Figueiredo & Steneck 2002, Figueiredo 2005, Villas Bôas *et al.* 2005, Tâmega & Figueiredo 2007).

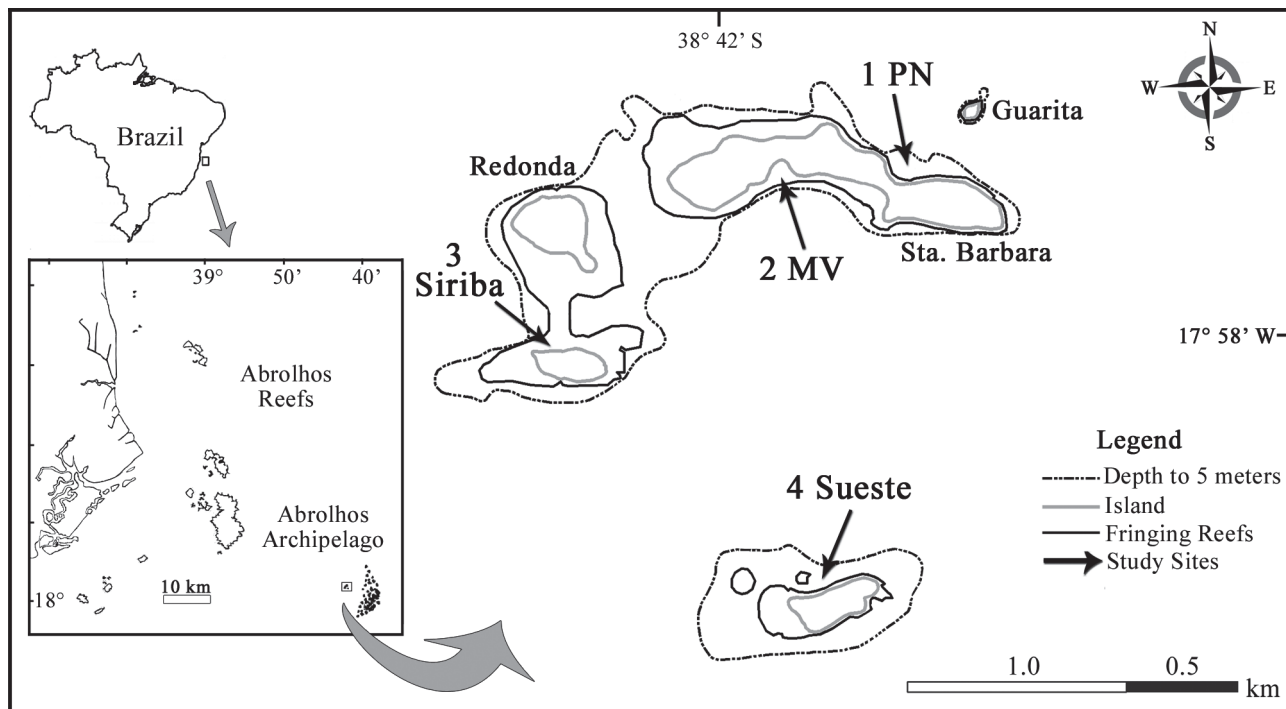


FIGURE 1. Archipelago of Abrolhos Marine National Park with study sites: 1—Porto Norte (PN), 2—Mato Verde (MV), 3—Siriba (Si) and 4—Sueste (Su).

Species of nongeniculate coralline algae were borrowed from collections taken by scuba diving or free diving in February, August, September, October and December of 2008 at reef crest and reef edge on the fringe reefs of

Abrolhos Archipelago in 1 to 8 m deep, south of Bahia, Brazil. The spatial distribution of these species was described in a previous study of Abrolhos Bank (Figueiredo 2005).

Samples of crustose coralline algae were removed with a hammer and spike and stored in nylon bags during the dive. The collected material was preserved in a solution of 4% formaldehyde in seawater. In the laboratory, we used a stereomicroscope (32–500 ×) and eyepiece with a millimeter reticle to observe the external morphological features of the thallus. Specimens with similar features were separated into form-functional groups (thin crust, thick crust and branched crust), following the classification of Steneck (1986). The samples were described according to the vegetative and reproductive features (Woelkerling 1988), and their growth forms were classified as encrusting and branched, following the classification of Woelkerling *et al.* (1993a). Histological sections were prepared following the methodology of Moura *et al.* (1997) with some modifications. Briefly, the samples were decalcified in nitric acid at 10%, immersed for 10 minutes in an alcohol dilution series (30, 60, 90 and 95%), embedded in historesin, cut with a rotary microtome and then stained with toluidine blue. The vegetative and reproductive structures were measured using an optical microscope eyepiece with a millimeter reticle, and the measurements were recorded in a spreadsheet. Photographs were taken by digital image capture with an optical microscope to illustrate the taxonomic features. For the identification of genera, Adey & Adey (1973), Woelkerling (1988), Irvine & Chamberlain (1994), Horta (2002) and Harvey *et al.* (2005) as well as specialized literature on the taxonomy of the group were consulted. The adopted taxonomic nomenclature followed that used for species in the tropical Atlantic (Littler & Littler 2000) because this is an ecological study.

For their identification, vegetative morphological features were considered, including the color of the thallus in the living alga, growth forms (encrusting, warty), edge (adherent or not, with entire forms, lobed or orbits on the surface), thickness of thallus, cell connections (secondary-pit or cell fusion), epithallial and perithallial cells (shape, size and number of layers), organization of the thallus (dimerous or monomerous), trichocytes (presence and arrangement), reproductive structures (tetraspores, bispores, uni or multiporate conceptacles), position of the thallus (elevated above the surface or sunken) and conceptacle shape (dimensions of the internal chambers).

Results

Our taxonomic analysis distinguished four species of nongeniculate coralline red algae: *Lithophyllum stictaeforme* (J.E. Areschoug) Hauck (Figs. 2–9), *Neogoniolithon atlanticum* Tâmega, Riosmena-Rodriguez, Mariath & Figueiredo *sp. nov.* (Figs. 10–15), *Porolithon pachydermum* (Foslie) Foslie (Figs. 16–24) and *Spongites fructiculosus* Kützing (Figs. 25–28). Comparison of the type materials to modern collections has showed that *L. congestum* is a heterotypic synonym of *L. stictaeforme*.

Subfamily **Lithophylloideae** Setchell 1943: 134

Lithophyllum stictaeforme (J.E. Areschoug) Hauck (1877: 292) (Figs. 2–9)

Basionym:—*Melobesia stictaeformis* Areschoug in Agardh (1852: 517).

Lectotype:—Designated and illustrated in Athanasiadis (1999: 738, fig. 1)

Type locality:—Mediterranean Sea (Athanasiadis 1999: 738, fig. 1)

Homotypic synonyms:—*Melobesia stictaeformis*, *Lithophyllum expansum* f. *stictaeforme* (Areschoug) Foslie (1901: 18).

Heterotypic synonyms:—*Melobesia frondosa* Dufour (1861: 39), *Lithophyllum expansum* f. *agariciforme* Hauck (1885: 269), *Lithophyllum bermudense* Foslie & M.A. Howe (1906: 132), *Dermatolithon bermudense* (Foslie & M. A. Howe) Foslie & M.A. Howe in Foslie (1909: 58), *Tenarea bermudensis* (Foslie & M.A. Howe) Adey (1970a: 6), *Titanoderma bermudense* (Foslie & M.A. Howe) Woelkerling, Y. M. Chamberlain & P.C. Silva (1985: 333), *Lithophyllum grandiusculum* (Montagne 1846: 138) Woelkerling, Penrose & Y.M. Chamberlain (1993b: 326), *Lithophyllum frondosum* (Dufour 1861: 39) G. Furnari, Cormaci & Alongi (1996: 117–121).

Nomenclature:—*Lithophyllum congestum* is a heterotypic synonym of *L. stictaeforme*. Thus, *L. stictaeforme*, as the older name, has taxonomic priority according to article 11 of the current botanical code (McNeill *et al.* 2011).

TABLE 1. Comparison of the characteristics of *L. stictaeforme* in this study to those from other works and closely related species. This study¹, Figueiredo & Steneck (2002)², Taylor (1960)³, Steneck & Adey (1976)⁴, Littler & Littler (2000)⁵, Adey *et al.* (1982)⁶, Verheij (1994)⁷, Nunes *et al.* (2008)⁸, Villas Bôas *et al.* (2009)⁹, Ringeltube & Harvey (2000)¹⁰, (nd) no data available, (*) data from specimens deposited in herbarium.

Features	<i>L. stictaeforme</i> Brazil ¹	<i>L. congestum</i> TRH	<i>L. congestum</i> Brazil ²	<i>L. congestum</i> Caribbean ³	<i>L. congestum</i> Caribbean ⁴	<i>L. congestum</i> Caribbean ⁵	<i>L. kotschyannum</i> Hawaii ⁶	<i>L. kotschyannum</i> Sulawesi ⁷	<i>L. stictaeforme</i> Brazil ⁸	<i>L. stictaeforme</i> Brazil ⁹	<i>L. tamiense</i> Australia ¹⁰
Position of the conceptacle in relation to thalli surface	Elevated	Elevated	Elevated	Elevated	Elevated	Elevated	Elevated	Elevated	Flat	Elevated	Elevated
Number of cell rows in conceptacle roof	6–8	6–8	nd	nd	6	nd	nd	5–10	5–7	5	5
Number of cell rows in conceptacle floor	13–16	13–17	nd	nd	nd	nd	nd	>15	11–12	14–15	8–10
Internal conceptacle height (µm)	149–193	157–185	nd	nd	65–108	80–210	80–210	175–225	105–182	150–160	180
External conceptacle diameter (µm)	300–360	290–340	200–600	300	nd	nd	350–450	nd	nd	nd	nd
Internal conceptacle diameter (µm)	291–302	273–305	nd	nd	194–302	216–300	250–370	300–400	202–262	230–275	260–400

TABLE 2. Comparison of the characteristics of *N. atlanticum* in this study to those from other works and closely related species. This study¹, Mateo-Cid & Pedroche (2004)², Woelkerling *et al.* (1993b)³, Woelkerling (1996)⁴, Penrose (1992)⁵, Adey *et al.* (1982)⁶, Lawson & John (1982)⁷, Kato *et al.* (2013)⁸ (nd) no data available.

Features	<i>N. atlanticum</i> Brazil ¹	<i>N. solubile</i> (lectotype) Porto Rico ²	<i>M. brassica-florida</i> (lectotype) South Africa ³	<i>N. brassica-florida</i> (type) Egypt ⁴	<i>N. fosliei</i> Australia ⁵	<i>N. fosliei</i> Mexico ²	<i>N. fosliei</i> Hawaii ⁶	<i>N. clavacymosum</i> Hawaii ⁶	<i>N. rufum</i> Hawaii ⁶	<i>N. mamillare</i> Africa ⁷	<i>N. trichotomum</i> Japan ⁸
Trichocyte arrangement	Absent	Solitary/ groups	Solitary/ groups	Solitary/ groups	Solitary/ groups	Solitary/ groups	Solitary	Solitary	Solitary/ groups	Solitary/ groups	Scattered
Position of the conceptacle in relation to thalli surface	Elevated	Elevated	Elevated	Elevated	Elevated	Elevated	Elevated	Elevated	Elevated	Elevated	Flush
Number of cell rows in conceptacle roof	7–8	nd	8–15	10–25	10–25	nd	nd	nd	nd	nd	nd
Number of cell rows in conceptacle floor	16–17	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd
Internal conceptacle height (µm)	217	180–300	nd	370–820	370–820	200–340	90–190	50–110	50–100	sd	nd
External conceptacle diameter (µm)	300–360	nd	nd	nd	nd	nd	700–1500	450–600	200–400	nd	nd
Internal conceptacle diameter (µm)	416–419	540–800	355–519	590–820	590–820	550–900	240–900	200–500	80–300	400–700	nd

TABLE 3. Comparison of the characteristics of *P. pachydermum* in this study to those from other works and closely related species. This study¹, Figueiredo & Steneck (2002)², Taylor (1960)³, Littler & Littler (2000)⁴, Adey *et al.* (1982)⁵, Lawson & John (1982)⁶, Keats & Chamberlain (1994)⁷, Woelkerling (1996)⁸, Ringeltaube & Harvey (2000)⁹, Mendoza-González *et al.* (2009)¹⁰, (nd) no data available, (*) data from specimens deposited in herbarium and (**) data obtained from published figures.

Features	<i>P. pachydermum</i> Brazil ¹	<i>P. pachydermum</i> (Lectotype)	<i>H. onkodes</i> (Lectotype)	<i>P. pachydermum</i> Brazil ^{2*}	<i>P. pachydermum</i> Caribbean ³	<i>P. pachydermum</i> Caribbean ⁴	<i>P. onkodes</i> Hawaii ⁵	<i>P. onkodes</i> Africa ⁶	<i>H. onkodes</i> South Africa ⁷	<i>H. onkodes</i> Australia ⁸	<i>H. onkodes</i> Australia ⁹	<i>H. onkodes</i> Mexico ¹⁰	<i>H. pachydermum</i> Mexico ¹⁰
Trichocyte arrangement	Solitary/ groups	Solitary/ groups	Solitary/ groups	Groups	Groups	Groups	Groups	nd	Groups	Groups	Groups	Solitary/ groups	Solitary
Position of the conceptacle in relation to thalli surface	Flat/ elevated	Flat	Flat	Elevated	Elevated	nd	Elevated	nd	Flat/ elevated	Elevated	Elevated	Flat/ elevated	Flat/ elevated
Number of cell rows in conceptacle roof	4–5	7–8	7–9	nd	nd	nd	nd	nd	5–6 **	3–6	6	4–8	3–4
Number of cell rows in conceptacle floor	12–14	14–16	15–16	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd
Internal conceptacle height (µm)	85–151	131–159	135–162	nd	nd	nd	30–140	68–85	60–130	109–150	nd	36–180	30–165
External conceptacle diameter (µm)	150–210	150–230	156–241	240–400	150–250	150–250	240–300	nd	130	nd	nd	nd	nd
Internal conceptacle diameter (µm)	153–199	168–233	165–249	200	nd	nd	110–230	165–210	115–250	164–250	130–260	141–255	63–255

TABLE 4. Comparison of the characteristics of *S. fruticosus* in this study to those from other works and closely related species. This study¹, Penrose (1991)², Basso & Rodondi (2006)³, Woelkerling (1996)⁴, Ringeltaube & Harvey (2000)⁵, Chamberlain (1993)⁶, Harvey *et al.* (2005)⁷, (nd) no data available.

Features	<i>S. fruticosus</i> Brazil ¹	<i>S. fruticosus</i> (lectotype) Mediterranean ²	<i>S. fruticosus</i> Mediterranean ³	<i>S. fruticosus</i> Australia ⁴	<i>S. fruticosus</i> Australia ⁵	<i>S. yendoii</i> South Africa ⁶	<i>S. yendoii</i> Australia ^{6,7}
Position of the conceptacle in relation to thalli surface	Elevated	Elevated	Elevated	Elevated	Elevated	Elevated	Elevated
Number of cell rows in conceptacle roof	5–12	8–12	nd	8–12	8–12	nd	3–5
Number of cell rows in conceptacle floor	13–18	nd	nd	nd	nd	nd	nd
Internal conceptacle height (µm)	160–200	275–410	130–250	275–410	nd	62–117	109–185
External conceptacle diameter (µm)	150–300	nd	nd	nd	nd	nd	nd
Internal conceptacle diameter (µm)	280–300	350–595	320–480	350–595	230–560	147–207	164–232 120–255

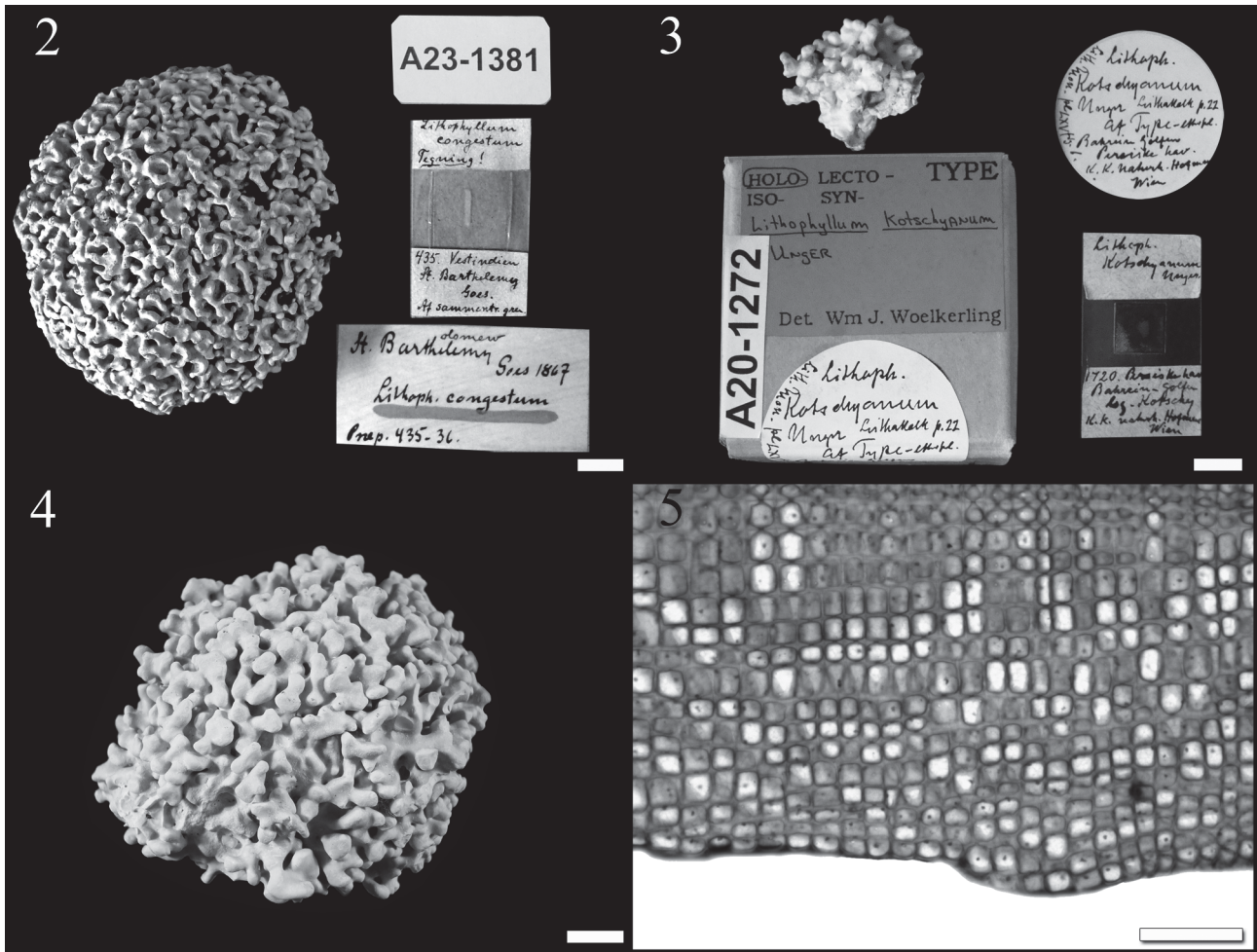


FIGURE 2. External morphology of *Lithophyllum congestum* (lectotype). **FIGURE 3.** External morphology of *L. kotschyianum* (lectotype). **FIGURE 4.** External morphology of *L. congestum* from Abrolhos. **FIGURE 5.** Longitudinal section of *L. congestum* from Abrolhos showing the dimerous cellular organisation. Scales: (2–4) 1 cm, (5) 50 μ m.

Description:—The plants are nongeniculate, with a branched growth form (Fig. 2); the colour could not be observed in the type material of *L. congestum* from THR A23-1381. The thallus is 1.75 cm thick, with an incrusting surface and an adherent margin with dense, irregular, elongate, anastomosed branches (Fig. 2), which are 6–14 mm high and 3–7 mm in diameter in the type material of *L. congestum* from THR A23-1381. The plants are nongeniculate, with a branched growth form (Fig. 3); the color could not be observed in the type material of *Lithophyllum kotschyianum* Unger (1858: 22) from THR A20-1272. The plants are nongeniculate, with a branched growth form (Fig. 4) and color ranging from wine to dark brown. The thallus is 200–400 μ m thick, with an incrusting surface and adherent margin with irregular, elongate, anastomosed branches (Fig. 4), which are 8–16 mm high and 4–9 mm in diameter. The internal thallus construction is dimerous (Fig. 5). There is one layer of rounded, pigmented epithallial cells that is with 3–6 μ m high and 5–10 μ m in diameter (Fig. 6). The internal thallus construction ranges from monomerous coaxial to dimerous in the type material of *L. congestum* from THR A23-1381 (Fig. 7). Sub-epithallial cells are square-rectangular in shape 13–19 μ m high and 9–12 μ m in diameter (Fig. 6). Perithallial cells are 8–12 μ m high and 6–8 μ m in diameter. The basal region comprises cylindrical cells that are 11–14 μ m high and 8–10 μ m in diameter. The cells of adjacent filaments are joined by secondary pit connections (Fig. 6). The trichocytes are isolated or present in groups with nine cells arranged horizontally, and they are 38–47 μ m high and 10–11 μ m in diameter (Fig. 6). Mature conceptacles are uniporate and elevated, with 6–8 cell layers in the conceptacle roof in the type material of *L. congestum* from THR A23-1381 (Fig. 8). Mature bisporangial conceptacles are uniporate and elevated, with 6–8 cell layers in the conceptacle roof (Fig. 9). The cells surrounding the conceptacle pore are arranged vertically in the type material of *L. congestum* from THR A23-1381 (Fig. 8). The cells surrounding the conceptacles pore are arranged vertically (Fig. 9). The external diameter of the conceptacles is 300–360 μ m. The conceptacle internal chamber is 157–185 μ m high and 273–305 μ m in diameter, with a central

columella in the type material of *L. congestum* from THR A23-1381 (Fig. 8). The conceptacle internal chamber is 149–193 μm high and 291–302 μm in diameter, with a present central columella (Fig. 9). The conceptacle chamber floor is 13–17 cell layers below the surrounding thallus surface in the type material of *L. congestum* from THR A23-1381 (Fig. 8). The conceptacle chamber floor is situated 13–16 cell layers below the surrounding thallus surface (Fig. 9). Mature zonate bispores that are 51–82 μm high and 28–46 μm in diameter are located on the periphery of the conceptacles (Fig. 9). Gametangial plants are not observed.

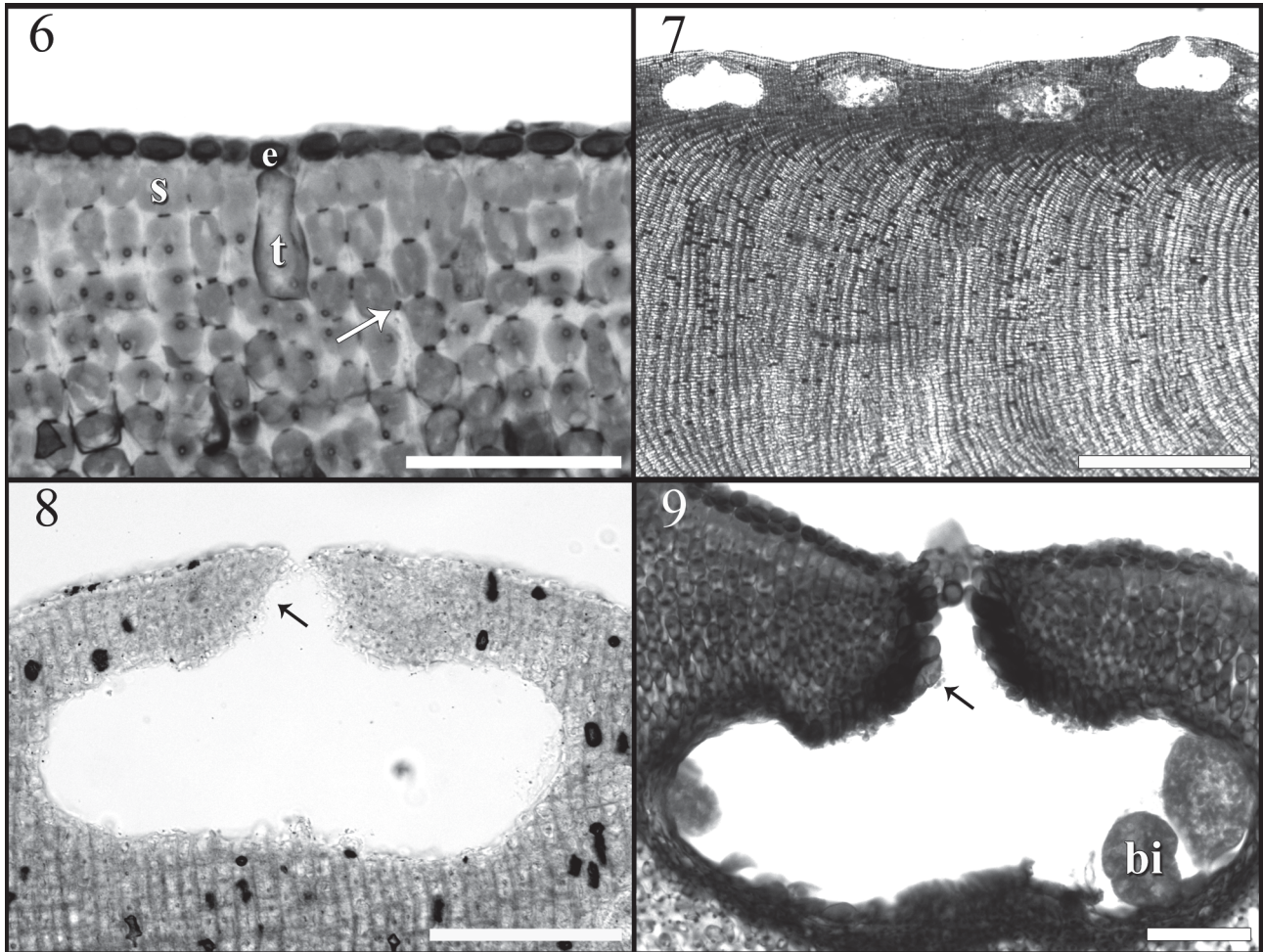


FIGURE 6. Longitudinal section of *Lithophyllum congestum* from Abrolhos showing the epithelial cells (e), sub-epithelial cells (s), trichocytes (t) and secondary pit connections (white arrow). **FIGURE 7.** Longitudinal section of *L. congestum* (Lectotype) showing the coaxial cellular organisation. **FIGURE 8.** Longitudinal section of *L. congestum* (lectotype) showing the empty conceptacles and cells around the pore (black arrow). **FIGURE 9.** Longitudinal section of *L. congestum* from Abrolhos showing the conceptacles with bispore (bi) and vertically arranged cells around the pore (black arrow). Scales: (6–9) 50 μm .

Remarks:—The conceptacles internal chamber is 149–193 μm high and 291–302 μm in diameter. The conceptacle roof consists of 6–8 cell layers, and the conceptacle floor consists of 13–16 cell layers. Comparisons to the type material of *L. congestum* revealed it to have conceptacle anatomy and measurements similar to those of *L. kotschyianum* and *L. stictaeforme* (Table 1); however, the type specimen of *L. kotschyianum* has an incomplete conceptacle, preventing the use of this older name.

Ecological observations:—Algae are found from the reef crest to the base of the reef at a depth of 4 m in fringe reefs.

Geographical distribution:—Adriatic Sea (Munda 1979), Australia (Woelkerling & Campbell 1992, Womersley 1996, Huisman 2000, Ringeltaube & Harvey 2000, Phillips 2002), Bermuda (Taylor 1960), Brazil (Villas Bôas *et al.* 2009, Creed *et al.* 2010), Canary Islands (John *et al.* 2004), Caribbean (Littler & Littler 2000), Chile (Ramírez & Santelices 1991), Colombia (Díaz-Pulido & Díaz-Ruiz 2003), Corsica (Coppejans 1979, Rodríguez Prieto *et al.* 1993, Furnari *et al.* 1996), Cuba (Suárez 2005), France (Furnari *et al.* 1996), Greece (Gerloff & Geissler 1974; Tsirika & Haritonidis 2005), Hispaniola (Betancourt & Herrera-Moreno 2001), Israel

(Einav 2007), Italy (Giaccone 1969, Cecere *et al.* 1996, Furnari *et al.* 1996, 1999, 2003, Rindi *et al.* 2002, Serio *et al.* 2006), Lesser Antilles (Taylor 1960), Madeira Island (Neto *et al.* 2001, John *et al.* 2004), Malta (Cormaci *et al.* 1997), New Zealand (Woelkerling & Campbell 1992, Bostock & Holland 2010), Puerto Rico (Taylor 1960, Ballantine *et al.* 2004), Salvage Island (John *et al.* 2004), Sardinia (Furnari *et al.* 2003), Senegal (John *et al.* 2004), Spain (Gallardo *et al.* 1985, Morais e Silva *et al.* 2008), Tanzania (Oliveira *et al.* 2005), Trinidad and Tobago (Duncan & Lee Lum 2006), Trinidad (Taylor 1960, Richardson 1975), Turkey (Taskin *et al.* 2008), United States (Taylor 1960), Virgin Islands (Taylor 1960).

Distribution in the study sites:—Abrolhos Archipelago in Brasil (Figueiredo & Steneck 2002, Tâmeaga & Figueiredo 2007, Creed *et al.* 2010), Abrolhos Archipelago at Santa Bárbara Island (18° 09' 09" S–38° 53' 27" W and 18° 11' 08" S – 38° 43' 24" W) and Siriba island (18° 00' 44" S–38° 53' 01" W), Chapeirão at Abrolhos Archipelago (18° 00' 14" S – 38° 42' 13" W), Parcel dos Abrolhos (17° 58' 51" S–38° 39' 35" W and 18° 00' 46" S – 38° 38' 22" W), Timbebas Reefs (17° 30' 22" S–39° 00' 47" W), Lixa Reefs (17° 40' 56" S 38° 57' 59" W), Areia Reefs (17° 36' 19" S – 39° 03' 03" W) and Pedra Leste (17° 47' 11" S–39° 02' 54" W).

Examined material:—Sample 1: 18° 09' 09" S–38° 53' 27" W, coll. *F.T. de S. Tâmeaga, M.A. de O. Figueiredo and R. Mariath, 31-8-2008*, RB 490643; Sample 2: 18° 11' 08" S–38° 43' 24" W, coll. *F.T. de S. Tâmeaga, 10-2-2008*, RB 490644; Sample 3: 18° 00' 44" S–38° 53' 01" W, coll. *F.T. de S. Tâmeaga, 27-10-2008*, R 209894.

Subfamily **Neogoniolithoideae** Kato et Baba 2011

***Neogoniolithon atlanticum* Tâmeaga, Riosmena-Rodriguez, Mariath & M. Figueiredo, sp. nov. (Figs. 10–15)**

Neogoniolithon atlanticum differs from related species of *Neogoniolithon* Setchell & L.R. Mason (1943: 89) because of the following features: (1) 7–8 cells in the tetrasporangial conceptacle roof, and (2) 16–17 cells in the tetrasporangial conceptacle floor.

Type:—BRAZIL. Abrolhos Archipelago at Porto Norte in Santa Bárbara Island, Bahia State, Northeastern of Brazil, 18° 09' 09" S, 38° 53' 27" O, coll. *F.T. de S. Tâmeaga, 31-8-2008*. Holotype: RB! 490645 (Jardim Botânico do Rio de Janeiro, Rio de Janeiro, Brazil).

Etymology:—The name *atlanticum* is derived from the area where the species was found for the first time.

Description:—The plants are nongeniculate, with an incrusting growth form (Fig. 10), ranging in colour from pink to brown. The surface is irregular, and the thallus is 500–600 µm thick with an adherent margin. The internal thallus construction is monomerous (Fig. 11). There is a one single layer of pigmented, rectangular epithallial cells that are 4 µm high and 6–7 µm in diameter (Fig. 12). Rectangular sub-epithallial cells are 5–7 µm high and e 4–6 µm in diameter (Fig. 12). Rectangular perithelial cells are 6 µm high and 5 µm in diameter. The ventral region comprises cylindrical cells that are 7–12 µm high and 15–29 µm in diameter. The cells of adjacent filaments are joined by cell-fusion (Fig. 12). Mature tetrasporangial conceptacles are uniporate and elevated above the surface of the thallus, with 7–8 cell layers in the conceptacle roof (Fig. 13). The cells surrounding the conceptacle pore are arranged horizontally (Fig. 13). The external diameter of the conceptacle chamber is 300–360 µm. The conceptacle internal chamber is 217 µm high and 416–419 µm in diameter, with a present central columella (Fig. 13). The conceptacle chamber floor is 16–17 cell layers below the surrounding thallus surface (Fig. 13). The mature zonate tetraspore is 64–113 µm high and 20–47 µm in diameter and is located peripheral to the conceptacle (Fig. 13).

Mature carpogonial conceptacles are uniporate and elevated above the surface of the thallus, with 11–18 cell layers in the conceptacle roof (Fig. 14). The cells surrounding the conceptacle pore are arranged horizontally (Fig. 14). The external diameter of the conceptacle is 300–360 µm. The conceptacle internal chamber is 276–515 µm high and 570–890 µm in diameter, with a central columella (Fig. 14). The conceptacle chamber floor is 16–21 cell layers below the surrounding thallus surface (Fig. 14). Mature carpospores that are 47–113 µm high and 20–55 µm in diameter are located on the conceptacle floor (Fig. 15). Trichocytes are not observed.

Ecological observations:—This species was found at the base of the reef, at a depth of 4 m in the fringe reefs.

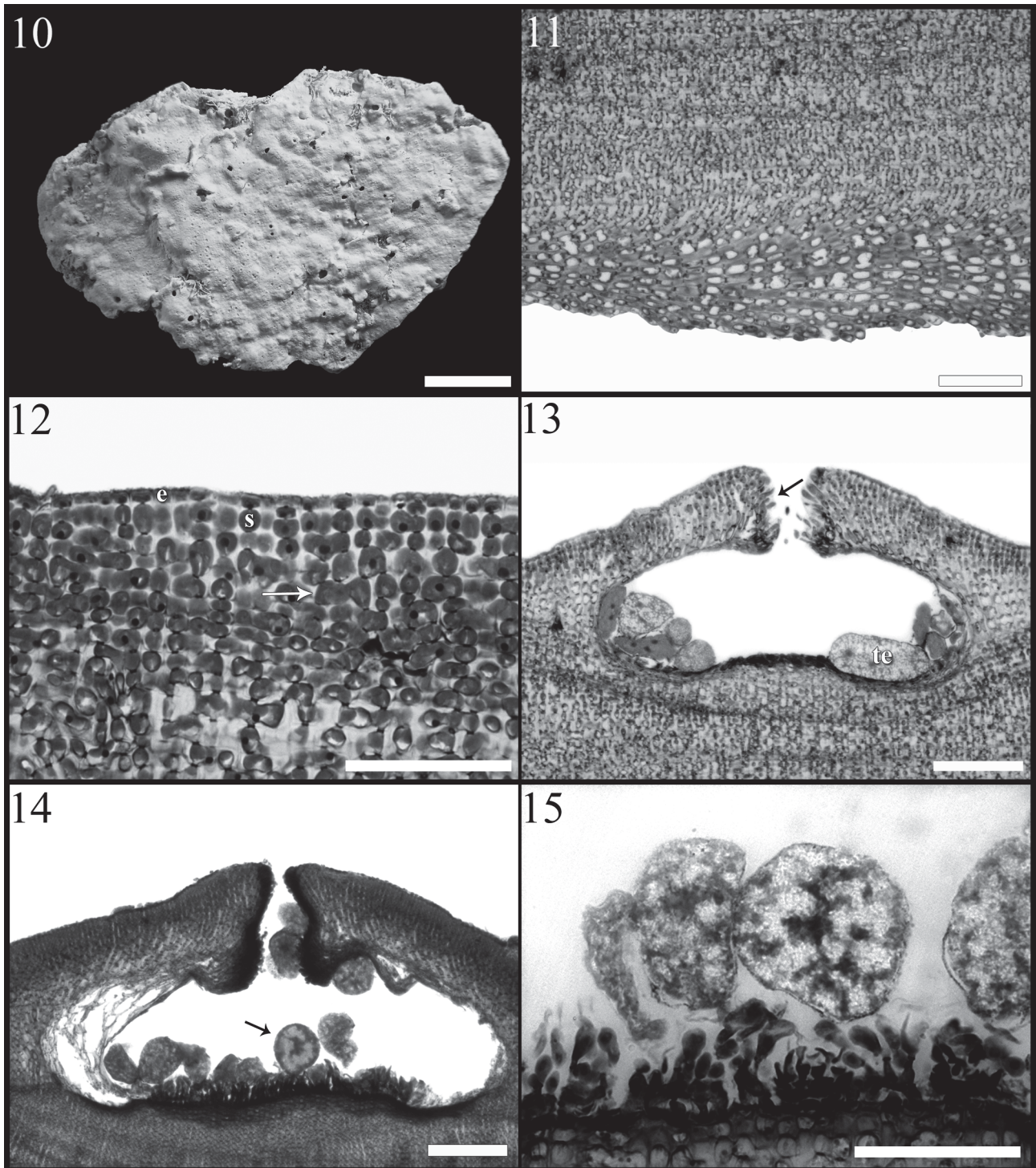


FIGURE 10. External morphology of *Neogoniolithon atlanticum* sp. nov. **FIGURE 11.** Longitudinal section of *N. atlanticum* sp. nov. showing a monomerous cellular organisation. **FIGURE 12.** Longitudinal section of *N. atlanticum* sp. nov. showing the epithallial cells (e), sub-epithallial cells (s), and cell fusion (white arrow). **FIGURE 13.** Longitudinal section of *N. atlanticum* sp. nov. showing the conceptacles with tetraspores (te) and cells around the pore arranged horizontally (black arrow). **FIGURE 14.** Longitudinal section of *N. atlanticum* sp. nov. showing the conceptacles with carpogonia (black arrow). **FIGURE 15.** Longitudinal section of *N. atlanticum* sp. nov. showing the carpospore in detail. Scales: (10) 1 cm; (11–14) 100 μ m, (12,15) 50 μ m.

Subfamily **Porolithoideae** Kato et Baba 2011

Porolithon pachydermum (Foslie) Foslie (1909: 57) (Figs. 16–24)

Basionym:—*Lithophyllum onkodes* f. *pachydermum* Foslie (1904: 5).

Homotypic synonyms:—*Lithophyllum pachydermum* (Foslie) Adey & Lebednik (1967: 47).

Lectotype:—TRH, A26-1553, St. Croix, U.S. Virgin Islands (West Indies); Ørsted no. 548. Previous references to typification were by Adey & Lebednik (1967) (as *Lithophyllum pachydermum*) and Adey (1970b) (as *Porolithon pachydermum*).
Isolectotype: BM (as *Lithophyllum pachydermum*).

Type locality:—St. Croix, U.S. Virgin Islands.

Description:—The plants are nongeniculate, with an incrusting growth form (Fig. 16); colour was not observable in the type material of *P. pachydermum* from THR A26-1553. The plants are nongeniculate, with an incrusting growth form (Fig. 17) and range in colour from pink to brown. The surface of the thallus is flat and 200–500 µm thick with an adherent margin. The internal thallus construction is pseudo-parenchymatous (Fig. 19). There is one layer of pigmented, rounded epithallial cells that are 6–12 µm high and 4–11 µm in diameter (Fig. 21). The sub-epithallial cells in type material of *P. pachydermum* from THR A26-1553 are cylindrical, 10–13 µm high and 4–7 µm in diameter (Fig. 20). The sub-epithallial cells are cylindrical, 10–14 µm high and 4–7 µm in diameter (Fig. 21). The perithallial cells are cylindrical, 7–12 µm high and 5–7 µm in diameter. The basal region comprises cylindrical cells that are 12–24 µm high and 5–9 µm in diameter (Fig. 19). The cells of adjacent filaments are joined by cell-fusion in the type material of *P. pachydermum* from THR A26-1553 (Fig. 20). Trichocytes are prominent on the surface of the thallus and are solitary or in groups of three or more, 22–30 µm high and 10–15 µm in diameter in the type material of *P. pachydermum* from THR A26-1553 (Figs 18, 20). The cells of adjacent filaments are joined by cell-fusion (Fig. 21). Trichocytes are prominent on the surface of the thallus, and are solitary or in groups of three or more, 24–30 µm high and 8–9 µm in diameter (Fig. 21). Mature conceptacles are uniporate and flat in the surface of the thallus, with 7–8 cell layers in conceptacle roof; they are sunken into the surface of the thallus when senescent in type the material of *P. pachydermum* from THR A26-1553 (Figs. 18, 22). Mature conceptacles are uniporate and flat in the surface of the thallus, with 7–9 cell layers in the conceptacle roof in the type material of *Hydrolithon onkodes* (Heydrich 1897: 6) D. Penrose & Woelkerling (1992: 83) from THR A26-1494 (Fig. 23). They are sunken into the surface of the thallus when senescent. Mature tetrasporangial conceptacles are uniporate and flat in the surface of the thallus, with 4–5 cell layers in the conceptacle roof (Fig. 24), and they are sunken into the surface of the thallus when senescent. The cells surrounding the conceptacle pore are arranged vertically in the type material of *P. pachydermum* from THR A26-1553 (Fig. 22). The cells surrounding the conceptacle pore are arranged vertically in the type material of *H. onkodes* from THR A26-1494 (Fig. 23). The cells surrounding the conceptacle pore are arranged vertically (Fig. 24), with elongated cells within the pore (Fig. 24). The external diameter of the conceptacle is 150–210 µm. The conceptacle internal chamber is 131–159 µm high and 168–233 µm in diameter in type the material of *P. pachydermum* from THR A26-1553 (Fig. 22) and 135–162 µm high and 165–249 µm in diameter in the type material of *H. onkodes* from THR A26-1494 (Fig. 23). The conceptacle internal chamber is 85–151 µm high and 153–199 µm in diameter (Fig. 24). The conceptacle chamber floor is 14–16 cell layers below the surrounding thallus surface in the type material of *P. pachydermum* from THR A26-1553 (Fig. 22) and 15–16 cell layers below the surrounding thallus surface in the type material of *H. onkodes* from THR A26-1494 (Fig. 23). The conceptacle chamber floor is situated into 12–14 cell layers below the surrounding thallus surface (Fig. 24). Mature zonate tetraspores are 38–56 µm high and 31–36 µm in diameter and are located on the conceptacle floor (Fig. 24). Gametangial plants are not observed.

Remarks:—The conceptacle internal chamber is 85–151 µm high and 153–199 µm in diameter. Mature tetrasporangial conceptacles have 4–5 cell layers in the roof and their chamber floor is 12–14 cell layers below the surrounding thallus surface.

Ecological observations:—The algae are found in fringe reefs, from the crest to the base of these reefs at a depth of 4 m, and are commonly associated with *Dendropoma irregulare* (Mollusca: Vermetidae).

Geographical distribution:—Abrolhos Archipelago in Brazil (Figueiredo 1997, Figueiredo & Steneck 2002, Tâmega & Figueiredo 2007), Bahamas, Barbados, Greater and Lesser Antilles, Jamaica, Puerto Rico, Virgins Islands, in the Caribbean (Taylor 1960, Littler & Littler 2000), Belize (Norris & Bucher 1982), Colombia (Díaz-Pulido & Díaz-Ruíz 2003), Cuba (Suárez 2005), Mexico (Mendoza-González & Mateo-Cid 1985).

Distribution in the study sites:—Abrolhos Archipelago at Santa Bárbara island (18° 09' 09" S–38° 53' 27" W and 18° 11' 08" S–38° 43' 24" W), Siriba island (18° 00' 44" S–38° 53' 01" W) and Sueste island (18° 06' 14" S–38° 57' 04" W), Chapeirão at Abrolhos Archipelago (17° 54' 25" S–38° 41' 25" W and 18° 00' 14" S–38° 42' 13" W), Parcel dos Abrolhos (17° 58' 51" S–38° 39' 35" W and 18° 00' 46" S–38° 38' 22" W), Timbebas Reef

(17°28'42"S–39°01'40"O, 17°30'22"S–39°00'47"O and 17°27'36"S–39°01'55"O), Lixa Reef (17° 40' 56" S–38° 57' 59" W), Areia Reef (17° 36' 19" S–39° 03' 03" W) and Pedra Leste (17° 47' 11" S–39° 02' 54" W).

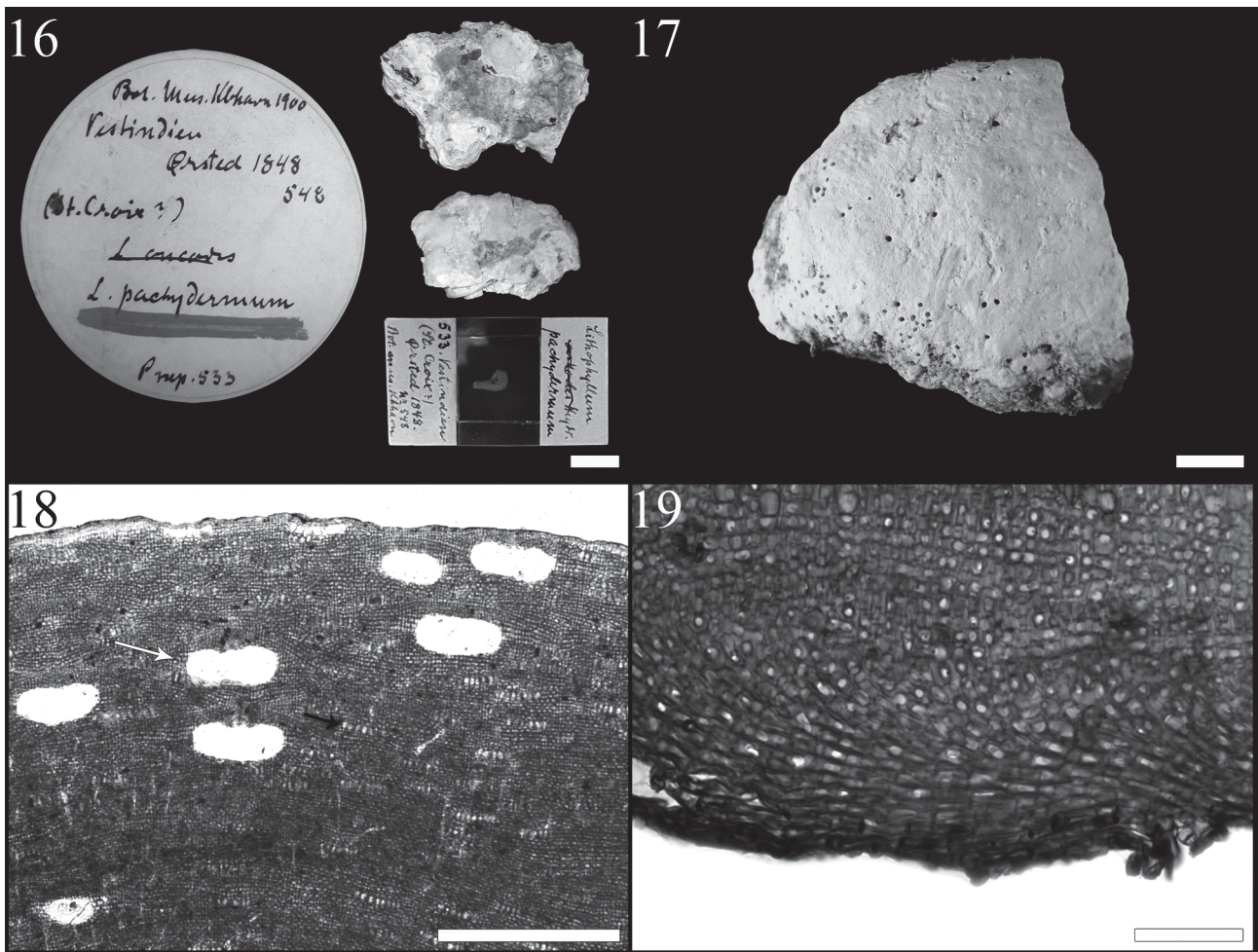


FIGURE 16. External morphology of *Porolithon pachydermum* (lectotype). **FIGURE 17.** External morphology of *P. pachydermum* from Abrolhos. **FIGURE 18.** Longitudinal section of *P. pachydermum* (lectotype) showing empty conceptacles (white arrow) and trichocyte field (black arrow) sunken in the thallus. **FIGURE 19.** Longitudinal section of *P. pachydermum* from Abrolhos showing a pseudo-parenchymatous cellular organisation. Scales: (16–17) 1 cm, (18–19) 50 µm.

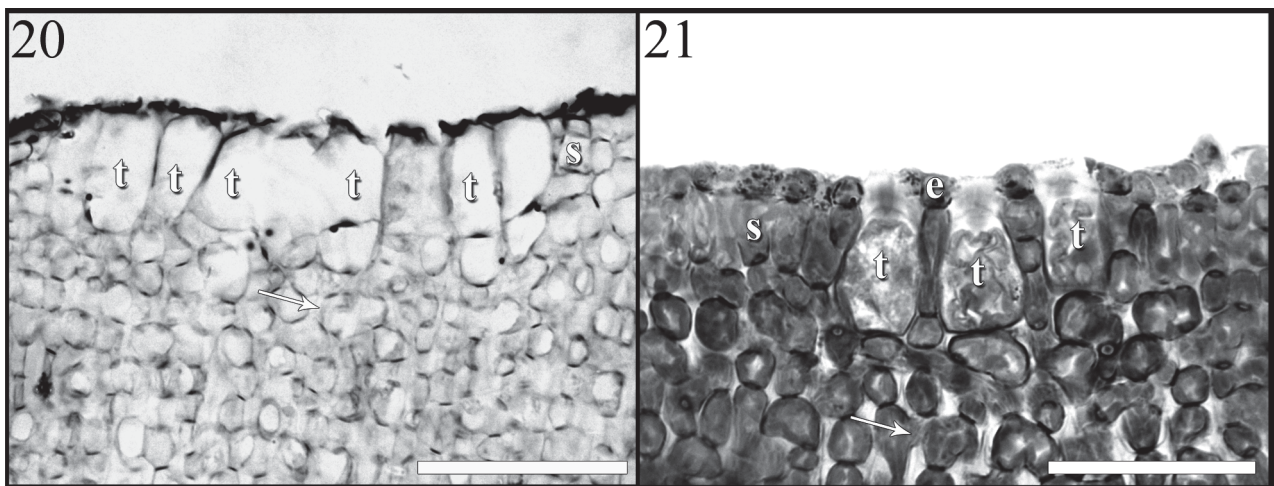


FIGURE 20. Longitudinal section of *Porolithon pachydermum* (lectotype) showing the sub-epithallial cells (s), trichocyte field (t) and cell fusion (white arrow). **FIGURE 21.** Longitudinal section of *P. pachydermum* from Abrolhos showing the epithallial cells (e), sub-epithallial cells (s), trichocyte field (t) and cell fusion (white arrow). Scales: (20–21) 50 µm.

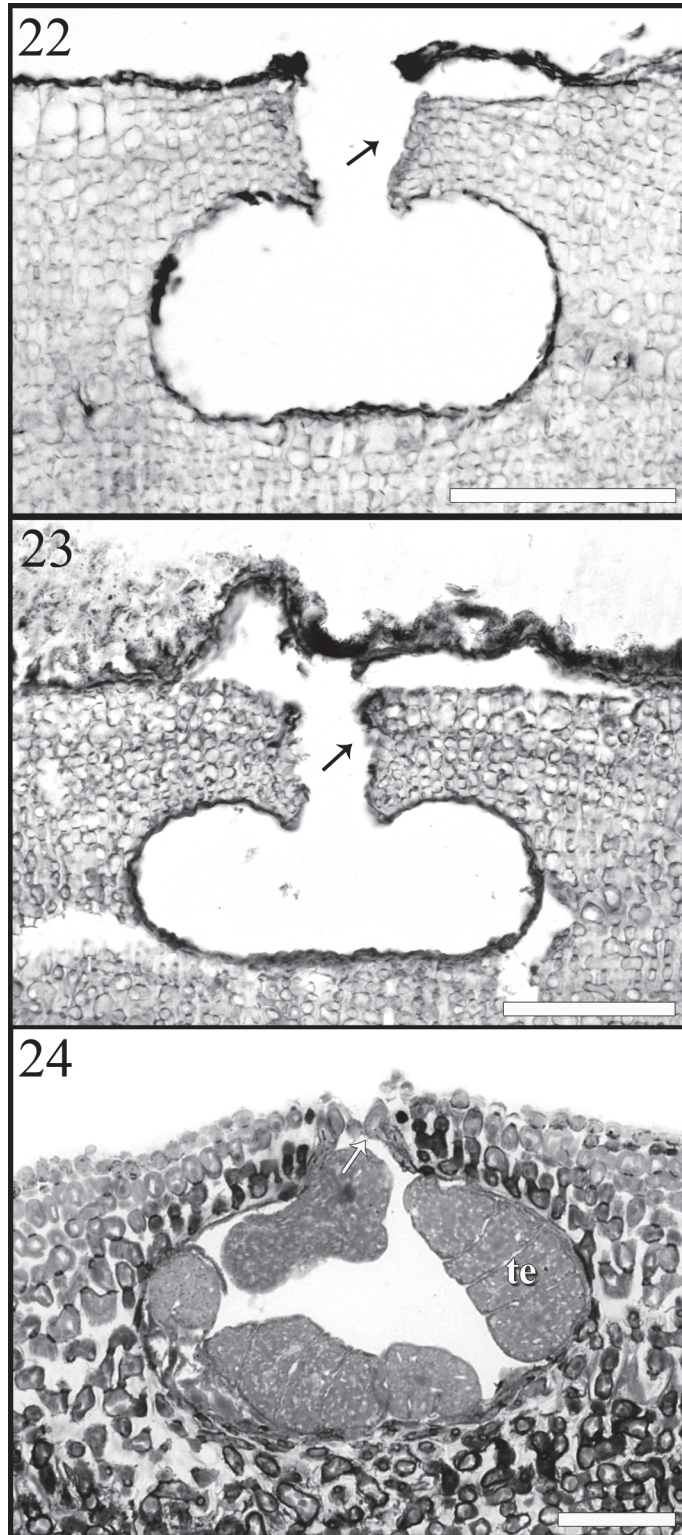


FIGURE 22. Longitudinal section of *Porolithon pachydermum* (lectotype) showing the empty conceptacles, with cells around the pore arranged vertically (black arrow). **FIGURE 23.** Longitudinal section of *Hydrolithon onkodes* (lectotype) showing the empty conceptacles, with cells around the pore arranged vertically (black arrow). **FIGURE 24.** Longitudinal section of *P. pachydermum* from Abrolhos showing the conceptacles with tetraspores (te), with cells around the pore arranged vertically (white arrow). Scales: (22–24) 50 μ m.

Examined material:—Sample 1: 18° 09' 09" S–38° 53' 27" W, coll. *F.T. de S. Tâmega, M.A. de O. Figueiredo and R. Mariath*, 31-8-2008, RB 490648; Sample 2: 18° 11' 08" S–38° 43' 24" W, coll. *F.T. de S. Tâmega*, 1-9-2008, RB 490649; Sample 3: 18° 00' 44" S–38° 53' 01" W, coll. *F.T. de S. Tâmega, M.A. de O. Figueiredo and R. Mariath*, 31-8-2008, R 209893.

Subfamily **Mastophoroideae** Setchell *sensu lato*

Spongites fruticosus Kützing (1841: 33) (Figs. 25–28)

Homotypic synonyms:—*Melobesia fruticulosa* (Kützing) Decaisne (1842: 126), *Lithothamnion fasciculatum* f. *fruticosum* (Kützing) Hauck (1883: 274), *Lithothamnion fruticosum* (Kützing) Foslie (1895: 46), *Paraspora fruticulosa* (Kützing) Heydrich (1900: 315).

Heterotypic synonyms:—*Lithothamnion ramulosum* Philippi (1837: 388), *Spongites stalactitica* Kützing (1841: 33), *Spongites ramulosus* (Philippi) Kützing (1869: 35), *Lithothamnion meneghianum* Vinassa (1892: 57), *Goniolithon verrucosum* Foslie (1900: 24–25), *Lithophyllum verrucosum* (Foslie) Foslie (1901: 21), *Neogoniolithon verrucosum* (Foslie) Adey (1970b: 10).

Lectotype:—L (Rijksherbarium, Leiden, Netherlands L943.8.134).

Type locality:—Mediterranean Sea (Silva *et al.* 1996).

Description:—The plants are nongeniculate, with warty growth forms (Fig. 25), and range in colour from pink to brown. The surface is irregular, and the thallus is 217–2000 µm thick with an adherent margin. The internal thallus construction is pseudo-parenchymatous (Fig. 26). There is one layer of pigmented, rounded epithallial cells that are 5–8 µm high and 7–10 µm in diameter (Fig. 27). The sub-epithallial cells are cylindrical, 8–13 µm high and 6–9 µm in diameter (Fig. 27). The perithallial cells are cylindrical, 6–7 µm high and 6–13 µm in diameter. The basal region comprises rectangular cells that are 12–27 µm high and 4–11 µm in diameter. The cells of adjacent filaments are joined by cell-fusion (Fig. 27). Trichocytes are prominent on the surface of the thallus or sunken, solitary or in groups of nine or more, arranged horizontally, with 28–37 µm high and 9–17 µm in diameter (Fig. 27). Mature tetrasporangial conceptacles are uniporate and elevated above the surface of thallus with 5–12 cell layers in the conceptacle roof (Fig. 28). The cells surrounding the conceptacle pore are arranged horizontally (Fig. 28). The external diameter of the conceptacle is 150–300 µm. The conceptacle internal chamber is 160–200 µm high and 280–300 µm in diameter with a present central columella and paraphyses (Fig. 28). The conceptacles chamber floor is 13–18 cell layers below the surrounding thallus surface (Fig. 28). Mature zonate tetraspores are 26–100 µm high and 21–48 µm in diameter, located peripherally or on the conceptacle floor (Fig. 28). Gametangial plants are not observed.

Remarks:—The conceptacles internal chamber is 160–200 µm high and 280–300 µm in diameter with a present central columella and paraphyses. The mature tetrasporangial conceptacles with 5–12 cell layers in the conceptacle roof, and their chamber floor is 13–18 cell layers below the surrounding thallus surface

Ecological features:—This alga was collected from fringe reefs, between the reef crest and the base of the reef at a depth of 4 m. This report represents the first record of this species in the southwest Atlantic.

Geographical distribution:—Adriatic Sea (Babbini & Bressan 1997), Algeria (Babbini & Bressan 1997), Australia and New Zealand (Penrose & Woelkerling 1992, Penrose 1996, Ringeltube & Harvey 2000, Phillips 2002, Bostock & Holland 2010), Balearic Islands (Babbini & Bressan 1997), Canary Islands (Woelkerling *et al.* 1998), Cape Verde Islands (John *et al.* 2004), Costa Rica (Fernández-Gracia *et al.* 2011), Corsica (Babbini & Bressan 1997), France (Babbini & Bressan 1997), Greece (Athanasiadis 1987, Babbini & Bressan 1997), India (Silva *et al.* 1996, Sahoo *et al.* 2001), Ireland (Guiry 1978), Italy (Cecere *et al.* 1996, Babbini & Bressan 1997, Furnari *et al.* 1999, Rindi *et al.* 2002, Basso & Rodondi 2006, Serio *et al.* 2006), Japan (Yoshida 1998), Korea (Lee & Kang 2001), Laccadive Island (Silva *et al.* 1996), Libya (Babbini & Bressan 1997), Madeira (Neto *et al.* 2001, John *et al.* 2004), Maldives (Silva *et al.* 1996), Mauritania (John *et al.* 2004), Mexico (Dawson 1960), Morocco (Babbini & Bressan 1997), Sardinia (Babbini & Bressan 1997), Pakistan (Silva *et al.* 1996), Senegal (John *et al.* 2004), Spain (Ramos Esplá 1985, Conde *et al.* 1996), Sri Lanka (Silva *et al.* 1996), Tunisia (Ben Maiz *et al.* 1987, Babbini & Bressan 1997) Turkey (Basso & Rodondi 2006, Taskin *et al.* 2008). In our opinion, records from the Maldives (Hackett 1977) need to be verified. Australia, Mediterranean and Red Sea (Basso & Rodondi 2006).

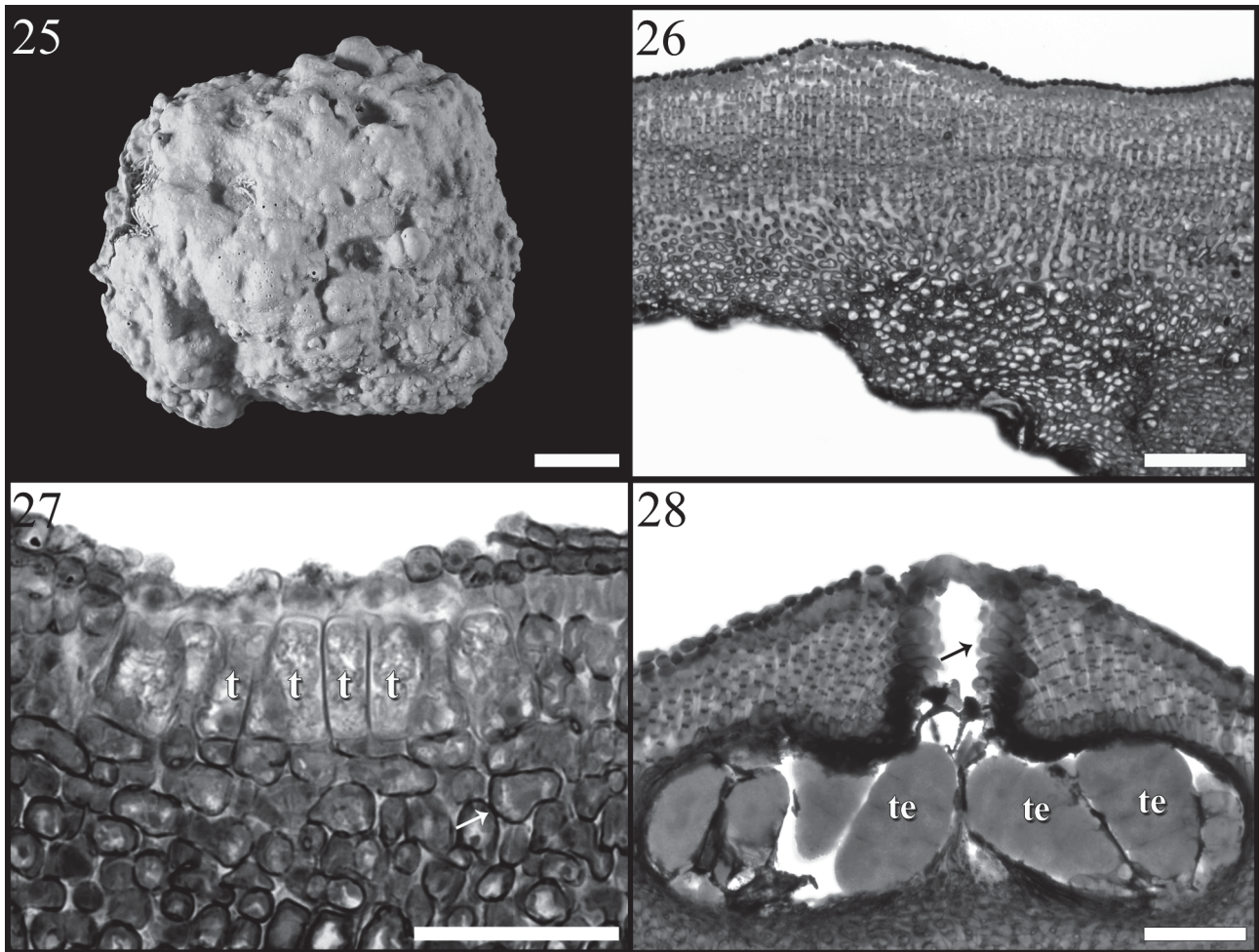


FIGURE 25. External morphology of *Spongites fructiculosus*. **FIGURE 26.** Longitudinal section of *S. fructiculosus* showing a pseudo-parenchymatous cellular organisation. **FIGURE 27.** Longitudinal section of *S. fructiculosus* showing the trichocyte field (t) and cell fusion (white arrow). **FIGURE 28.** Longitudinal section of *S. fructiculosus* showing the conceptacles with tetraspores (te) and cells around the pore arranged horizontally (black arrow). Scales: (25) 1 cm; (26–28) 50 μ m.

Distribution at the study sites:—Abrolhos Archipelago at Porto Norte in Santa Bárbara Island (18° 09' 09" S – 38° 53' 27" W) and Mato Verde (18° 11' 08" S – 38° 43' 24" W), Siriba Island (18° 00' 44" S – 38° 53' 01" W) and Sueste Island (18° 06' 14" S – 38° 57' 04" W).

Examined material:—Sample 1: 18° 09' 09" S–38° 53' 27" W, coll. *F.T. de S. Tâmega, M.A. de O. Figueiredo and R. Mariath, 31-8-2008*, RB 490650; Sample 2: 18° 11' 08" S–38° 43' 24" W, coll. *F.T. de S. Tâmega, M.A. de O. Figueiredo and R. Mariath, 31-8-2008*, RB 490651; Sample 3: 18° 00' 44" S – 38° 53' 01" W, coll. *F.T. de S. Tâmega, 27-10-2008*, R 209890, Sample 4: 18° 06' 14" S–38° 57' 04" W, coll. *F.T. de S. Tâmega, 15-12-2008*, R 209891.

Discussion

In the Abrolhos Archipelago, the shallow reefs are dominated by *L. stictaeforme* and *P. pachydermum* (Figueiredo & Steneck 2002, Figueiredo 2005, Tâmega & Figueiredo 2007). In this study, *L. stictaeforme* is mainly characterised by anastomosed branches with lumps. The inner conceptacles roof is 149–193 μ m in height and 291–302 μ m in diameter. The conceptacle roof contains 6–8 cell layers, and the conceptacles floor is located 13–16 cell layers below the surrounding thallus surface. The herein described specimens show close similarities with those reported previously for the species at the same study site (Figueiredo & Steneck 2002, Tâmega & Figueiredo 2007) and in the Caribbean (Steneck & Adey 1976).

The vegetative and reproductive features of *L. stictaeforme* identified in this study were compared to samples of (1) *L. congestum* from previous studies carried out in Abrolhos (Figueiredo & Steneck 2002) and descriptions of samples from the Caribbean (Taylor 1960, Steneck & Adey 1976, Littler & Littler 2000), to (2) *L. stictaeforme* from the Brazilian reefs at Cumuruxatiba (Nunes *et al.* 2008) and from rhodolith beds (Villas Bôas *et al.* 2009), to (3) *Lithophyllum kotschyianum* Unger from Hawaii (Adey *et al.* 1982) and the Sulawesi Islands (Verheij 1994) and to (4) *Lithophyllum tamiense* (Heydrich 1897: 1) Verheij (1994: 103) from Australia (Ringeltube & Harvey 2000) (Table 1). The comparison showed similarities in the vegetative organisation of the thallus, the epithallial and perithallial cells and the reproductive structures (shape, size and number of cells on the roof of the tetrasporangial conceptacles; Table 1).

The overlap of vegetative and reproductive features between *L. congestum* and *L. kotschyianum* observed in this study suggests that these species are likely heterotypic synonyms. In fact, *L. kotschyianum* in the Pacific Ocean is considered to be *L. congestum* in the Atlantic Ocean, occupying the same habitats as this species in shallow waters (Adey *et al.* 1982). Similarly, *L. stictaeforme* in coastal reefs occupies the same habitats as *L. congestum* in the Abrolhos reefs in Brazil (Nunes *et al.* 2008). The information on the type material of *L. congestum* shows that both have the same conceptacle anatomy and sizes as similar to *L. kotschyianum* and *L. stictaeforme* (Table 1), however the type samples of *L. kotschyianum* have incomplete conceptacles, which makes this older name unusable. Thus, *L. stictaeforme*, as the older name, has taxonomic priority according to article 11 of the current botanical code (McNeill *et al.* 2011).

The vegetative and reproductive features of *Neogoniolithon atlanticum* Tâmega, Riosmena-Rodriguez, Mariath & Figueiredo *sp. nov.* identified in this study were compared with recent publications (Table 2). This comparison failed to show greater similarity in the shape and size of the tetrasporangial conceptacles compared to *Melobesia brassica-florida* Harvey (1849: 110) (described by Woelkerling *et al.* 1993b) from South Africa or to *Neogoniolithon clavacymosum* Adey, Townsed & Boykins (1982: 21–23), *Neogoniolithon mamillare* Setchell & L.R. Manson (1943: 91) and *Neogoniolithon rufum* Adey, Townsed & Boykins (1982: 9–11) (described by Adey *et al.* 1982) from Hawaii. However, these species are distinguished by the absence of trichocytes, the number of cells on the roof of the tetrasporangial conceptacles and the position of the tetraspores. Molecular information strongly suggests that *N. fosliei* have several cryptic species to be defined (Kato *et al.* 2013). Due to a lack of overlap in the characteristics analyzed, we propose *N. atlanticum* as a new species of *Neogoniolithon*.

The genus *Porolithon* was initially characterised by the presence of trichocytes organised into horizontal fields and a multi-layered hypothallium (Adey 1970a, Adey *et al.* 1982, Penrose & Woelkerling 1988, 1992). Under the current criteria, the presence of trichocytes has not been considered an important taxonomic feature as their presence can be attributed to environmental conditions (Woelkerling 1985). Trichocytes arranged singly or in groups were recorded as *Hydrolithon* (Foslie 1905: 7) Foslie (1909: 55) (Keats & Chamberlain 1994, Woelkerling 1996, Ringeltaube & Harvey 2000) and *Spongites* Kützing (1841: 30) (Penrose & Woelkerling 1988, 1992), respectively.

As the analysis of vegetative features is not sufficient to distinguish the genera *Hydrolithon*, *Porolithon* and *Spongites* (Woelkerling 1985, Penrose & Woelkerling 1988), the observation of reproductive features is necessary (Penrose & Woelkerling 1992). However, Kato *et al.* (2011) concluded that differences in trichocyte arrangement could be used to separate the two supported lineages at a generic level: *Hydrolithon* for horizontally arranged fields of trichocytes with interspersed vegetative filaments, and *Porolithon* (resurrected) for horizontally arranged, tightly packed fields of trichocytes without interspersed vegetative filaments. Similarities in the formation of cells around the pores of tetrasporangial conceptacles led the latter authors to propose that *Porolithon* is a heterotypic synonym of *Hydrolithon*. The distinction between *Hydrolithon* and *Spongites* was also based on the features of the pore channels, which in *Hydrolithon* are aligned, with elongated cells that do not protrude into the channel and are arranged perpendicular to the epithallus. In *Spongites*, in contrast, the cells are elongated, aligned within the pore channel and arranged parallelly to the epithallus.

In this study, *P. pachydermum* is characterized mainly by prominent trichocytes present on the surface of the thallus that are solitary or in groups, as was observed for specimens at the same study site (Figueiredo & Steneck 2002, Tâmega & Figueiredo 2007) and in the Caribbean (Taylor 1960, Littler & Littler 2000). Furthermore, it has conceptacles that are 150–210 µm in outer diameter, with an inner chamber that is 85–151 µm high and 153–199 µm in diameter, a roof of 5–7 cell layers and floor located 12–13 cell layers below the surrounding thallus surface. According to Adey *et al.* (1982), *Porolithon onkodes* (Heydrich 1897: 6) Foslie (1909: 57) in the Pacific Ocean is

considered to be *P. pachydermum* in the Atlantic, as it is dominant in shallow waters and occupies the same habitats. According to Mendoza-González *et al.* (2009), after consulting the respective lectotypes of these species, *H. onkodes* appears to be closely related to *H. pachydermum*. Both *P. onkodes* and *P. pachydermum* are easily identified in the field by the presence of trichocyte fields visible on the surface of the thallus (Adey *et al.* 1982). Bailey *et al.* (2004) used molecular biology techniques, but not morphological features, and combined *P. pachydermum* with *Hydrolithon pachydermum* (Foslie 1904: 4) Bailey, Gabel & Freshwater (2004: 8), as did Broom *et al.* (2008), who recognised genetic similarities between *H. pachydermum* and *H. onkodes*. Kato *et al.* (2011) used molecular analyses of SSU rDNA and *psbA* sequences to divide Japanese coralline algae into independent polyphyletic lineages for the Mastophoroideae genera examined (*Hydrolithon*, *Neogoniolithon*, *Pneophyllum* Kützinger (1843: 385), *Porolithon* and *Spongites*). They also proposed the establishment of three new subfamilies, Hydrolithoideae (including *Hydrolithon*), Porolithoideae (including the resurrected genus *Porolithon*) and Neogoniolithoideae (including *Neogoniolithon*).

In this study, the vegetative and reproductive features of *P. pachydermum* were compared to those of *P. onkodes* and *Hydrolithon onkodes*, as described in other studies (Table 3). This comparison shows similarities in the vegetative (organisation of the thallus, shape of the epithallial cells, arrangement of the trichocytes) and reproductive structures (shape and size of the tetrasporangial conceptacles, number of cells on the conceptacles roof) in *P. pachydermum* (Taylor 1960, Littler & Littler 2000, Figueiredo & Steneck 2002), *P. onkodes* and *H. onkodes* (Adey *et al.* 1982, Lawson & John 1982, Keats & Chamberlain 1994, Woelkerling 1996, Ringeltaube & Harvey 2000). The overlap in the vegetative and reproductive features among *P. pachydermum* and *P. onkodes* observed after consulting their type materials confirms the similarities in the anatomical features of these species.

The genus *Spongites* is characterised by the absence of an endophytic thallus, haustoria, filaments composed of palisade cells and filaments arranged in a monomerous coaxial in regions of the thallus, and by the presence of a vegetative thallus composed of several layers of cells (Woelkerling 1988). In this study, *Spongites fructiculosus* Kützinger (1841: 33) is characterised mainly by a conceptacle with an external diameter of 150–300 µm, an inner chamber that is 160–200 µm high and 280–300 µm in diameter, a roof with 5–12 cell layers and a floor located 13–18 cell layers below the surrounding thallus surface.

We compared the vegetative and reproductive features of *S. fructiculosus* from localities elsewhere in relation to *Spongites yendoi* (Foslie 1900: 25) Y.M. Chamberlain (1993: 102). This comparison showed similarities in the vegetative (surface and organisation of the thallus, form of the epithallial and perithallial cells, arrangement of the trichocytes) but several differences in the reproductive structures (shape and size of tetrasporangial conceptacles and number of cells over the roof of conceptacles, Table 4) who also has been noted by Penrose (1991), Woelkerling (1996), Ringeltaube & Harvey (2000) and Basso & Rodondi (2006).

The measurements of the height and internal diameter of the tetrasporangial conceptacles and the number of cell layers on the conceptacle roof are similar to those found previously for the same species (Penrose 1991, Woelkerling 1996, Ringeltaube & Harvey 2000, Basso & Rodondi 2006). According to Penrose (1991), *S. fructiculosus* and *S. yendoi* are distinguished mainly by the larger conceptacles in *S. fructiculosus* (> 450 µm) compared to those in *S. yendoi* (<250 µm).

In the studied coral reef sites, *L. stictaeforme* and *P. pachydermum* were the most common species and are mainly found in the shallow edge of the fringing reefs of Abrolhos Archipelago, as observed for the Abrolhos Bank. These results corroborate the synonymy (*sensu* Adey *et al.* 1982) of *P. pachydermum* and *H. onkodes* and between *L. congestum* and *L. kotschyianum*. This occurrence of *S. fructiculosus* is the first record of the species in the southwestern Atlantic. We therefore recommend that the taxonomy of coralline algae important in reef construction to be reviewed following modern taxonomic criteria.

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