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Taxonomic study of crustose coralline algae off the northeastern Brazilian coast

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Abstract

This work presents a detailed morphoanatomical study of crustose coralline algae species from the northeastern Brazilian coast, in the north of Bahia state. Nine species have been recognized: *Sporolithon episporum*, *Lithophyllum stictaeforme*, *Spongites yendoi*, *Spongites* sp., *Mesophyllum erubescens*, *Phymatolithon masonianum*, *Phymatolithon calcareum*, *Lithothamnion crispatum* and *Lithothamnion brasiliense*. *Phymatolithon masonianum* and *Phymatolithon calcareum* constitute the first record of these species for the northern coast of Brazil. An identification key, as well as descriptions, illustrations, comparisons with related taxa, and geographical distributions for Brazil as well as global geographic distributions are presented. Additionally, some ecological implications are discussed focusing the need of more studies about this neglected group of coralline red algae.

Keywords: Atlantic West, Calcareous algae, Rhodolith, Taxonomy

Introduction

Crustose coralline algae (CCA), until recently, were grouped in the order Coralinalles (Rhodophyta), which was composed by three families: Corallinaceae, Hapalidiaceae, and Sporolithaceae (Harvey *et al.* 2005). However, based on molecular studies, Le Gall *et al.* (2010) proposed a change of status for the family Sporolithaceae, raising it to a new order Sporolithales, comprising a single family.

CCA are cosmopolitan, and occupy a diverse range of habitats, varying from the intertidal zone to depths of 366 m (Littler *et al.* 1985, Steneck 1986, Foster 2001). Their defining characteristic is the impregnation of their cell walls with carbonate in the form of calcite, giving them a rigid texture, which is not observed in other groups of red algae (Chamberlain 1983, Bailey & Chapman 1998). Because of their wide ecological and geographical distributions, CCA have different growth forms (Woelkerling *et al.* 1993), making them taxonomically complex. Some CCA initially develop from fragments that stand out from other coralline algae fixed to the substrate, and continue their development as free-living structures, forming sedimentary deposits (Dias 2000). The forms that grow on the substrate are referred to as rhodoliths when composed mainly (>50%) of CCA (Foster 2001, Harvey & Woelkerling 2007). CCA are recognized to be important carbonate builders in the tropical zone of the Atlantic Ocean, forming reefs and rhodolith beds, especially in Brazil (Riul *et al.* 2009, Amado-Filho *et al.* 2012a, Amado-Filho *et al.* 2012b, Pereira-Filho *et al.* 2012). They also provide refuge areas, habitat, and pasture for numerous species of fish and invertebrates, as well as influence the settlement and recruitment of marine invertebrates through the action of attractive chemicals associated with the surface of CCA, which are known to lead to the establishment of a variety of species of larvae (Farr *et al.* 2009).

The characteristics generally utilized for the identification of CCA in level of species are: the growth form (arborescent, discoid, encrusting, fruticose, foliose, layered, lumpy, warty or ribbon-like) (Woelkerling *et al.* 1993),

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the way secondary cell connections occur (as pit connections or fusion cells), epithallial cells shape and number of layers, organization of the thallus (monomerous or dimerous), trichocytes (presence and location), the kind of tetrasporangial conceptacles they produce (uniporate or multiporate), the conceptacle position relating to the thallus surface (raised, flush, or flat), and the shape of the conceptacle (dimensions of the cavities, the presence of rings and columella) (Woelkerling 1988, Harvey & Woelkerling 2007, Farr *et al.* 2009). Therefore, reproductive characteristics have been critical to the specific delimitation in this group, which requires that specimens be fertile for identification.

Recent taxonomic studies on the Brazilian coast have helped to expand our knowledge of the diversity of CCA, including the description of some new species, as *Lithophyllum depressum* Villas-Boas, Figueiredo & Riosmena-Rodriguez in Villas-Boas *et al.* (2009: 245) and *Sporolithon tenue* Bahia, Amado-Filho, Maneveldt et W. H. Adey (2013: 3) (Villas-Boas *et al.* 2009, Mariath *et al.* 2012 and Bahia *et al.* 2014). To date, 41 valid species have been recorded for the Brazilian coast (Horta 2002, Figueiredo & Steneck 2002, Tâmega & Figueiredo 2005, Amado-Filho *et al.* 2007, Nunes *et al.* 2008, Villas-Boas *et al.* 2009, Amado-Filho *et al.* 2010, Farias *et al.* 2010, Bahia *et al.* 2010, Bahia *et al.* 2011, Henriques *et al.* 2011, Horta *et al.* 2011, Pereira-Filho *et al.* 2011, Amado-Filho *et al.* 2012a, b, Mariath *et al.* 2012, Bahia *et al.* 2013, Mariath *et al.* 2013). A few studies in the state of Bahia have investigated the taxonomy and ecology of CCA and most of them were accomplished in the southern limit of this region (Figueiredo & Steneck 2002, Nunes *et al.* 2008, Amado-Filho *et al.* 2012b, Mariath *et al.* 2012 and Bahia *et al.* 2013).

The aim of this report is to present a taxonomic study of CCA off the overlooked north coast of Bahia state, based on morphological and anatomical characteristics, as well as to contribute to the knowledge of the algal diversity of the Bahian and Brazilian coasts.

Material and Methods

Material for examination was collected in ten areas distributed along the north coast of the state of Bahia, on the continental platform of the cities of Salvador, Camaçari, Mata de São João, Entre Rios and Conde (Figure 1). The samples were collected in 2011 and 2012 from the intertidal zone during low spring tides, and from the subtidal zone (9–26 m depth) by SCUBA diving and Petersen dredge. The specimens were preserved in 4% formalin seawater.

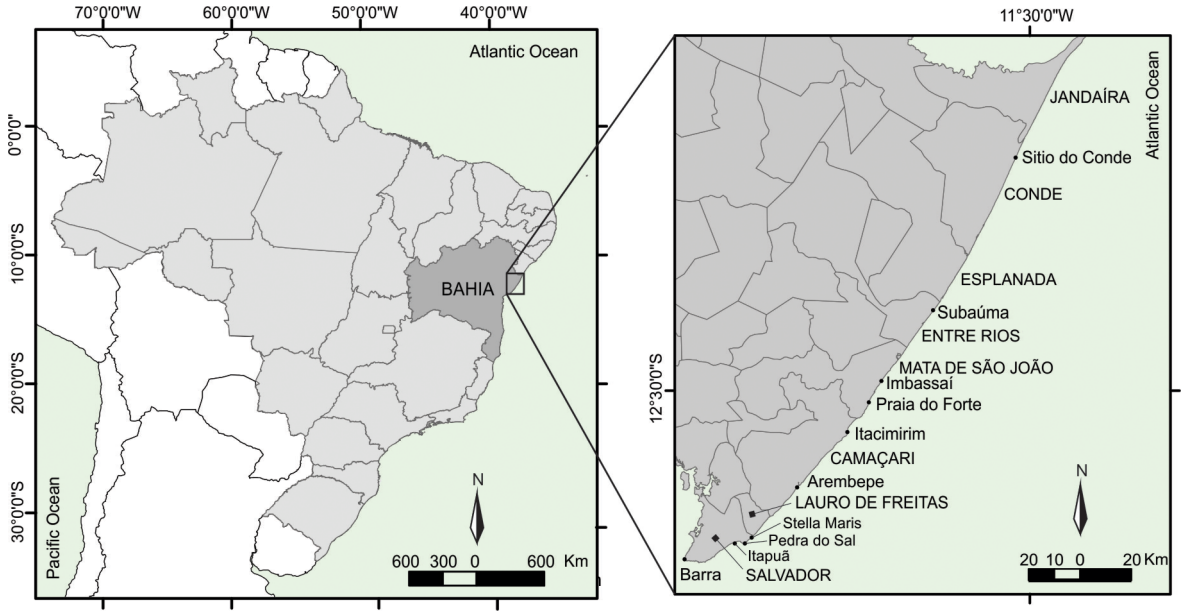

FIGURE 1: Map of the Brazil showing the coast of Bahia sampling sites.

For optical microscopy analysis the material was decalcified with 0.6 M HNO_3 for 24 hours, followed by dehydration using an ethanol series (30, 50, 70, 90 and 100%), infiltration and inclusion in methacrylate glycol

resin in accordance with the instructions supplied in the "Historesin embedding Kit" Leica, Reichert-Jung. Sections (6–12 µm thick) were cut by using a Leica microtome (Model 2040) and stained with acidified aqueous toluidine blue (Riosmena-Rodriguez 1993, Moura *et al.* 1997). For scanning electron microscopy (SEM), the dry specimens were fractured looking for diagnostic features and placed in stubs using carbon tapes, following the procedures decribed by Chamberlain (1993). The specimens were deposited in the Alexandre Leal Costa Herbarium (ALCB), Federal University of Bahia.

Results

Identification key:

1. Tetra/bisporangia cruciately divided, arranged in calcified compartments..... *Sporolithon episporum*
- Tetra/bisporangia zonately divided, arranged in conceptacles..... 2.
2. Uniporate tetra/bisporangial conceptacle..... 3.
- Multiporate tetra/bisporangial conceptacle..... 4.
3. Cells of adjacent filaments joined by secondary pit-connections ..... *Lithophyllum stictaeforme*
- Cells of adjacent filaments joined by cell fusions ..... 5.
4. Rounded or flattened epithallial cells..... 6.
- Flared epithallial cells ..... 7.
5. Trichocytes present ..... *Spongites yendoi*
- Trichocytes absent..... *Spongites* sp.
6. Subepithallial initials as long as or longer than the cells immediately subtending them..... *Mesophyllum erubescens*
- Subepithallial initials as short as or shorter than the cells immediately subtending them ..... 8.
7. Tetra/bisporangial conceptacles protruding above thallus surface, with depressions around the pore ..... *Lithothamnion crispatum*
- Tetra/bisporangial conceptacles flushed or slightly elevated from the thallus surface, without depressions around the pore ..... *Lithothamnion brasiliense*
8. Tetra/bisporangial conceptacles with vegetative cells inside..... *Phymatolithon masonianum*
- Tetra/bisporangial conceptacles without vegetative cells inside..... *Phymatolithon calcareum*

SPOROLITHALES Le Gall & Saunders in Le Gall *et al.* (2010: 305)
Sporolithaceae Verheij (1993: 195)
Sporolithon episporum (Howe) Dawson (1960b: 40)
Archaeolithothamnion episporum Howe (1919: 2)

Figures: 2 A–G and 3 A–F.

Description: Non-geniculate thallus forming free-living rhodoliths or attached to the substrate, growth form encrusting or lumpy. Color varying from grayish to brownish-red. Thallus pseudoparenchymatous with monomerous construction. Epithallial cells single and flared, 5–7.5 µm long and 6–9.2 µm in diameter. Subepithallial initials as long as or longer than the cells immediately subtending them, 8–12.5 µm long and 7–9 µm in diameter. Cells from the perithallus are 8–12.3 µm long and 5–11 µm in diameter. Cells from the hypothallus are 6–9 µm long and 11–17 µm in diameter. Cells from adjacent filaments are joined by secondary pit-connections and few cell fusions. Calcified compartments are 58–77.3 µm long and 32–48 µm in diameter, forming sori that protrude above the thallus surface, surrounded by calcified paraphyses and located seven layers below the epithallial cells. Calcified compartment roofs are two cells thick, including the epithallial cells; pore is 11–20 µm in diameter, surrounded by 9–11 rosette cells. Cruciately divided tetrasporangia, 68–77.2 µm long and 26–30 µm in diameter, supported by a stalk cell. Mature uniporate carposporangial conceptacles flush with the surrounding thallus surface, 143–192 µm long and 108–189 µm in diameter. Conceptacle wall formed by vertically elongated cells. Carposporangia, 68–77.2 µm long and 26–30 µm in diameter, arising from the floor of the conceptacle. Male specimens not observed.

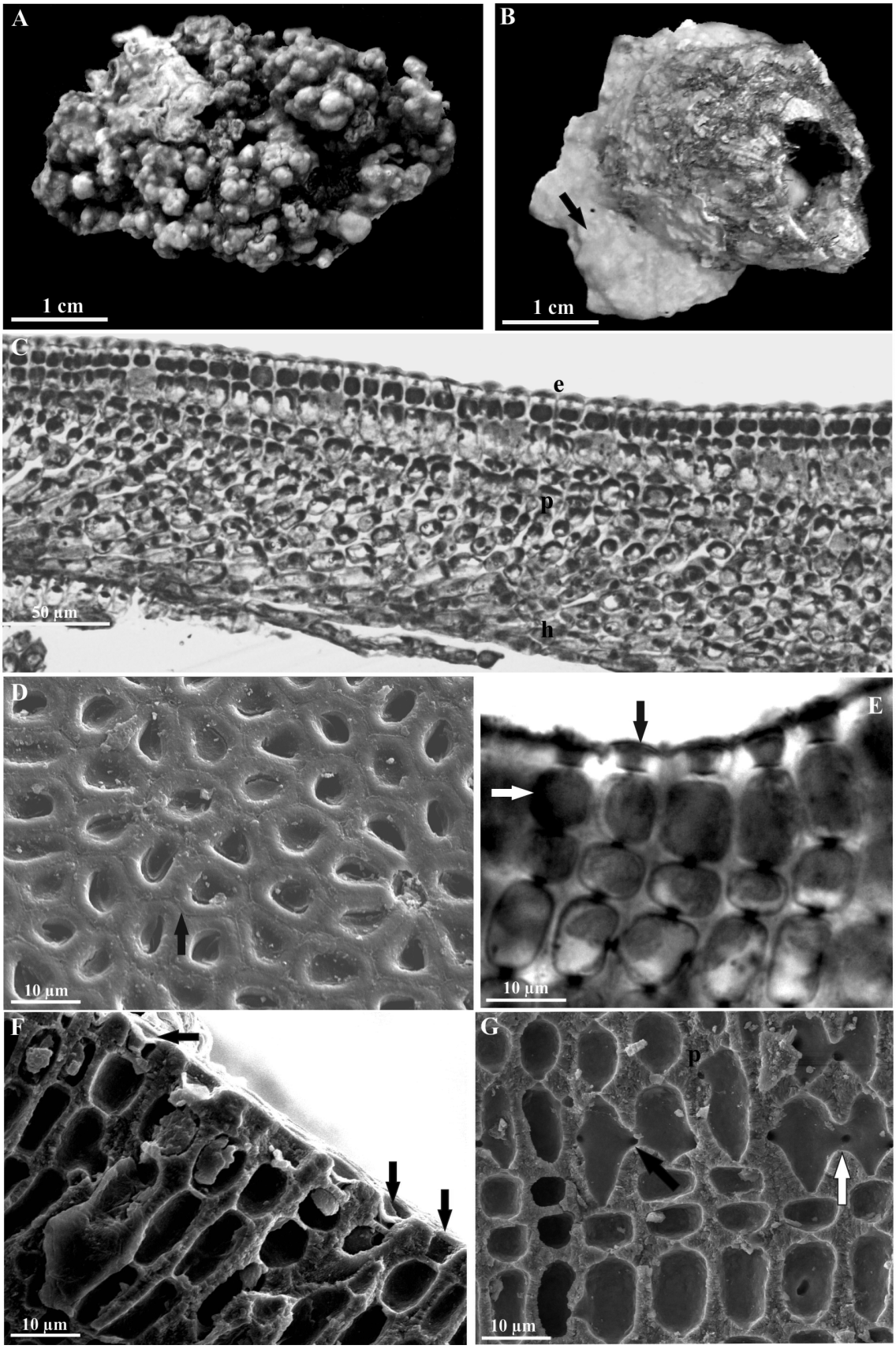

FIGURE 2 A–G: General aspects and micrographs of *Sporolithon episporum* (Howe) Dawson. **A.** General aspects of a sporophytic thallus. **B.** General aspects of a carposporophytic thallus (arrow). **C.** Longitudinal section showing monomerous construction (e—epithallial, p—perithallial, h—hypothallial). **D.** Epithallial cells in surface view, SEM (Scanning Electron Microscope). **E.** Longitudinal section showing flared epithallial cells (black arrow), and subepithallial initials as long as or longer than the cells immediately subtending them (white arrow). **F.** Longitudinal fracture showing flared epithallial cells, SEM (arrows). **G.** Longitudinal section showing cells of adjacent filaments joined by secondary pit-connections (black arrow), and cell fusions (white arrow).

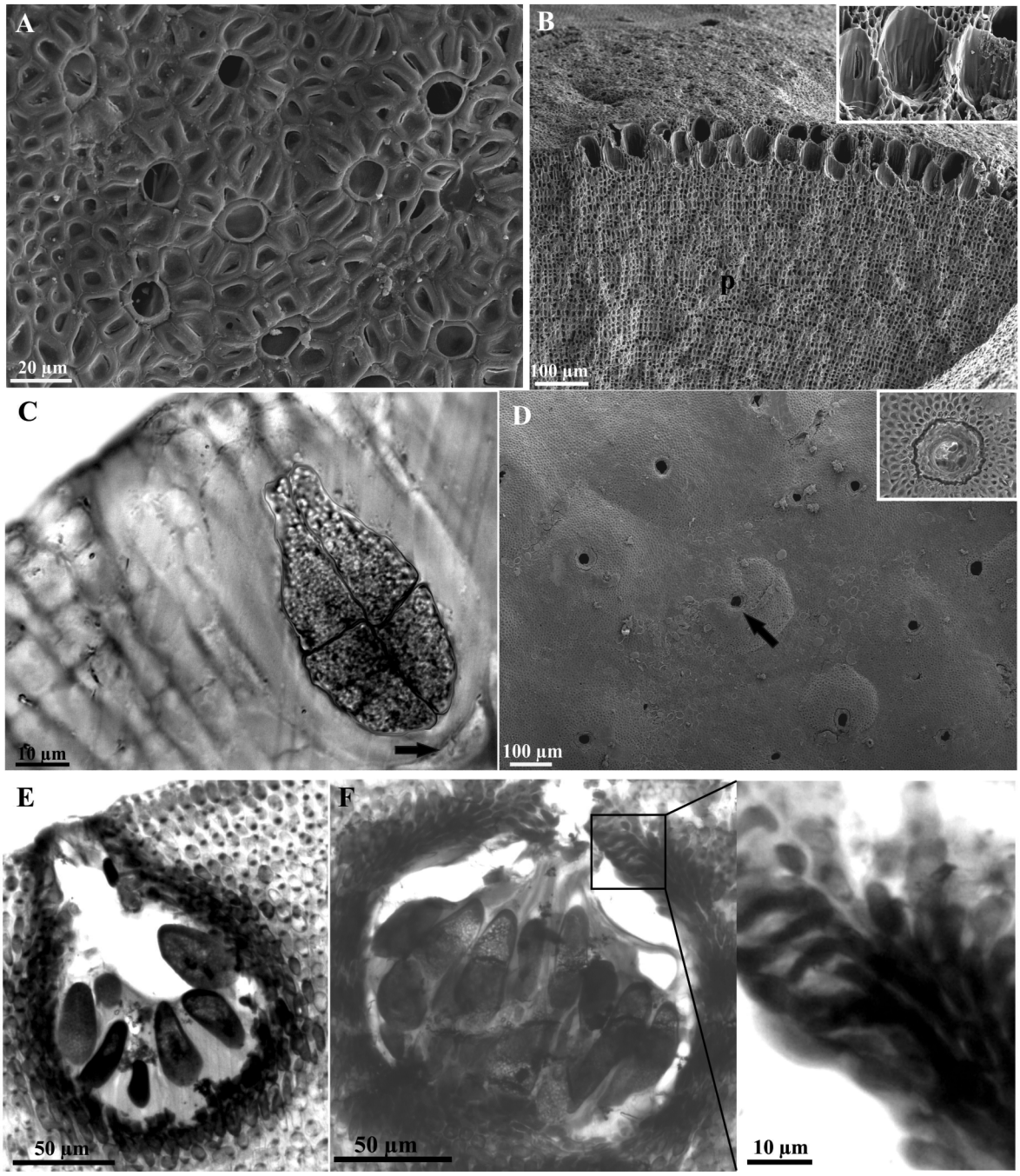

FIGURE 3 A–F: Micrographs of *Sporolithon episporum* (Howe) Dawson. **A.** Calcified compartments in surface view, SEM. **B.** Longitudinal fracture showing calcified compartments (detail). **C.** Longitudinal section showing cruciately divided tetrasporangia supported by a stalk cell (arrow). **D.** Uniporate carposporangial conceptacles in surface view, SEM. **E.** Longitudinal section of carposporangial conceptacles with carposporangia inside. **F.** Carposporangial conceptacle with detail of elongated cells that surround the chamber.

Material examined: BRASIL. Bahia: Salvador, Pedra do Sal, 12°57'06"S, 38°20'42"W, 05 April 2012, *I.O. Costa et al. s.n.* (ALCB 103448); Salvador, Stella Maris, 12°56'22"S, 38°19'41"W, 05 April 2012, *I.O. Costa et al. s.n.* (ALCB 103449); Camaçari, Arembepe, 12°44'25"S, 38°08'58"W, 07 May 2012, *I.O. Costa et al. s.n.* (ALCB 103451), 12 July 2012, *CETREL s.n.* (ALCB 103450); Mata de São João, Praia do Forte, 12°34'42"S, 38°00'06"W, 07 October 1998, *C. Coimbra s.n.* (ALCB 103452); Mata de São João, Imbassaí, 12°30'11"S, 37°57'36"W, 28 August 2011, *I.O. Costa et al. s.n.* (ALCB 103453); Conde, Sítio do Conde, 11°51'11"S, 37°33'49"W, 30 August 2011, *I.O. Costa et al. s.n.* (ALCB 103454, ALCB 103455♀).

TABLE 1: Comparison between descriptions of sporophytic specimens of *Sporolithon episporum* based on vegetative and reproductive features (+ = present, - = absent; ND = not disclosed). [1] Yamaguishi-Tomita (1976)—Brazil, [2] Keats & Chamberlain (1993)—South Africa and Panama, [3] Nunes *et al.* (2008)—Brazil.

Characters (measured in µm)	*S. episporum* (this study)	*S. episporum* [2] (holotype)	*S. episporum* [1]	*S. episporum* [2]	*S. episporum* [3]
Epithallial cell length	5–7.5	4–5	3–3.5	3.5–6	ND
Epithallial cell diameter	6–9.2	5–10	6–10	8.5–11	3–4
Perithallial cell length	8–12.3	5–20	8–15	5–21	9–15
Perithallial cell diameter	5–11	5–9	7–9	6–13	5–10
Hypothallial cell length	6–9	12–47	12–24	9–31	28–36
Hypothallial cell diameter	11–17	4–10	5–9	5–12	12–16
Calcified compartment length	58–77.3	50–70	80–100	95–112	60–90
Calcified compartment diameter	32–48	25–40	40–45	33–50	30–50
Tetrasporangia length	68–77.2	>50	ND	74–96	60–90
Pore diameter (calcified compartments)	11–20	16–30	ND	16–20	9–15
Number of cells around the pore	9–11	12–16	ND	8–12	12–14

TABLE 2: Comparison between descriptions of carposporophytic specimens of *Sporolithon* based on vegetative and reproductive features (+ = present, - = absent; ND = not disclosed). [1] Verheij (1992)—Indonesia, [2] Woelkerling (1996)—Australia, [3] Harvey *et al.* (2002)—Australia.

Characters (measured in µm)	*S.episporum* (this study)	*S. episoredion* [1]	*S. durum* [2]	*S. durum* [3]
Epithallial cell length	4.5–6.2	ND	7–10	3–4
Epithallial cell diameter	5–11	ND	2–5	5–10
Perithallial cell length	10–21.6	ND	ND	ND
Perithallial cell diameter	6.5–8.3	ND	ND	ND
Hypothallial cell length	11–20.5	ND	6–23	5–27
Hypothallial cell diameter	5–8	ND	5–12	3–13
Carposporangial conceptacle length	143–192	950–1300	70–370	125–180
Carposporangial conceptacle diameter	108–189	500–900	80–445	200–220
Carposporangia length	68–77.2	200–375	105–119	ND

Comments: Plants found growing at the midlittoral zone in the front region of the reef and rhodolith presence in the subtidal zone to 23 m in depth. Epiphyted by *Aglaothamnion herveyi* (M.A.Howe) N.E. Aponte, D.L.Ballantine, & J.N.Norris (1994: 232–237), *Centroceras clavulatum* (C.Agardh) Montagne (1846: 140), *Dictyota mertensii* (Martius) Kützing (1859: 15), *Enantiocladia duperreyi* (C.Agardh) Falkenb. in Schmitz (1889: 447), *Gelidium coarctatum* Kützing (1868: 21), *Gracilaria domingensis (*Kützing) Sonder ex Dickie (1874: 149), *Gracilaria* sp., *Herposiphonia secunda* (C.Agardh) Ambronn (1880: 197), *Hydropuntia secunda* Gurgel & Fredericq (2004: 156), *Hypnea musciformis* (Wulfen) J.V.Lamouroux (1813: 43), *Hypnea nigrescens* Greville ex J. Agardh (1851: 443–444), *Jania adhaerens* J.V. Lamouroux (1816: 270), *Padina gymnospora* (Kütz.) Sond. (1871: 47), *Pterosiphonia pennata* (C.Agardh) Sauvageau (1897: 287), *Spatoglossum schroederi* (C.Agardh) Kützing (1859: 21) and *Vidalia obtusiloba* (Mertens ex C.Agardh) J.Agardh (1863: 1123).

Distribution on the Brazilian coast: Bahia (Nunes *et al.* 2008, Bahia *et al.* 2010, Amado Filho *et al.* 2012b), Ceará (Yamaguishi-Tomita 1976), Paraíba (Riul *et al.* 2009), Arquipélago de Fernando de Noronha (Burgos 2011, Amado Filho *et al.* 2012a).

Global distribution: Caribbean Islands, Indonesia, New Zealand, Pacific Islands, Panama, South Africa, Tanzania, Venezuela (Guiry & Guiry 2014).

CORALLINALES Silva & Johansen (1986: 250)
Corallinaceae J. V. Lamouroux (1812: 185)
Lithophylloideae Setchell (1943: 134)
Lithophyllum stictaeforme (Areschoug in J. Agardh) Hauck (1877: 292)
Melobesia stictaeformis Areschoug in J. Agardh (1852: 517)
Synonyms: *Lithophyllum expansum* f. *stictaeforme* (Areschoug in J. Agardh) Foslie (1900a: 18), *Melobesia frondosa* Dufour (1861: 39), *Lithophyllum frondosum* (Dufour) Furnari, Cormaci et Alongi (1996: 121), *Lithophyllum expansum* Phillippi (1837: 389), *Lithophyllum bermudense* Foslie & M.A.Howe (1906: 132).

Figure: 4 A–H.

Description: Non-geniculate thallus forming free-living rhodoliths or attached to the substrate, growth form encrusting or lumpy. Color varying from grayish to brownish-red. Thallus pseudoparenchymatous with dimerous construction. Epithallial cells single and rounded or flattened, 7–8.3 µm long and 7.8–10 µm in diameter. Subepithallial initials as long as or longer than the cells immediately subtending them, 13–16 µm long and 8–10.5 µm in diameter. Cells from the perithallus are 10–20 µm long and 8–15 µm in diameter. Cells from the hypothallus are 8.5–17 µm long and 7–17.5 µm in diameter. Trichocytes not observed. Cells of the adjacent filaments are joined by secondary pit-connections. Cell fusion not observed. Uniporate tetrasporangial conceptacles, 77–117 µm long and 185–258.3 µm in diameter, chambers are more or less elliptical. Conceptacle roofs are 5–6 cells thick, including the epithallial cells, pore without an apical plug. Central columella present. Conceptacle chamber floor positioned at 12-14 cell layers below the surface of the thallus. Zonately divided tetrasporangia, 58–89 µm long and 19–30 µm in diameter. Gametangial thallus not observed.

Material examined: BRASIL. Bahia: Salvador, Itapuã, 12°57'22"S, 38°21'31"W, 29 September 2011, *I.O. Costa et al. s.n.* (ALCB 103460); Camaçari, Arembepe, 12°44'25"S, 38°08'58"W, 12 July 2012, *CETREL s.n.* (ALCB 103444), Itacimirim, 12°36'53"S, 38°02'31"W, 29 October 2010, *N.A. Andrade et al. s.n.* (ALCB 100348); Entre Rios, Subaúma, 12°14'10"S, 37°46'05"W, 29 August 2011, *I.O. Costa et al. s.n.* (ALCB 103445).

Comments: Plants found growing at the midlittoral zone in the front region of the reef and at the subtidal zone between 9 and 25 m depth. Epiphyted by *Anadyomene stellata* (Wulfen in Jacq.) C. Agardh (1823: 400), *Bryothamnion triquetrum* (S.G.Gmelin) M.A.Howe (1915: 222), *Caulerpa mexicana* Sond. *ex* Kütz. (1849: 496), *Caulerpa prolifera* (Forssk.) J.V.Lamour. (1809: 332), *Corynomorpha clavata* (Harvey) J. Agardh (1872: 4), *Corallina officinalis* Linnaeus (1758: 805), *Dictyopteris delicatula* J.V.Lamour. (1809: 332), *Gelidiella acerosa* (Forsskal) Feldmann & G. Hamel (1934: 533)*, Gelidium coarctatum, Gracilaria domingensis*, *Gracilaria* sp., *Grateloupia filicina* (J.V.Lamouroux) C.Agardh (1822: 223), *Jania cubensis* Mont. *ex* Kütz. (1849: 709-710), *Jania subulata* (Ellis & Solander) Sond. (1846: 186), *Sargassum* sp. and *Ulva fasciata* Delile (1813: 297).

Distribution on the Brazilian coast: Bahia (Nunes *et al.* 2008, Amado Filho *et al.* 2012b), Espírito Santo (Villas-Boas *et al.* 2009, Amado Filho *et al.* 2010), Arquipélago de Fernando de Noronha (Burgos 2011), Santa Catarina (Martins *et al.* 2012).

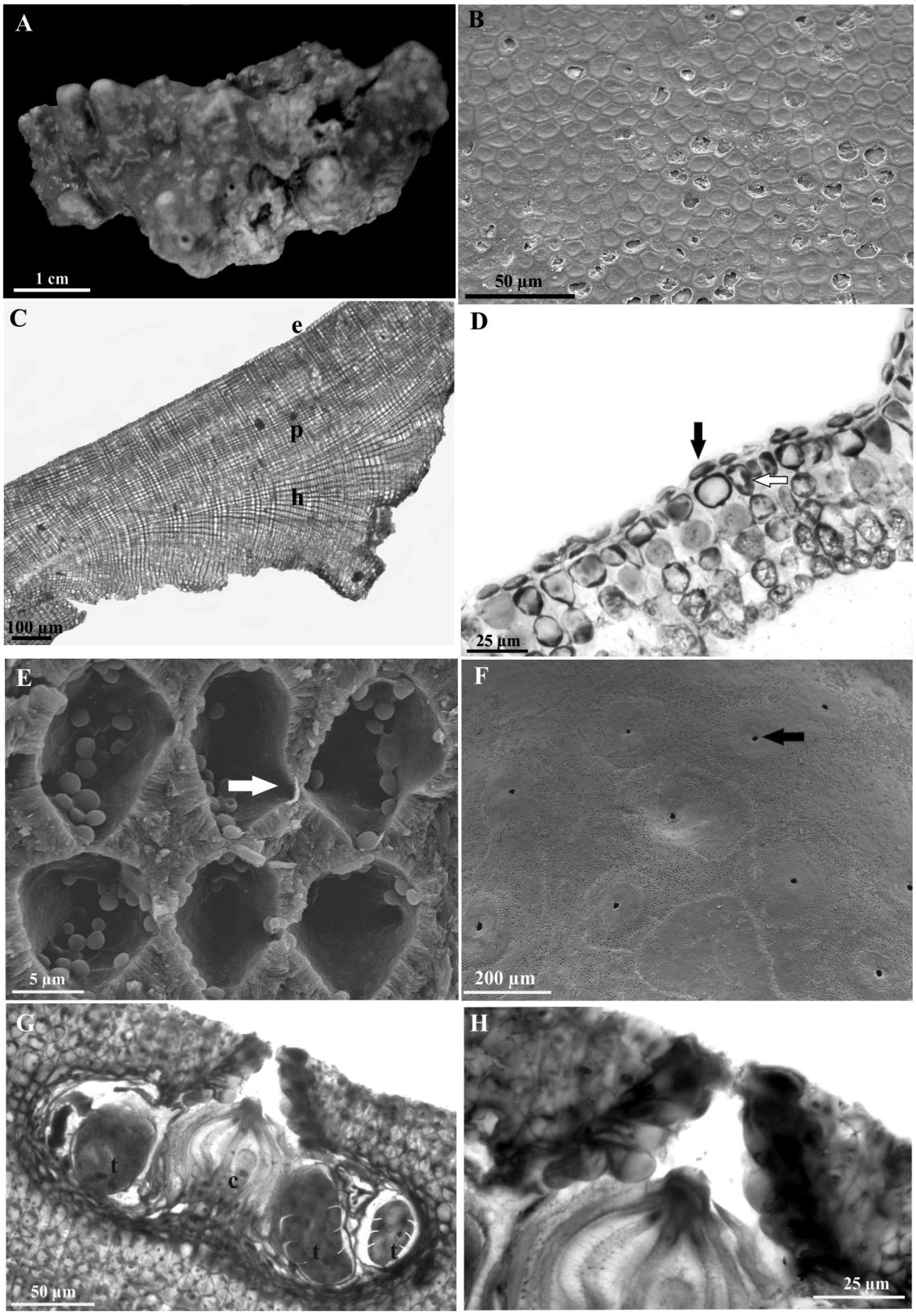

FIGURE 4 A–H: General aspects and micrographs of *Lithophyllum stictaeforme* (Areschoug in J. Agardh) Hauck. **A.** General aspects. **B.** Epithallial cells in surface view, SEM. **C.** Longitudinal section showing dimerous construction (e—epithallial, p—perithallial, h—hypothallial). **D.** Longitudinal section showing rounded or flattened epithallial cells (black arrow), and subepithallial initials as long as or longer than the cells immediately subtending them (white arrow). **E.** Longitudinal fracture of the cells of adjacent filaments joined by secondary pit-connections (arrow), SEM. **F.** Uniporate tetrasporangial conceptacles in surface view, SEM. **G.** Longitudinal section of tetrasporangial conceptacles with central columella (c) and zonately divided tetrasporangia (t). **H.** Detail of the pore canal from the tetrasporangial conceptacle.

Global distribution: Australia, Bermuda, Canary Islands, Chile, Colombia, Florida, France, Greece, Israel, Italy, Mexico, New Zealand, Pelagic Islands and Spain (Guiry & Guiry 2014).

TABLE 3: Comparison between descriptions of sporophytic specimens of *Lithophyllum stictaeforme* based on vegetative and reproductive features (+ = present, - = absent; ND = not disclosed). [1] Furnari *et al.* (1996)—as *L. frondosum*—Mediterranean Sea, [2] Athanasiadis (1999)—as *L. expansum*—France, [3] Nunes *et al.* (2008)—Brazil, [4] Villas-Boas *et al.* (2009)—Brazil, [5] Harvey *et al.* (2009)—Australia.

Characters (measured in µm)	*L. stictaeforme* (this study)	*L. stictaeforme* [2] (Lectótipo)	*L. stictaeforme* [1]	*L. stictaeforme* [3]	*L. stictaeforme* [4]	*L. stictaeforme* [5]
Epithallial cell length	7–8.3	ND	4–8	2–3	8–12	3–6
Epithallial cell diameter	7.8–10	ND	10–16	5–9	5–8	4–11
Perithallial cell length	10–20	10–24	15–45	ND	20–22	8–35
Perithallial cell diameter	8–15	12–17	10–20	ND	9–13	11–20
Hypothallial cell length	8.5–17	8–24	12–22	ND	ND	ND
Hypothallial cell diameter	7–17.5	7–25	15–50	ND	ND	ND
Tetrasporangial conceptacle length	77–117	100–175	<120	105–180	125–135	(55) 75–110
Tetrasporangial conceptacle diameter	185–258.3	375–475	200–450	202–262	220–230 (295)	(230) 260–390
Tetrasporangia length	50–89	ND	85–120	ND	ND	ND
Number of cells in the roof of tetrasporangial conceptacle	5–6	5–10	5–9	5–7	3–7	(3)4–6
Position of the floor of the conceptacle chamber (number of cells)	12–14	16–17	> 10	11–13	6–10	-

Mastophoroideae Setchell (1943: 134)

Spongites yendoi (Foslie) Chamberlain (1993: 100)

Goniolithon yendoi Foslie (1900a: 25)

Synonyms: *Lithophyllum yendoi* (Foslie) Foslie (1900b: 20), *Pseudolithophyllum yendoi* (Foslie) Adey (1970: 14), *Lithophyllum natalense* Foslie (1907: 27).

Figure: 5 A–G.

Description: Non-geniculate thallus forming free-living rhodoliths or attached to the substrate, growth form encrusting. Color varying from grayish to brownish-red. Thallus pseudoparenchymatous with monomerous construction. Epithallial cells single and more or less elliptical, 5–7.6 µm long and 7.5–9 µm in diameter. Subepithallial initials markedly longer than subtending ones, 9.5–13.7 µm long and 6–8.8 µm in diameter. Cells from the perithallus are 8–12.1 µm long and 6.5–9 µm in diameter. Cells from the hypothallus are 13–17.2 µm long and 8–11 µm in diameter. Trichocytes arranged in horizontal rows, 18–25 µm long and 12–18.7 µm in diameter.

Cells of the adjacent filaments are linked by lateral cell fusions. Secondary pit-connection not observed. Uniporate tetrasporangial conceptacles, 75–116.2 µm long and 102–266 µm in diameter, chambers are more or less elliptical. Conceptacle roofs 3–6 cells thick, including the epithallial cells, pore without an apical plug. Central columella present. Conceptacle chamber floor formed by 3–5 cell layers; tetrasporangial conceptacle pore canals lined by cells that are orientated parallel to the thallus surface, projected into the canal. Zonately divided tetrasporangia, 38–90 µm long and 19–45 µm in diameter. Gametangial thallus not observed.

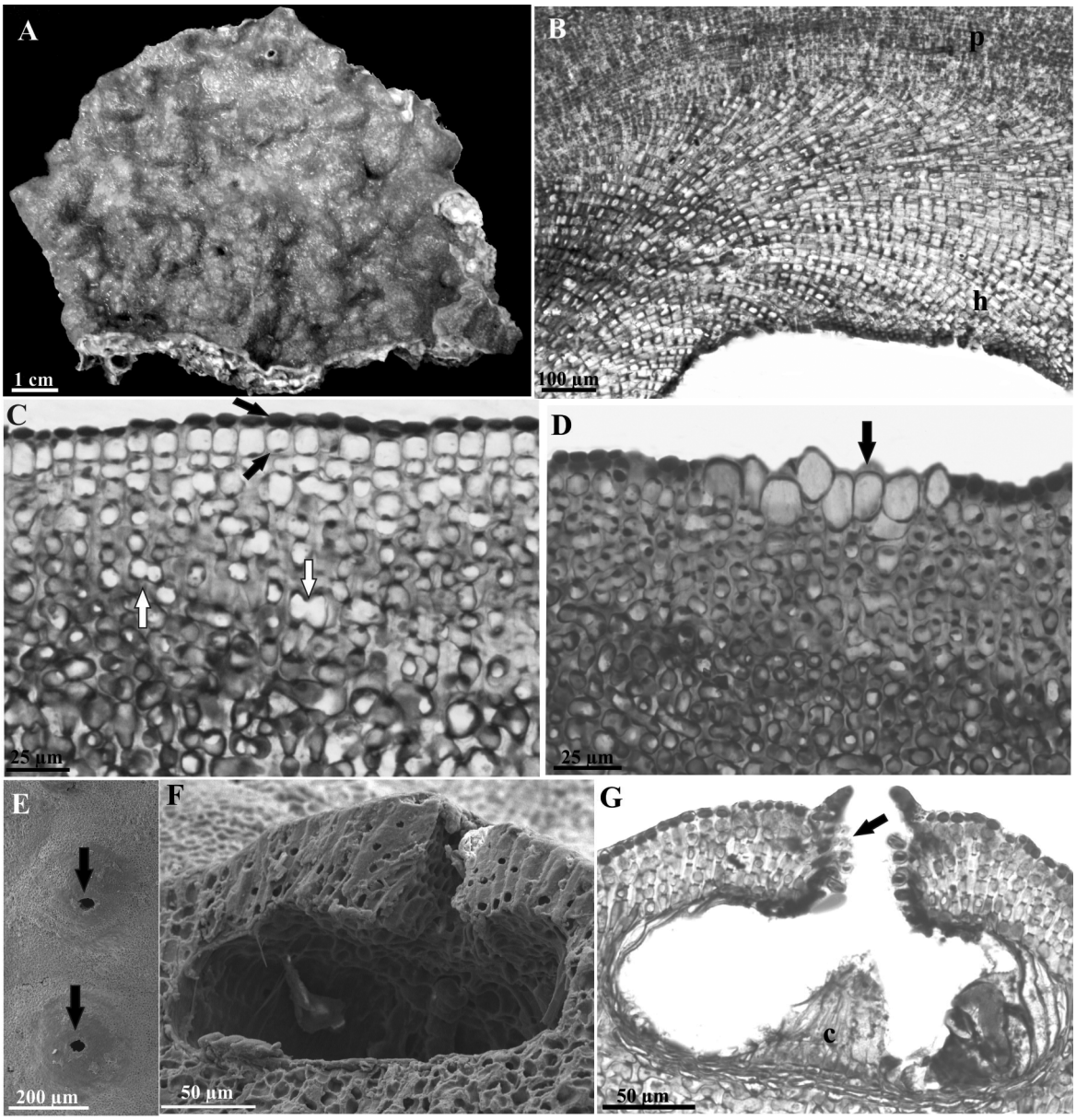

FIGURE 5 A–G: General aspects and micrographs of *Spongites yendoi* (Foslie) Chamberlain. **A.** General aspects. **B.** Longitudinal section showing monomerous construction (e—epithallial, p—perithallial, h—hypothallial). **C.** Longitudinal section showing rounded or flattened epithallial cells, subepithallial initials as long as or longer than the cells immediately subtending them (black arrows), and cells of adjacent filaments joined by cell fusions (white arrows). **D.** Longitudinal section showing trichocytes grouped in horizontal row (arrow). **E.** Uniporate tetrasporangial conceptacles in surface view, SEM, showing pores (arrows). **F.** Longitudinal fracture, SEM, uniporate tetrasporangial conceptacles. **G.** Longitudinal section of the tetrasporangial conceptacle showing pore canals lined by cells orientated parallel to the thallus surface, projected into the pore canal (arrow), and presence of central columella (c).

Material examined: BRASIL. Bahia: Salvador, Itapuã, 12°57'22"S, 38°21'31"W, 29 September 2011, *I.O. Costa et al. s.n.* (ALCB 103456, ALCB 103457); Camaçari, Arembepe, 12°44'25"S, 38°08'58"W, 12 July 2012, *CETREL s.n.* (ALCB 103458).

Comments: Plants found growing in the subtidal zone at depths between 9 and 25 m.

Distribution on the Brazilian coast: Espírito Santo (Henriques *et al.* 2011), Bahia (Costa *et al.* in press).

Global distribution: Alaska, Australia, Indian Ocean Islands, Indonesia, Japan, Mozambique, Namibia, New Zealand, South Africa (Guiry & Guiry 2014) and Mexico (Fragoso & Rodriguez 2002, Mateo-Cid *et al.* 2007).

TABLE 4: Comparison between descriptions of sporophytic specimens of *Spongites yendoi* based on vegetative and reproductive features (+ = present, - = absent; ND = not disclosed). [1] Chamberlain (1993)—Japan, [2] Penrose (1996)—Australia, [3] Mateo-Cid *et al.* (2007)—Mexico, [4] Henriques *et al.* (2011)—Brazil, [5] Basso & Rondoni (2006)—Mediterranean Sea.

Characters (measured in µm)	*S. yendoi* (this study)	*S. yendoi* [1] (lectotype)	*S. yendoi* [2]	*S. yendoi* [3]	*S. yendoi* [4]
Trichocytes	+	+	+	+	-
Trichocyte length	18–25	15	ND	15–17.5	-
Trichocyte diameter	12–18.7	8	ND	12.5–15	-
Epithallial cell length	5–7.6	ND	ND	2.5–3	2–3
Epithallial cell diameter	7.5–9	ND	ND	4–6	6–8
Perithallial cell length	8–12.1	3–10	2–6	ND	4–8
Perithallial cell diameter	6.5–9	3–8	5–22	ND	6–10
Hypothallial cell length	13–17.2	6–12	ND	ND	10–19
Hypothallial cell diameter	8–11	3–8	ND	ND	3–7
Tetrasporangial conceptacle length	75–116.2	80	109–185	80–150	105–110
Tetrasporangial conceptacle diameter	102–266	170	164–232	180–295	280–290
Tetrasporangia length	38–90	ND	ND	32.5–75	17–20
Number of cells in the roof of tetrasporangial conceptacle	3–6	ND	3–5	ND	3–8

Spongites sp.

Figure: 6 A–G.

Description: Non-geniculate thallus forming free-living rhodoliths or attached to substrate, growth form encrusting or lumpy. Color varying from grayish to brownish-red. Thallus pseudoparenchymatous with monomerous construction. Epithallial cells single and rounded or flattened, 4.1–5.35 µm long and 5–6.4 µm in diameter. Subepithallial initials as long as or longer than the cells immediately subtending them, 3.5–7.1 µm long and 3.4–5.4 µm in diameter. Cells from the perithallus are 3–4.5 µm long and 4–6 µm in diameter. Cells from the hypothallus are 8–12 µm long and 4–6 µm in diameter. Trichocytes not observed. Cells of the adjacent filaments are joined by cell fusions. Secondary pit-connections not observed. Uniporate carposporangial conceptacles, 53 µm long and 118.6 µm in diameter. Conceptacle roofs 3–5 cells thick, including the epithallial cells. Conceptacle chamber floor formed by 3–4 cell layers. Carposporangia, 14.4–25 µm long and 23–30.1 µm in diameter, enclosing small gonimoblast filaments that originated from an evident central fusion cell measuring 13.5 µm long and 27.5 µm in diameter. Tetrasporangial and male thallus not observed.

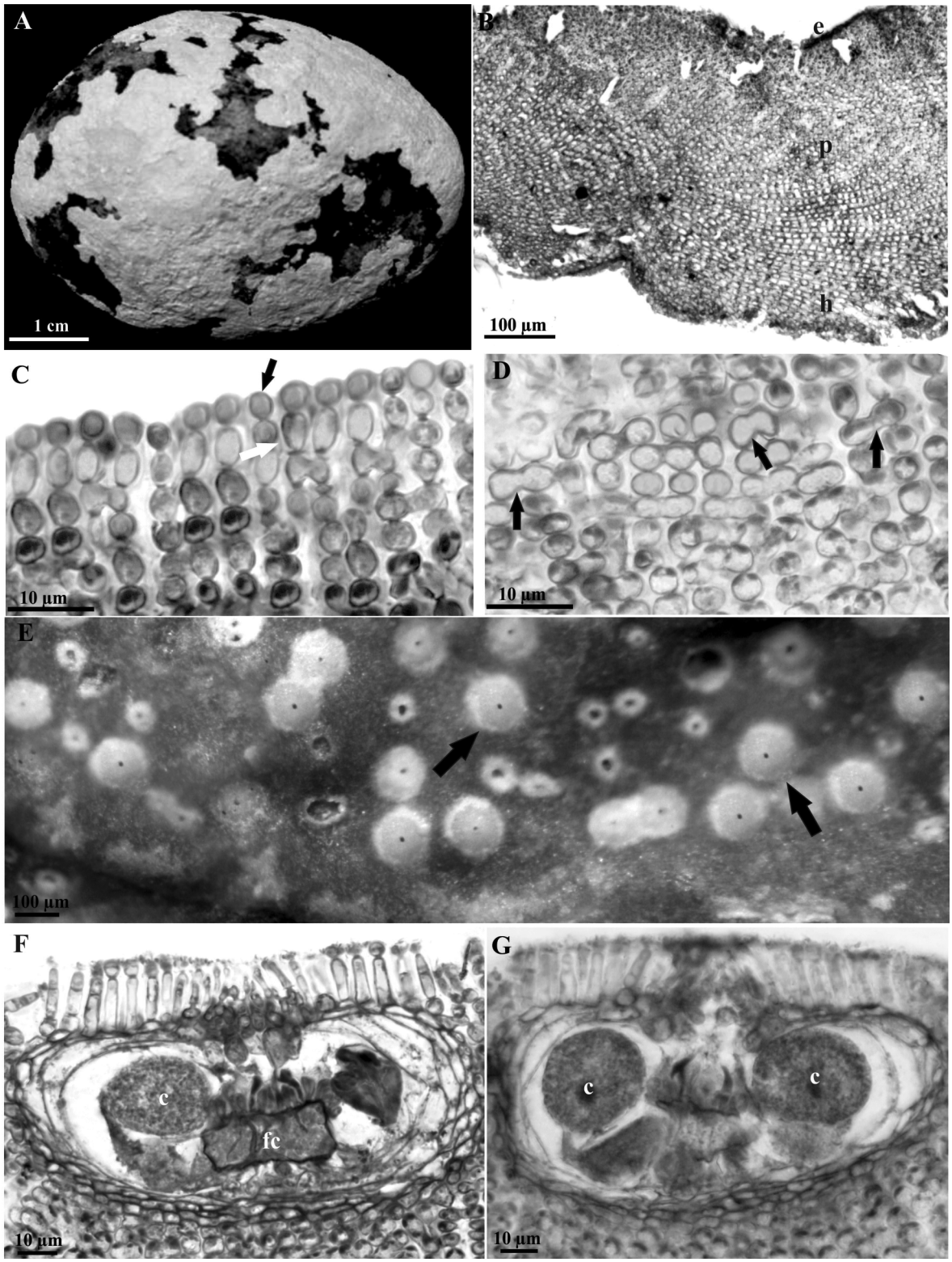

FIGURE 6 A–G: General aspects and micrographs of *Spongites* sp. **A.** General aspects. **B.** Longitudinal section showing monomerous construction (e—epithallial, p—perithallial, h—hypothallial). **C.** Longitudinal section showing rounded or flattened epithallial cells (black arrow), and subepithallial initials as long as or longer than the cells immediately subtending them (white arrow). **D.** Longitudinal section of the cells of adjacent filaments joined by cell fusions (arrows). **E.** Uniporate carposporangial conceptacles in surface view (arrows). **F.** Longitudinal section of carposporangial conceptacles showing large fusion cell (fc) and carposporangia (c). **G.** Longitudinal section of carposporangial conceptacles showing carposporangia (c).

Material examined: BRASIL. Bahia: Salvador, Barra, 13°00'11"S, 38°32'01"W, 28 September 2011, *I.O. Costa et al. s.n.* (ALCB 103443); Mata de São João, Imbassaí, 12°30'11"S, 37°57'36"W, 28 August 2011, *I.O. Costa et al. s.n.* (ALCB 103710).

Comments: Plants found growing in the midlittoral zone in the front region of the reef and in the subtidal zone at depths between 9 and 17 m. Epiphyted by *Bryothamnion seaforthii* (Turner) Kütz. (1843: 433), *B. triquetrum*, *Centroceras clavulatum, Chondracanthus acicularis* (Roth) Fredericq in Hommersand, Guiry, Fredericq & Leister (1993: 117)*, Digenea simplex* (Wulfen) C. Agardh (1822: 389), *Enantiocladia duperreyi* and *Pterosiphonia pennata.*

TABLE 5: Comparison between descriptions of carposporophytic specimens of *Spongites* based on vegetative and reproductive features (+ = present, - = absent; ND = not disclosed). [1] Mateo-Cid *et al.* (2007)—Mexico, [2] Penrose (1996)—Australia.

Characters (measured in µm)	*Spongites* sp. (this study)	*S. yendoi* (this study)	*S. yendoi* [1]	*S. fruticulosus* [2]	*S. hyperellus* [2]
Trichocytes	-	+	+	-	+
Epithallial cell length	4.1–5.35	5–7.6	2.5–3	4–11	ND
Epithallial cell diameter	5–6.4	7.5–9	4–6	6–18	ND
Perithallial cell length	3–4.5	8–12.1	ND	6–28	2–14
Perithallial cell diameter	4–6	6.5–9	ND	5–22	2–8
Hypothallial cell length	8–12	13–17.2	ND	10–32	ND
Hypothallial cell diameter	4–6	8–11	ND	5–17	ND
Carposporangial conceptacle length	53	-	80–150	295–320	109–128
Carposporangial conceptacle diameter	118.6	-	240–300	575–595	136–150
Carposporangia length	14.4–25	-	105–108	ND	ND
Number of cells in the roof of carposporangial conceptacle	4–5	-	ND	8–12	3–7
Fusion cell	High and long	-	ND	Compressed and long	Flattened

Hapalidiaceae Gray (1864: 22)
Melobesioideae Bizzozero (1885: 109)
Mesophyllum erubescens (Foslie) M. Lemoine (1928: 252)
Lithothamnion erubescens Foslie (1900b: 9-10)
Synonyms: *Lithothamnion erubescens* f. *madagascarense* Foslie (1901: 3–4), *Lithothamnion erubescens* f. *haingsisianum* Weber-van Bosse & Foslie in Foslie (1901: 4), *Lithothamnion erubescens* f. *subflabellatum* Foslie (1904: 31–36), *Lithothamnion madagascarense* (Foslie) Foslie (1906: 19), *Mesophyllum madagascariense* (Foslie) Adey (1970: 25).

Figure: 7 A–I.

Description: Non-geniculate thallus forming free-living rhodoliths or attached to the substrate, growth form lumpy or fruticose. Color varying from grayish to brownish-red. Thallus pseudoparenchymatous with monomerous construction. Epithallial cells single and rounded or flattened, 4.5–7 µm long and 6–8.6 µm in diameter. Subepithallial initials as long as or longer than the cells immediately subtending them, 9.4–10.8 µm long and 5.7–7.7 µm in diameter. Cells from the perithallus are 8–12 µm long and 4–8 µm in diameter. Cells from the hypothallus are 11–17 µm long and 3,5–6 µm in diameter. Trichocytes dispersed at the thallus surface. Cells of the adjacent filaments joined by cell fusions. Secondary pit-connections not observed. Multiporate tetrasporangial

conceptacles, 153–243.8 µm long and 196–385 µm in diameter. Conceptacle roofs 4–6 cells thick, including the epithallial cells. Conceptacle chamber floor formed by more than four cell layers. The basal cells from the filaments which line the pore canal are longer than the other cells of the same filaments. Zonately divided tetra/bisporangia, 104.5–124.1 µm long and 51.45–84.87 µm in diameter. Gametangial thallus not observed.

Material examined: BRASIL. Bahia: Salvador, Barra, 13°00'11"S, 38°32'01"W, 28 September 2011 *P.A. Horta et al. s.n.* (ALCB 103461); Salvador, Itapuã, 12°57'22"S, 38°21'31"W, 29 September 2011, *I.O. Costa et al. s.n.* (ALCB 103462); Salvador, Stella Maris, 12°56'22"S, 38°19'41"W, 05 April 2012, *I.O. Costa et al. s.n.* (ALCB 103446); Camaçari, Arembepe, 12°44'25"S, 38°08'58"W, 07 May 2012, *I.O. Costa et al. s.n.* (ALCB 103459), Camaçari, Itacimirim, 12°36'53"S, 38°02'31"W, 01 February 2007, *J.M.C. Nunes et al. s.n.* (ALCB 103447); Mata de São João, Praia do Forte, 12°34'42"S, 38°00'06"W, 07 October 1998, *C. Coimbra s.n.* (ALCB 103678).

Comments: Plants found growing in the midlittoral zone in the protected region of the reef and in the subtidal zone at depths between 9 and 25 m. Epiphyted by *Jania adhaerens* e *Palisada perforata* (Bory de Saint-Vincent) K.W.Nam (2007: 54).

TABLE 6: Comparison between descriptions of sporophytic specimens of *Mesophyllum erubescens* based on vegetative and reproductive features (+ = present, - = absent; ND = not disclosed). [1] Verheij (1993)—Indonesia, [2] Keats & Chamberlain (1994)—South Africa, [3] Nunes *et al*. (2008)—Brazil, [4] Horta *et al.* (2011)—Brazil.

Characters (measured in µm)	*M. erubescens* (this study)	*M. erubescens* [4] (holotype)	*M. erubescens* [1]	*M. erubescens* [2]	*M. erubescens* [3]	*M. erubescens* [4]
Trichocytes	+/-	+/-	+/-	+/-	+/-	+/-
Epithallial cell length	4.5–7	2–3	5–10	2–3	5	2–4
Epithallial cell diameter	6.1–8.6	5–8	4–11	6–7	5–8	4–9
Perithallial cell length	8–12	5–23	5–10	5–10	5–10	14–21
Perithallial cell diameter	4–8	5–14	4–11	4–7,5	5–12	5–8
Hypothallial cell length	11–17	14–30	8–15	7–22	ND	11–20
Hypothallial cell diameter	3,5–6	5–14	ND	5–8	ND	3–6
Tetrasporangial conceptacle length	153–243.8	90–180	ND	85–125	150	84–153
Tetrasporangial conceptacle diameter	196–385	200–354	350–475	210–300	195–310	254–551
Tetrasporangia length	104.5–124.1	–	ND	130–170	100–160	76–119
Number of cells in the roof of tetrasporangial conceptacle	4–6	4–6	4–7	4–7	4–5	5–7
Basal cells of the conceptacle canal more elongated than other roof	+	+	+	+	+	+
Conceptacles buried in the thallus	+	-	+	+	+	+

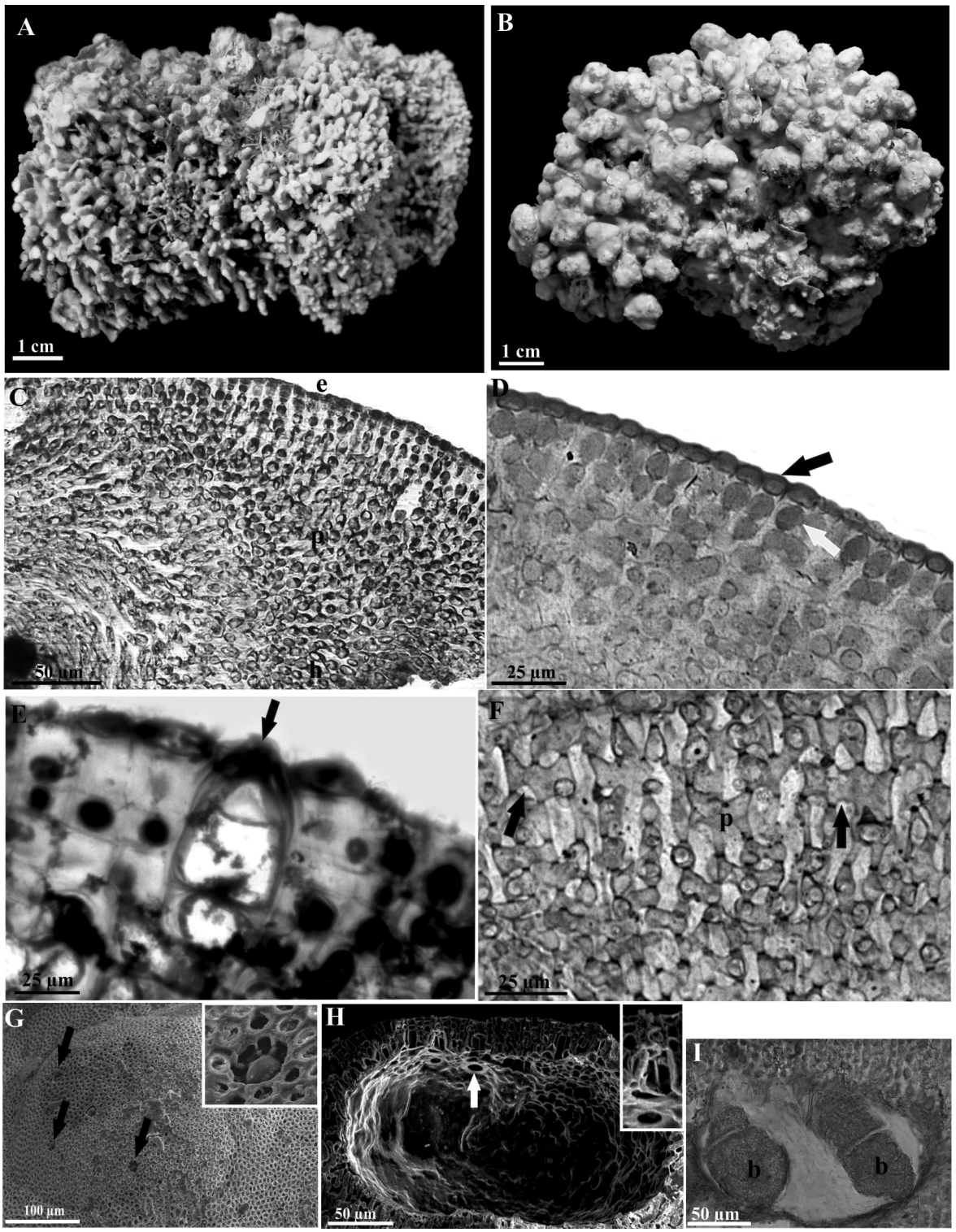

FIGURE 7 A–I: General aspects and micrographs of *Mesophyllum erubescens* (Foslie) M. Lemoine. **A.** General aspects, fruticose growth-form. **B.** General aspects, lumpy growth-form. **C.** Longitudinal section showing monomerous construction (e—epithallial, p—perithallial, h—hypothallial). **D.** Longitudinal section showing rounded or flattened epithallial cells (black arrow), and subepithallial initials as long as or longer than the cells immediately subtending them (white arrow). **E.** Longitudinal section showing isolated trichocytes (arrow). **F.** Longitudinal section of the cells of adjacent filaments joined by cell fusions (arrows). **G.** Multiporate tetrasporangial conceptacles in surface view, SEM, showing pores (arrows), detail apical plug. **H.** Longitudinal fracture, SEM, multiporate tetrasporangial conceptacles showing pore (arrow), with detail of the basal cell of conceptacle canal longer than the other cells of the filament. **I.** Longitudinal section of the bisporangial conceptacle with bisporangia (b).

Distribution on the Brazilian coast: Bahia (Figueiredo & Steneck 2002, Nunes *et al.* 2008, Figueiredo *et al.* 2007, Bahia *et al.* 2010), Arquipélago de Fernando de Noronha (Foslie 1900, Burgos 2011), Santa Catarina (Horta *et al.* 2011), Espírito Santo (Amado Filho *et al.* 2010).

Global distribution: Australia, Canary Islands, China, Indian Ocean Islands, India, Indonesia, Japan, Kenya, Korea, Madagascar, New Zealand, Pacific Islands, Senegal, South Africa, and Tanzania (Guiry & Guiry 2014).

Lithothamnion crispatum Hauck (1878: 289)

Synonyms: *Lithophyllum crispatum* (Hauck) Hauck (1885: 270), *Archaeolithothamnion crispatum* (Hauck) Foslie (1898: 3), *Lithothamnion brasiliense* f. *heteromorpha* Foslie (1900b: 4), *Lithothamnion superpositum* Foslie (1900: 8), *Lithothamnion fruticulosum* f. *confinis* Foslie (1904: 4), *Lithothamnion philippii* Foslie f. *crispata* (Hauck) Foslie (1904: 13), *Lithothamnion indicum* Foslie (1907: 7), *Lithothamnion heteromorphum* (Foslie) Foslie (1908: 10), *Mesophyllum superpositum* (Foslie) Adey (1970: 26).

Figure: 8 A–I.

Description: Non-geniculate thallus forming free-living rhodoliths, growth form lumpy or fruticose. Color varying from grayish to brownish-red. Thallus pseudoparenchymatous with monomerous construction. Epithallial cells single and flared, 2–5 µm long and 6–10 µm in diameter. Subepithallial initials as long as or longer than the cells immediately subtending them, 7–17 µm long and 4–10 µm in diameter. Cells from the perithallus are 7–20 µm long and 4–10 µm in diameter. Cells from the hypothallus are 16–30 µm long and 7–14 µm in diameter. Cells of the adjacent filaments are joined by cell fusions. Secondary pit-connections not observed. Multiporate tetrasporangial conceptacle roof protruding above the surrounding thallus surface, chambers 100–165 µm long and 240–320 µm in diameter. Conceptacle roofs 4–6 cells thick, including the epithallial cells. Pore conceptacle with 7–9 µm in diameter, presence of depressions around the pore which is surrounded by 5–6 rosette cells. Tetrasporangia not observed. Gametangial thallus not observed.

TABLE 7: Comparison between descriptions of sporophytic specimens of *Lithothamnion crispatum* based on vegetative and reproductive features (+ = present, - = absent; ND = not disclosed). [1] Basso *et al.* (2011)—Adriatic Sea, [[2] Keats *et al.* (2000)—South Africa, [3] Harvey *et al.* (2003)—Australia, [4] Farias *et al.* (2010)—Brazil, [5] Bahia *et al.* (2010)—Brazil—as *L. superpositum*].

Characters (measured in µm)	*L. crispatum* (this study)	*L. crispatum* [1] (lectotype)	*L. crispatum* [2]	*L. crispatum* [3]	*L. crispatum* [4]	*L. crispatum* [5]
Epithallial cell length	2–5	3–5.5	4–11	3–5	2–5	2,5–4
Epithallial cell diameter	6–10	7–14.5	7–11	8–11	6–12	5–8
Perithallial cell length	7–20	4.5–23	4–11.5	ND	13–24	ND
Perithallial cell diameter	4–10	7–18	7–11	ND	7–13	ND
Hypothallial cell length	16–30	9–39	10–40	ND	10–30	ND
Hypothallial cell diameter	7–14	4.5–16	7–9	ND	2–10	ND
Tetrasporangial conceptacle length	100–165	153	105–187	125–170	150–230	110–225
Tetrasporangial conceptacle diameter	240–320	306	125–370	390–440	250–525	220–450
Tetrasporangia length	–	ND	75–110	90–165	85–115	100–145
Number of cells in the roof of tetrasporangial conceptacle	4–6	ND	ND	4–5	ND	3–5
Number of cells in a rosette around the pore of the tetrasporangial conceptacle	5–6	ND	5–7	ND	ND	5–6
Depressions around the pores of tetrasporangial conceptacle	+	+	+	+	+	+

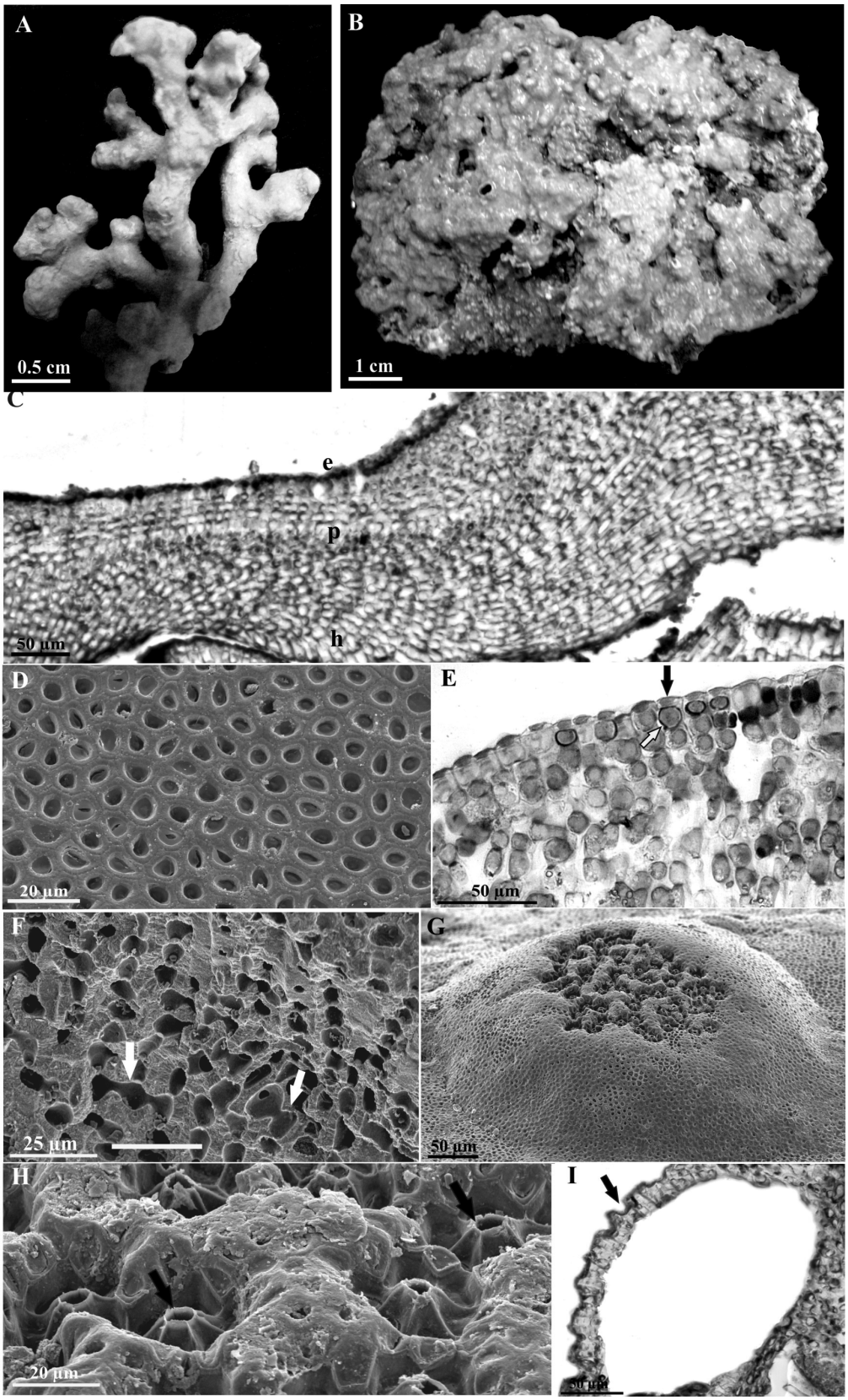

FIGURE 8 A–I: General aspects and micrographs of *Lithothamnion crispatum* Hauck. **A.** General aspects, fruticose growth-form. **B.** General aspects, lumpy growth-form. **C.** Longitudinal section showing monomerous construction (e—epithallial, p—perithallial, h—hypothallial). **D.** Epithallial cells in surface view, SEM. **E.** Longitudinal section showing flared epithallial cells (black arrow), and subepithallial initials as long as or longer than the cells immediately subtending them (white arrow). **F.** Longitudinal fracture of the cells of adjacent filaments joined by cell fusion (arrows), SEM. **G.** Multiporate tetrasporangial conceptacles in surface view, SEM. **H.** Detail of the multiporate tetrasporangial conceptacles showing depressions around the pore (arrows), SEM. **I.** Longitudinal section of the tetrasporangial conceptacle showing depressions around the pore (arrow).

Material examined: BRASIL. Bahia: Camaçari, Itacimirim, 12°36'53"S, 38°02'31"W, 29 October 2010, *N.A. Andrade et al. s.n.* (ALCB 100349); Camaçari, Arembepe, 12°44'25"S, 38°08'58"W, 12 July 2012, *CETREL s.n.* (ALCB 103681).

Comments: Plants found growing in the subtidal zone at depths between 20 and 23 m.

Distribution on the Brazilian coast: Rio Grande do Norte (Farias *et al.* 2010—as *L. superpositum*), Fernando de Noronha (Amado Filho *et al.* 2012a), Bahia (Figueiredo & Steneck 2002, Bahia *et al.* 2010, Farias *et al.* 2010—as *L. superpositum*, Amado Filho *et al.* 2012b—as *L. crispatum*), Santa Catarina (Farias—2010—as *L. superpositum*).

Global distribution: Adriatic, Algeria, Australia, Corsica, Costa Rica, Croatia, France, Greece, Indian Ocean Islands, Indonesia, Italy, Korea, Libya, Mauritania, New Zealand, Panama, South Africa, Spain, Sudan, Turkey and Yemen (Guiry & Guiry 2014).

Lithothamnion brasiliense Foslie (1900b: 4)

Figure: 9 A–H.

Description: Non-geniculate thallus forming free-living rhodoliths, growth form lumpy or fruticose. Color brownish-red. Thallus pseudoparenchymatous with monomerous construction. Epithallial cells single and flared, 3–5 µm long and 5–10 µm in diameter. Subepithallial initials as long as or longer than the cells immediately subtending them, 6–15 µm long and 6–14 µm in diameter. Cells from the perithallus are 6–20 µm long and 6–12 µm in diameter. Cells from the hypothallus are 9–22 µm long and 6–12 µm in diameter. Cells of the adjacent filaments are joined by cell fusions. Secondary pit-connections not observed. Multiporate tetrasporangial conceptacle roof protruding above the surrounding thallus surface, chambers 126–155 µm long and 300–500 µm in diameter. Conceptacle roofs 4–6 cells thick, including the epithallial cells. Pore conceptacle with 7–14 µm in diameter, surrounded by 5–7 rosette cells. Tetrasporangia not observed. Gametangial thallus not observed.

Material examined: BRASIL. Bahia: Salvador, Itapuã, 12°57'22"S, 38°21'31"W, 14 October 2011, *J.M.C. Nunes et al. s.n.* (ALCB 103682); Camaçari, Arembepe, 12°44'25"S, 38°08'58"W, 12 July 2012, *CETREL s.n.* (ALCB 103683), Itacimirim, 12°36'53"S, 38°02'31"W, 01 February 2007, *J.M.C. Nunes et al. s.n.* (ALCB 103684).

TABLE 8: Comparison between descriptions of sporophytic specimens of *Lithothamnion brasiliense* based on vegetative and reproductive features (+ = present, - = absent; ND = not disclosed). [1] Foslie (1900)—Brazil, [2] Horta (2000)—Brazil, [3] Bahia *et al.* (2010)—Brazil.

Characters (measured in µm)	*L. brasiliense* (this study)	*L. brasiliense* [1] (holotype)	*L. brasiliense* [2]	*L. brasiliense* [3]
Epithallial cell length	3–5	ND	2.4–5	3–4
Epithallial cell diameter	5–10	ND	4–10	5–8
Perithallial cell length	6–20	14–24	5–38	ND
Perithallial cell diameter	6–12	8–14	4–12	ND
Hypothallial cell length	9–22	ND	5–40	ND
Hypothallial cell diameter	6–12	ND	4–18	ND
Tetrasporangial conceptacle length	126–155	ND	97–200	100–180
Tetrasporangial conceptacle diameter	300–500	450–600	330–750	300–500
Tetrasporangia length	-	100	130–186	ND
Number of cells in the roof of tetrasporangial conceptacle	4–6	ND	ND	4–6
Number of cells in a rosette around the pore of the tetrasporangial conceptacle	5–7	ND	ND	6–8

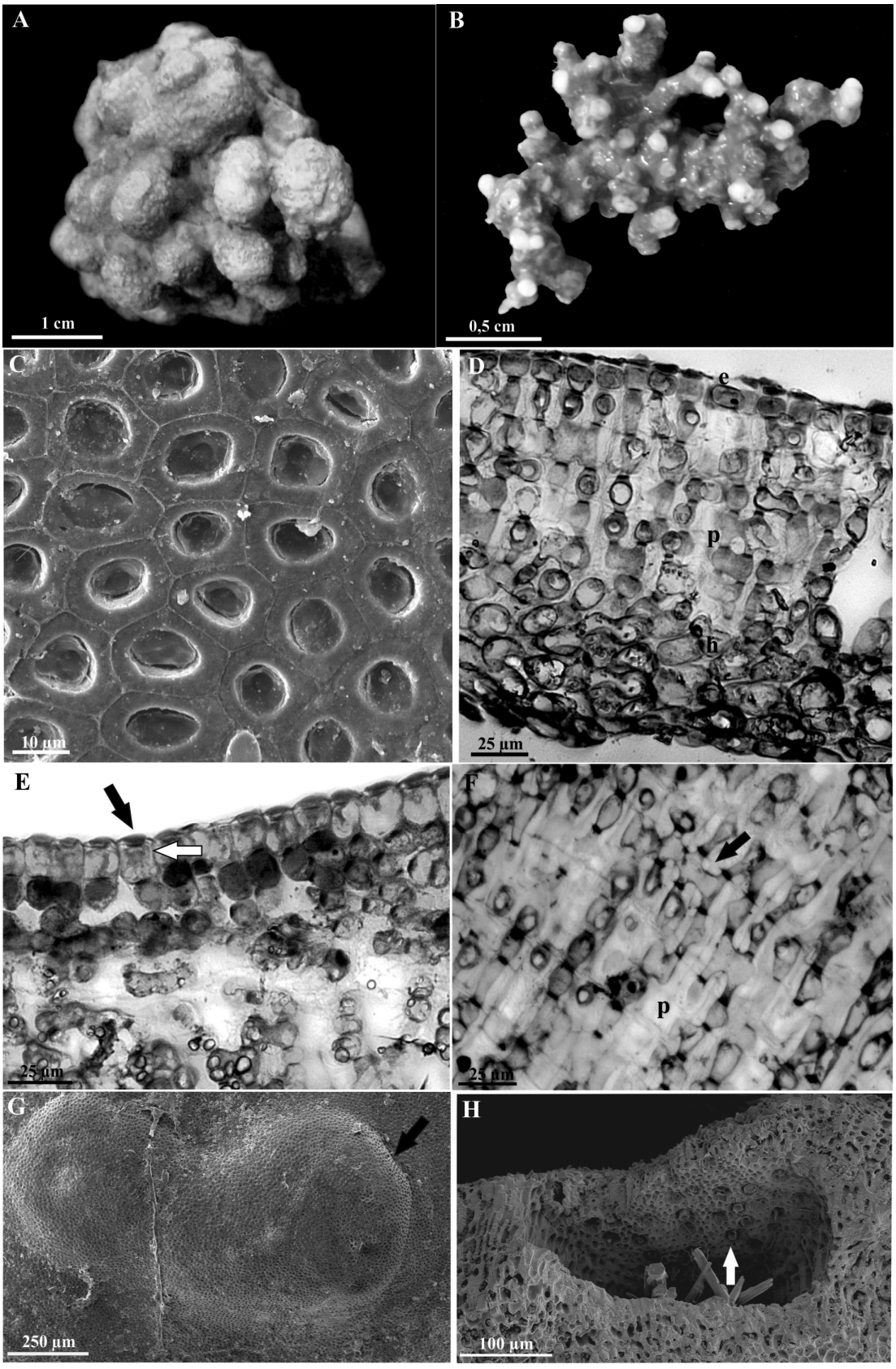

FIGURE 9 A–H: General aspects and micrographs of *Lithothamnion brasiliense* Foslie. **A.** General aspects, fruticose growth-form. **B.** General aspects, lumpy growth-form. **C.** Epithallial cells in surface view, SEM. **D.** Longitudinal section showing monomerous construction (e—epithallial, p—perithallial, h—hypothallial).**E.** Longitudinal section showing flared epithallial cells (black arrow), and subepithallial initials as long as or longer than the cells immediately subtending them (white arrow). **F.** Longitudinal section of the cells of adjacent filaments joined by cell fusions (arrows). **G.** Multiporate tetrasporangial conceptacles in surface view, SEM. **H.** Longitudinal section of the tetrasporangial conceptacle showing the pore (arrow).

Comments: Plants found growing in the midlittoral zone at the front region of the reef and in the subtidal zone at depths between 22 and 25 m.

Distribution on the Brazilian coast: Bahia (Bahia *et al.* 2010), São Paulo (Foslie 1900b, Taylor 1960, Horta 2000).

Global distribution: Restricted to Brazil (Foslie 1900b, Taylor 1960, Horta 2000, Bahia *et al.* 2010).

Phymatolithon masonianum Wilks & Woelkerling (1994: 195)

Figure: 10 A–F.

Description: Non-geniculate thallus forming free-living rhodoliths, growth form lumpy. Color brownish-red. Thallus pseudoparenchymatous with monomerous construction. Epithallial cells single and rounded or flattened, 5–6.5 µm long and 7.2–10 µm in diameter. Subepithallial initials as short as or shorter than the cells immediately subtending them, 4.9–7.5 µm long and 7–10 µm in diameter. Cells from the perithallus are 7.2–18.8 µm long and 4.2–11.5 µm in diameter. Cells from the hypothallus are 15–28.5 µm long and 8.7–13.8 µm in diameter. Trichocytes not observed. Cells of the adjacent filaments joined by cell fusions. Secondary pit-connections not observed. Multiporate tetrasporangial conceptacles flush with the thallus surface, chambers 85.8–183.1 µm long and 188–350.5 µm in diameter, with vegetative cells inside. Conceptacle roofs 4–6 cells thick, including the epithallial cells. Conceptacle chamber floor formed by 2–3 cell layers. Immature tetra/bisporangia, 101–132.4 µm long and 33–44.6 µm in diameter. Gametangial thallus not observed.

TABLE 9: Comparison between descriptions of sporophytic specimens of *Phymatolithon masonianum* based on vegetative and reproductive features (+ = present, - = absent; ND = not disclosed). [1] Wilks & Woelkerling (1994)— Australia, [2] Woelkerling (1996)—Australia, [3] Horta (2000)—Brazil, [4] Mendoza & Cabioch (1998)—France.

Characters (measured in µm)	*P. masonianum* (this study)	*P. masonianum* [1] (holotype)	*P. masonianum* [2]	*P. masonianum* [3]
Epithallial cell length	5–6.55	2–5	2–5	3–5
Epithallial cell diameter	7.2–10	4–13	4–13	5–10
Perithallial cell length	7.2–18.8	5–15	5–30	5–35
Perithallial cell diameter	4.2–11.5	5–10	5–15	5–12
Hypothallial cell length	15–28.5	10–30	ND	18–40
Hypothallial cell diameter	8.7–13.8	7–15	ND	7–16
Tetrasporangial conceptacle length	85–183.1	125–175	95–175	80–150
Tetrasporangial conceptacle diameter	188–350.5	250–500	220–500	170–350
Tetrasporangia length	101–132.4	75–125	70–125	ND
Number of cells in the roof of tetrasporangial conceptacle	5–6	5–7	5–7	5 –7
Vegetative cells within tetrasporangial conceptacle	+	+	+	+

Material examined: BRASIL. Bahia: Salvador, Arembepe, 12°44'25"S, 38°08'58"W, 12 July 2012, *CETREL s.n.* (ALCB 103679).

Comments: Plants found growing in the subtidal zone to 23 m depth.
Distribution on the Brazilian coast: Santa Catarina (Horta 2000) e Bahia (this study).
Global distribution: Australia (Wilks & Woelkerling 1994, Woelkerling 1996).

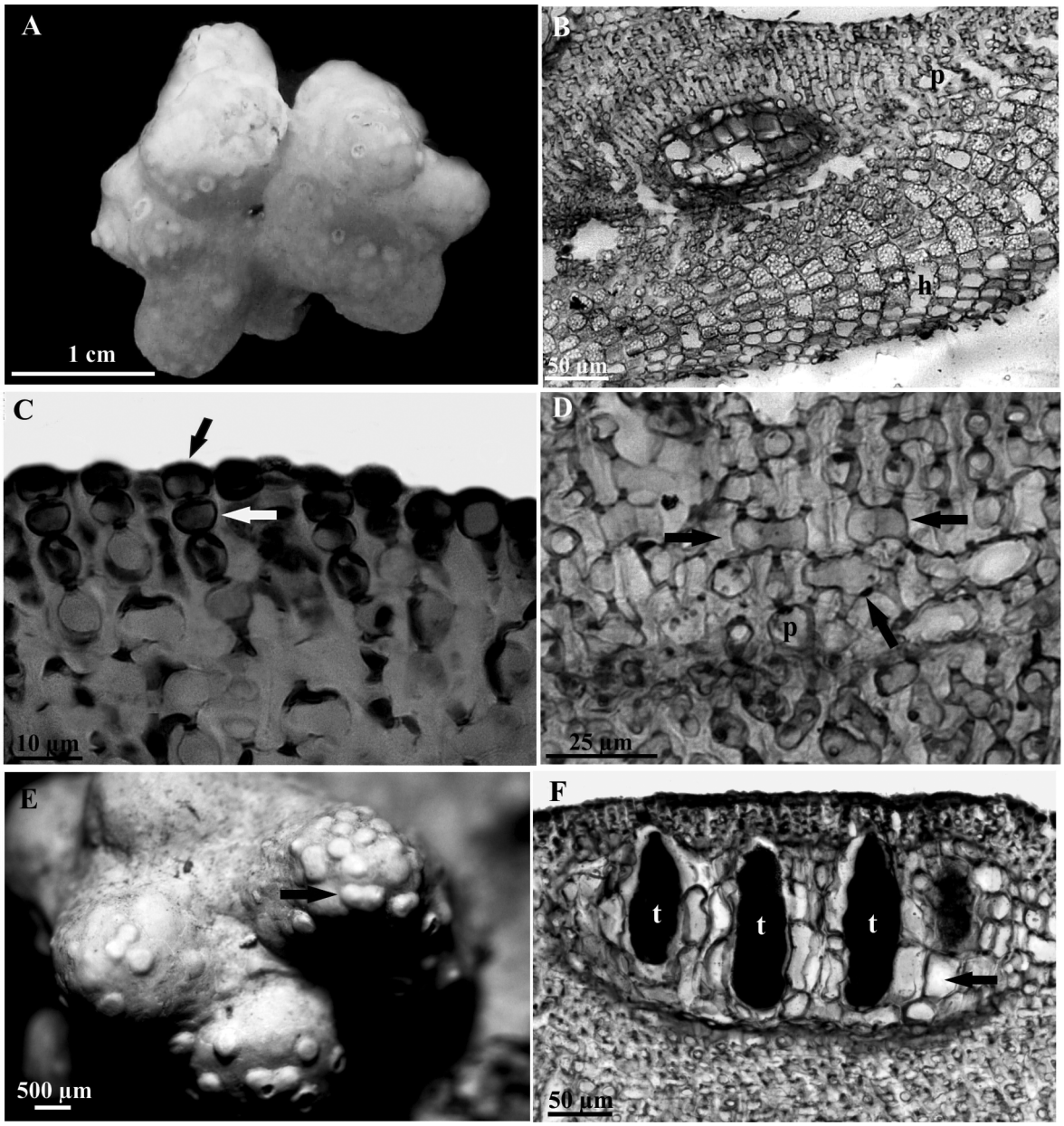

FIGURE 10 A–F: General aspects and micrographs of *Phymatolithon masonianum* Wilks & Woelkerling. **A.** General aspects. **B.** Longitudinal section showing monomerous construction (p—perithallial, h—hypothallial). **C.** Longitudinal section showing rounded or flattened epithallial cells (black arrow), and subepithallial initials as short as or shorter than the cells immediately subtending them (white arrow). **D.** Longitudinal section of the cells of adjacent filaments joined by cell fusions (arrows). **E.** Multiporate tetrasporangial conceptacles in surface view (arrow). **F.** Longitudinal section of the tetrasporangial conceptacle with immature tetrasporangia (t) surrounded by vegetative cells (arrow).

Phymatolithon calcareum (Pallas) Adey et Mckibbin (1970: 100)

Millepora calcarea Pallas, Elenchus Zoophyt., P. van Cleef (1766: 265)

Synonyms: *Nullipora calcarea* (Pallas) Lamarck (1801: 574), *Melobesia calcarea* (Pallas) Harvey (1849: 110), *Spongites calcarea* (Pallas) Kützing (1849: 699), *Lithothamnion calcareum* (Pallas) Areschoug (1852: 523), *Lithothamnion polymorphum* (Linnaeus) Areschoug in J. Agardh (1852: 524), *Lithophyllum calcareum* (Pallas) Foslie (1898: 9).

Figure: 11 A–G.

Description: Non-geniculate thallus overlaying other crustose coralline algae, growth form encrusting. Color varying from grayish to brownish-red. Thallus pseudoparenchymatous with monomerous construction. Epithallial cells single and rounded or flattened, 3.5–5.6 µm long and 4–6 µm in diameter. Subepithallial initials as short as or shorter than the cells immediately subtending them, 5.2–7 µm long and 4–5.75 µm in diameter. Cells from the perithallus are 7–9 µm long and 5–7.5 µm in diameter. Cells from the hypothallus 7–13 µm long and 5–9 µm in diameter. Trichocytes not observed. Cells of the adjacent filaments joined by cell fusions. Secondary pit-connections not observed. Multiporate tetrasporangial conceptacle roof protruding above the surrounding thallus surface, chambers 60.7–101.5 µm long and 100.8–163.8 µm in diameter. Conceptacle roofs 4–7 cells thick, including the epithallial cells. Conceptacle chamber floor formed by 2–3 cell layers. Zonately divided tetra/bisporangia, 60–64.5 µm long and 28–45.5 µm in diameter. Gametangial thallus not observed.

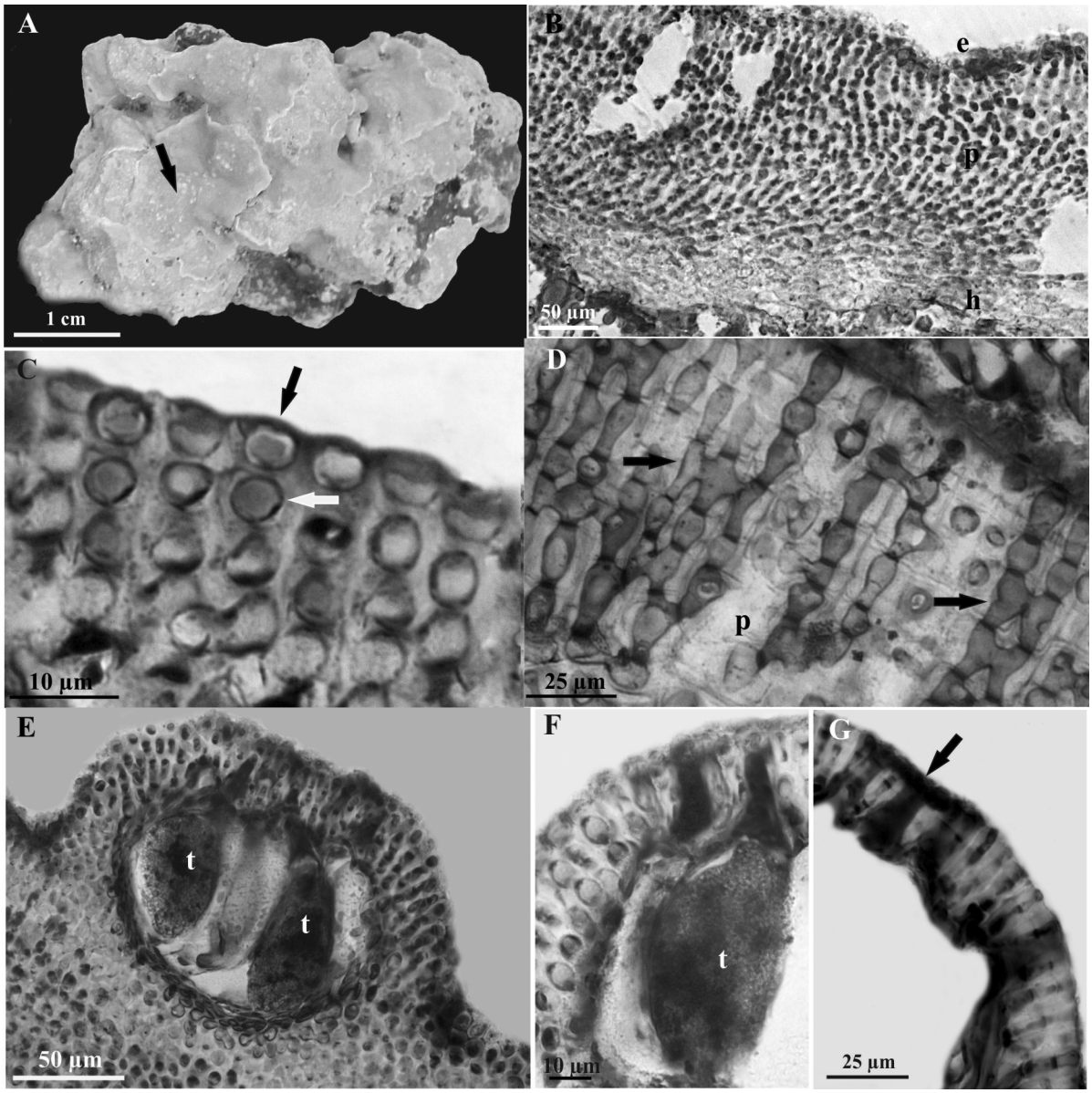

FIGURE 11 A–G: General aspects and micrographs of *Phymatolithon calcareum* (Pallas) Adey et McKibbin. **A.** General aspects (arrow). **B.** Longitudinal section showing monomerous construction (e—epithallial, p—perithallial, h—hypothallial). **C.** Longitudinal section showing rounded or flattened epithallial cells (black arrow), and subepithallial initials as short as or shorter than the cells immediately subtending them (white arrow). **D.** Longitudinal section of the cells of adjacent filaments joined by cell fusions (arrows). **E.** Longitudinal section of the multiporate tetrasporangial conceptacle with immature tetrasporangia (t). **F.** Detail of the multiporate tetrasporangial conceptacle with tetrasporangia (t) and pore. **G.** Detail of the multiporate tetrasporangial conceptacle pore with apical plug (arrow).

Material examined: BRASIL. Bahia: Salvador, Barra, 13°00'11"S, 38°32'01"W, 27 May 2012, *I.O. Costa s.n.* (ALCB 103680).

Comments: Plants found growing in the midlittoral zone in the protected region of the reef, overlaying *Lithophyllum stictaeforme.*

Distribution on the Brazilian coast: Santa Catarina (Horta 2000), Rio de Janeiro (Taylor 1960—como *Lithothamnion polymorphum*) e Bahia (this study).

Global distribution: Australia, Chile, Canada, Colombia, Ethiopia, France, Greece, England, Ireland, Italy, Japan, New Zealand, Portugal, Spain, Sudan and Tunisia (Guiry & Guiry 2014).

TABLE 10: Comparison between descriptions of sporophytic specimens of *Phymatolithon calcareum* based on vegetative and reproductive features (+ = present, - = absent; ND = not disclosed). [1] Woelkerling & Irvine (1986)—England, [2] Mendoza & Cabioch (1998)—France, [3] Horta (2000)—Brazil, [4] Konar *et al.* (2006)—Alaska.

Characters (measured in μm)	*P. calcareum* (this study)	*P. calcareum* [1] (neotype)	*P. calcareum* [2]	*P. calcareum* [3]	*P. calcareum* [4]
Epithallial cell form	Rounded	Rounded	Rounded	Flared	Rounded
Epithallial cell length	3.5–5.6	4–8	ND	2–4	4–11
Epithallial cell diameter	4–7	7–12	ND	5–11	0.83–1.66
Perithallial cell length	7–9	8–18	5–10	3–14	ND
Perithallial cell diameter	5–7.5	7–10	3–5	3–10	ND
Hypothallial cell length	7–13	ND	10–15	5–15	2.5–13
Hypothallial cell diameter	5–9	ND	4–5	3–10	2–12.5
Tetrasporangial conceptacle length	60.7–101.5	ND	70–120	100–130	80–170
Tetrasporangial conceptacle diameter	100.8–163.8	96–190	120–250	250–450	80–200
Tetrasporangia length	60–64.5	125	50	–	80–140
Number of cells in the roof of tetrasporangial conceptacle	4–6	ND	ND	ND	ND
Vegetative cells within tetrasporangial conceptacle	–	–	–	–	–

Discussion

The results show that the reef formations in the midlittoral and shallow subtidal zones of the northern state of Bahia contain nine species of CCA, distributed in two orders (Sporolithales and Coralinalles), three families (Sporolithaceae, Corallinaceae, and Hapalidiaceae), and three subfamilies (Lithophylloideae, Mastophoroideae, and Melobesoideae).

Among the observed taxa, we expected a major representation of the Sporolithaceae family once eight species of *Sporolithon* have been described to the Brazilian northeastern coast. This group is represented in our coast by *S. africanum* (Foslie) J. Afonso-Carillo (1984: 142), *S. australasicum* (Foslie) N. Yamaguishi-Tomita ex M. J. Wynne (1986: 2258), *S. episporum*, *S. erythraeum* (Rothpletz) Kylin (1956: 205), *S. howei* (Lemoine) N. Yamaguishi-Tomita ex M. J. Wynne (1986: 2258), *S. pacificum* E. Y. Dawson (1960a: 38-40), *S. ptychoides* Heydrich (1897: 67-69), *S. tenue* (Yamaguishi-Tomita 1976, Nunes *et al.* 2008, Riul *et al.* 2009, Bahia *et al.* 2010, Bahia *et al.* 2011, Amado Filho *et al.* 2012a, Amado Filho *et al.* 2012b, Bahia *et al.* (2014). Six of these have been reported by

Tomita-Yamaguishi (1976), and her identifications and descriptions were based on the size of the tetrasporangial chambers, pore density, number of hypothallial layers, and texture of the thallus. According to modern concepts of coralline algal taxonomy, these characters are not sufficient for a precise identification of CCA (Verheij 1993). However, we hypothesize that this diversity are related with the specie concept and methodological limitation observed in the 70's. A series of vegetative and reproductive characteristics are required in addition to those used by the author, such as: epithallial cell shape, subepithallial initials size, type of connection between adjacent filaments, and the location of tetrasporangial sori. Among the cited species, *S. episporum* is the more frequent found in the Atlantic tropical coast, and has been also recorded in the Indian, and Pacific Oceans. In Brazil, it is only recently found off the northeast coast of the country.

The specimens in this study were identified as *S. episporum* by satisfying the criteria set by Keats & Chamberlain (1993) and Nunes *et al.* (2008) (Table 1). There have been few descriptions of the structure and development of the carposporangial conceptacles in *Sporolithon*, being restricted to *S. durum* (Foslie) Townsend & Woelkerling (1995: 86-91) (Townsend *et al.* 1995, Woelkerling 1996, Harvey *et al.* 2002) and *S. episoredion* (Adey, Townsend & Boykins) Verheij (1992: 501). *S. episoredion* has carposporangial conceptacles much larger than those found in the present study (Verheij 1992, Table 2). Both specimens identified as *S. episporum* and specimens of *S. durum* have similar vegetative structure and the size of the carposporangial conceptacles. These two species are considered to be very closely related, and have been separated mainly by the relative proportions of their secondary pit-connections and cell fusions. *S. durum* exhibits adjacent filaments that are mainly connected by cell fusions, and the presence of secondary pit-connections between the filaments is rare (Woelkerling 1996). In *S. episporum,* the opposite is the case. However, the use of this feature has been contested by some authors (Townsend *et al.* 1995, Harvey *et al.* 2002). Harvey *et al.* (2002) reported that the proportion of secondary pit-connections and cell fusion varies in specimens of *S. durum* found in Australia, and that this feature should not be used to separate the two species. Townsend *et al.* (1995) suggested that the diagnostic characters of *S. durum* and *S. episporum* overlap each other, and although in *S. durum* the tetrasporangia are larger in height and diameter, these two taxa are conspecific. The structures observed at the carposporophyte stage from *S. episporum* and *S. durum* are not sufficient to separate the two species (Table 2). However, as both species show remarkable features, such as the proportion of pit-connections and cell fusion, they should be kept as distinct taxa until a study of their populations is conducted that proves that this characteristic has no taxonomic significance. This study represents the first description of the carposporophyte stage in *S. episporum*.

The genus *Lithophyllum* has been characterized according to Woelkerling (1983), Campbell & Woelkerling (1990), Harvey & Woelkerling (2007), and Farr *et al.* (2009), by the following features: the presence of uniporate tetrasporangial conceptacles, zonately divided tetrasporangia, the cells from adjacent filaments joined by secondary pit-connections, and rounded or flattened epithallial cells. The Brazilian coast has described until now six species of *Lithophyllum*: *L. congestum* (Foslie) Foslie (1900a: 20), *L. coralline* (P. L. Crouan & H. M. Crouan) Heydrich (1897a: 47), *L. depressum*, *L. johansenii* Woelkerling & Campbell (1992: 61-67), *L. margaritae* (Hariot) Heydrich (1901: 530), and *L. stictaeforme* (Figueiredo & Steneck 2002, Tâmega & Figueiredo 2005, Nunes *et al.* 2008, Vilas Boas *et al.* 2009, Amado Filho *et al.* 2010, Bahia *et al.* 2010, Amado Filho *et al.* 2012b, Martins *et al.* 2012). The characteristics used for positioning the species within this genus include the diameter of the tetrasporangial conceptacle, the number of cell layers from the floor of the tetrasporangial conceptacles to the surface of the thallus, and number of cell layers in the roof of these conceptacles. The diagnostic features observed in the specimens studied agree with the descriptions and illustrations provided by Athanasiadis (1999) for *Lithophyllum expansum sensu* Lemoine, which is considered a synonym of *L. stictaeforme.* Nunes *et al.* (2008) cited the first occurrence of *L. stictaeforme* in Bahia, and features of the specimens studied by these authors are corroborated in the present study (Table 3). *L. stictaeforme* has been recorded in the Atlantic and Pacific Oceans. In Brazil, it is found off the northeastern, southeastern, and southern coasts.

Spongites yendoi has been recorded in the Atlantic, Indian, and Pacific Oceans. In Brazil, it has been recorded off the southeastern coast (Henriques *et al.* 2011). The specimens referred to by Henriques *et al.* (2011) have characteristics similar to the specimens of the present study (Table 4), except for the absence of trichocytes in the samples from Espírito Santo. The occurrence and position of trichocytes is considered important in the delimitation of *Spongites* species; however, their presence is known to vary according to environmental conditions, and they are commonly found on species occurring in conditions of high temperature and luminosity (Woelkerling 1985). The samples examined in the present study were collected at a depth of 9–25 m, whereas those described by Henriques

et al. (2011) were collected at a depth of 50 m. Specimens of this study described as *S. yendoi* presented characteristics that coincided with diagnostic features reported by several authors (Table 4) (Penrose & Woelkerling 1992, Chamberlain 1993, Penrose 1996, Mateo-Cid *et al.* 2007, Henriques *et al.* 2011).

The specimens of *Spongites* sp. have characteristics that position them consistently in the genus *Spongites*, namely, a thallus with monomerous construction, epithallial cells rounded or flattened, subepithallial initials as short as or shorter than the cells immediately subtending them, cells of adjacent filaments joined by cell fusion, and carposporangial conceptacles containing an evident fusion cell. However, because of the scarcity of fertile material, tetrasporophytes were not found; therefore, the cited characteristics were not sufficient to determine the species of the exemplar. As can be seen in Table 5, *Spongites* sp. have vegetative characteristics that are similar to those in *S. yendoi*, *S. fruticulosa* Kützing (1841: 33), and *S. hyperella* (Foslie) Penrose (1996: 275). However, *Spongites* sp. present carposporangial conceptacles that are considerably smaller than those found in the above-mentioned species, besides having a fusion cell with a very different form from those found in the above taxa (Table 5). Therefore, it is still necessary to examine other fertile samples to confirm the taxon to which the studied specimen belongs.

The genus *Mesophyllum* has been described by many authors, among them Woelkerling & Harvey (1993), Keats & Chamberlain (1994), Keats & Maneveldt (1997), Athanasiadis *et al.* (2004), and Horta *et al.* (2011). The diagnostic features of the genus include a thallus with a monomerous construction, the coaxial cells of hypothallial filaments, the cells of adjacent filaments joined by cell fusion, epithallial cells rounded or flattened, subepithallial initials as long as or longer than the cells immediately subtending them, multiporate tetrasporangial conceptacles, unbranched mother cells of spermatangia, occurring both in the roof and in the floor of the conceptacle, and a dumbbell-shaped chamber of the carposporangial conceptacle. In Brazil, only two species of *Mesophyllum* have been reported: *M. erubescens* and *M. engelhartii* (Foslie) W. H. Adey (1970: 23) (Foslie 1900b, Figueiredo & Steneck 2002, Figueiredo *et al.* 2007, Nunes *et al.* 2008, Amado Filho *et al.* 2010, Bahia *et al.* 2010, Burgos 2011, Horta *et al.* 2011, Amado Filho *et al.* 2012a, b), which differ principally by the size and shape of the cells lining the pore canals of the tetrasporangial conceptacles. According to Keats & Chamberlain (1994), Ringeltaube & Harvey (2000), and Horta *et al.* (2011), the following characteristics are used for their identification: tetrasporangial conceptacle location and size, the shape of the cells that line the pore canals of the tetrasporangial conceptacles, and the number of cells that form the roof of the conceptacle. The aforementioned characteristics were essential for identifying the specimens analyzed in this study as *M. erubescens* (Table 6). This species is found in the Atlantic, Indian, and Pacific Oceans. In Brazil, its occurrence has been recorded off the northeastern, southeastern, and southern coasts.

Six species of *Lithothamnion* are found off the Brazilian coast: *L. brasiliense*, *L. crispatum*, *L. glaciale* Kjellman (1883: 123), *L. muelleri* Lenormand ex Rosanoff (1866: 101), *L. occidentale* (Foslie) Foslie (1908: 3-4), and *L. sejunctum* Foslie (1906: 3). Keats *et al.* (2000), Harvey *et al.* (2003), Bahia *et al.* (2010), Farias *et al.* (2010), and Basso *et al.* (2011) have set the following criteria for species identification in the genus *Lithothamnion*: the size of the tetrasporangial conceptacle, the number of cell layers that constitute the roof of tetrasporangial conceptacles, and the presence or absence of depressions around the pores of tetrasporangial conceptacles (Table 7). The presence of this latter characteristic has been considered decisive in identifying specimens of *Lithothamnion* as *L. crispatum*. According to Harvey *et al.* (2003), depressions around the pore result from the disintegration of the cells of elevated filaments that surround the pore canal.

Lithothamnion crispatum is found in the Atlantic, Indian, and Pacific Oceans and was originally reported in the Adriatic Sea at a depth of 25 m (Hauck 1878). However, the species underwent various nomenclatural changes, and material type was only designated in 1995 by Woelkerling and Verheij. After reviewing the type, Cabioch & Mendoza (1998) concluded that the designated lectotype was infertile. Basso *et al.* (2011) carried out a complete description based on the discovery of empty tetrasporangial conceptacles in the lectotype, and additional material of the species. The character "degenerated cells in rosettes around the pores of tetrasporangial conceptacles forming depressions" was used by some authors to synonymize species of *Lithothamnion* (*L. indicum* and *L. heteromorphum* for *L. superpositum* Keats *et al.* 2000, Farias *et al.* 2010), and was also used by Basso *et al.* (2011) to establish the conspecificity of *L. superpositum* with *L. crispatum*, the latter having nomenclatural priority. In Brazil, its occurrence has been recorded in the northeast and south.

Lithothamnion brasiliense was originally described by Foslie (1900b) in the municipality of São Sebastião, São Paulo State, and records of its occurrence have been confined to Brazil. The characteristics observed in the

examined material correspond to those already identified by Foslie (1900b), Taylor (1960), Horta (2000), and Bahia *et al.* (2010) (Table 8). The specimens collected by Horta (2000) occurred between 12 and 22 meters and those collected by Bahia *et al.* (2010) between 5 and 15 meters. The specimens in this study were collected in the midlittoral zone, and between 22 and 25 m in the subtidal zone, thereby expanding the known range of depths at which this species occur. *L. brasiliense* has similar characteristics to those of *L. crispatum*; however, the main characteristic that distinguishes the two species is related to the occurrence of depressions around the pores of tetrasporangial conceptacles in *L. crispatum,* which do not occur in *L. brasiliense*.

The genus *Phymatolithon* differs from other genera of Melobesoideae for being the only member of this subfamily that has subepithallial initials as short as or shorter than the cells immediately subtending them (Wilks & Woelkerling 1994, Woelkerling 1996, Harvey *et al.* 2003). Two species of *Phymatolithon* have been found in Brazil: *P. masonianum* and *P. calcareum* (Taylor 1960, Horta 2000), which are distinguished from each other mainly by the fact that *P. masonianum* presents vegetative cells inside the multiporate tetrasporangial conceptacles, whereas *P. calcareum* does not (Wilks & Woelkerling 1994, Woelkerling 1996, Horta 2000). *P. calcareum* was characterized by Woelkerling & Irvine (1986) and Mendoza & Cabioch (1998) by the cells of the perithallial and hypothallial filaments, the tetrasporangial conceptacles, and the tetrasporangia (Table 9 and 10). *P. masonianum* was originally described off southeast Australia by Wilks & Woelkerling (1994); in Brazil, it has only been reported in the south (Horta 2000). The present study is the first to report this species off the northeastern coast of Brazil. *P. calcareum* has been reported in the Atlantic and Pacific Oceans, and the first report of this species in Brazil was made by Taylor (1960). Horta (2000) studied the species using new observation techniques (Scanning Electron Microscopy); however, the specimens referred to by the author differed from the specimens of the present study by having flared epithallial cells. The present study is the first to report this species off the northeastern coast of Brazil.

This study represents an important contribution to the knowledge of the distribution of CCA off the Brazilian coast, with the first reports of two taxa in the tropical province off western Atlantic Coast (Horta *et al.* 2001). Therefore, our results also reinforce that this group represents an important gap in the knowledge about the South Atlantic flora and complementary efforts are needed once some reproductive and morphological aspects are informative and complement the information about the described species. Despite the importance of molecular studies, this manuscript brings light to the taxonomic diversity of CCA of the Brazilian tropical coast, subsiding studies about physiology and ecology of the important benthic formations. Coral reefs in this region, due to overfishing and coastal pollution, are passing through shifts in their physiognomies, and CCA are important players, now (Steneck 1986) and in the future (Martins *et al.* 2009), for the resilience of these environments. On a much larger scale, there is growing evidence that CCA communities play a crucial role in $CaCO_3$ cycles of continental shelf ecosystems (Milliman 1993), which upon change from ocean acidification may cause profound effects on the world's oceans. With Brazil having some of the largest communities of CCA in the world, specifically rhodolith beds (Amado-Filho et. al 2012b), it is important to place urgency on the detailed research and taxonomy of these species. Considering the process of global warming, ocean acidification and coastal eutrophication predicted for the next decades, we should urgently invest in complementary studies of these organisms, introducing or diffusing molecular tools to improve our understanding of the diagnoses of species and evolutionary relationships understanding.

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