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Floristic composition of crustose coralline algae from the St. Peter and St. Paul Archipelago, a summit of the Mid-Atlantic Ridge

THALITA MENDES CRESPO[1], RICARDO DA GAMA BAHIA[1], GAVIN WILLIAM MANEVELDT[2] & GILBERTO MENEZES AMADO FILHO[1,*]

[1] *Diretoria de Pesquisa Científica, Instituto de Pesquisas Jardim Botânico do Rio de Janeiro, Brazil*
[2] *Department of Biodiversity and Conservation Biology, University of the Western Cape, South Africa*
* *Corresponding author*

Abstract

Crustose Coralline Algae (CCA) are important constituents of tropical coral reef environments throughout the world's oceans, acting as structural reinforcement and recruitment cues. Despite their importance and their ubiquity, very little is known of the biodiversity of CCA in remote areas of the world's oceans. On the Saint Peter and Saint Paul Archipelago (SPSPA), located in the central equatorial Atlantic Ocean, CCA occur abundantly in intertidal rock pools and the surrounding subtidal zones. This study represents the first attempt at detailing the CCA species composition for the archipelago along a depth interval between 0 to 70 m. Seven taxa of CCA were identified: Corallinaceae sp., *Hydrolithon rupestre, Hydrolithon* sp., *Lithophyllum johansenii, Lithothamnion muelleri, Mesophyllum engelhartii,* and *Titanoderma pustulatum pustulatum*. A decrease in CCA species richness and change in species composition was seen from shallow to deeper zones that can be explained by a significant reduction in temperature and photon irradiance observed bellow 30 m depth.

Key words: Corallinales, *Hydrolithon rupestre*, *Hydrolithon* sp., *Lithophyllum johansenii, Lithothamnion muelleri, Mesophyllum engelhartii, Titanoderma pustulatum*, Specific composition, Light and Temperature

Introduction

The Saint Peter and Saint Paul Archipelago (SPSPA), Brazil, located approximately 960 km off the Brazilian coast and 1890 km south-west of Senegal, West Africa, consists of a remote group of ten small islands located in the central equatorial Atlantic Ocean (0° 55' 10" N, 29° 20' 33" W) (Serafini *et al* 2010). The archipelago is a summit of the Mid-Atlantic Ridge with an emerged area of 17,000 m^2 and a maximum altitude of 18 m. The archipelago is of great biogeographic interest due to the isolation and small size of its islands (Edwards & Lubbock 1983; Edwards 1984).

The climate of the archipelago is influenced by the Intertropical Convergence Zone with southeast trade wind velocities between 4 and 7 $m.s^{-1}$. Annual air temperatures average is around 27 ± 1 °C and sea surface temperatures are reported to vary between 24.0 and 28.5 °C (Soares *et al*. 2009). Maximum monthly-accumulated precipitation of 370 mm occurs in April while the lowest values occur between August and November (Soares *et al.* 2009).

The archipelago possesses several rock pools where geniculate and non-geniculate or crustose coralline algae (CCA) (Corallinales and Sporolithales) are found, showing a wide vertical distribution around the islands (Edwards & Lubbock 1983). The sub-tidal zone of the archipelago drops steeply to 60 m depth. According to Edwards & Lubbock (1983), three bionomic zones can be observed, namely: i. a *Palythoa* (Zoanthids) zone 0 to 5 m depth in which CCA are found only occasionally; ii. a *Caulerpa racemosa* (Forsskål) J.Agardh (1873: 35–36) zone 5 to 33 m depth in which CCA occur as an understory of the dense populations of the green alga *Caulerpa racemosa*; and iii. a *Caulerpa* sub-zone below 33 m depth in which several species of algae, including the brown alga *Dictyota dichotoma* (Hudson) J.V. Lamouroux (1809a: 42), the green alga *Bryopsis pennata* J.V. Lamouroux (1809b:) and the red alga *Gelidiopsis planicaulis* (W.R.Taylor) W.R Taylor (1960: 353) and CCA occur. The above macroalgae are found down to 40 m depth while 45 to 60 m depth, only CCA occur.

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CCA are ubiquitous and widely distributed around the world, occurring from the poles to the tropics, and from intertidal areas to 274 m depth (Steneck, 1986 and Littler & Littler, 2000). CCA are recognized as important components of tropical coral reefs where they act as binding agents, cementing together unconsolidated sediment, dead coral and debris, and create stable substrates for coral settlement (Bosence 1983; Diaz-Pulido *et al*. 2007).

Despite their wide distribution and their ecological and biogeographical importance, till now, there exist neither documented nor detailed accounts of CCA from the SPSPA. Most of the recent works on CCA from Brazil (e.g. Amado-Filho *et al*., 2012; Villas-Boas *et al*., 2009; Pereira-Filho *et al*., 2012) is related to unattached, free-living, rhodolith-forming species, with little modern focus on the attached CCA. The aim of the present study was to determine the species composition of the attached CCA along a depth gradient 0–70 m at the SPSPA.

Materials and Methods

Epilithic CCA samples were collected in a cove at SPSPA and along a contiguous vertical sea wall below it during two scientific expeditions (September 2010 and June 2011) between Ilhota Belmonte and Ilhota São Pedro and Ilhota São Paulo (Fig. 1). CCA were sampled along three depth intervals: 0–29 m, 30–49 m, and 50–70 m.

For CCA identification, scanning electron microscopy (SEM) techniques following Keats *et al*. (1993), and histological methods following Maneveldt & van der Merwe (2012) were employed. Identification of CCA species was based on both vegetative and reproductive characters according to recent monographic accounts by Penrose (1991), Keats & Chamberlain (1994), Irvine & Chamberlain (1994), Maneveldt (2005), Harvey *et al*. (2006), Basso & Rodondi (2006), Harvey & Woelkerling (2007) and Villas-Boas *et al.* (2009). Voucher specimens, including slides, were deposited in the herbarium of the Rio de Janeiro Botanical Garden (RB).

Photon irradiance and temperature were recorded *in situ* with a HOBO UA-002-64 / date Logger and UEMIS dive computer from 5, 15, 33, 45, and 65 m depth (n = 5 for each depth) to determine possible relationships between these variables and the CCA species compositions as a function of depth. Data are presented as means ± standard deviation (SD).

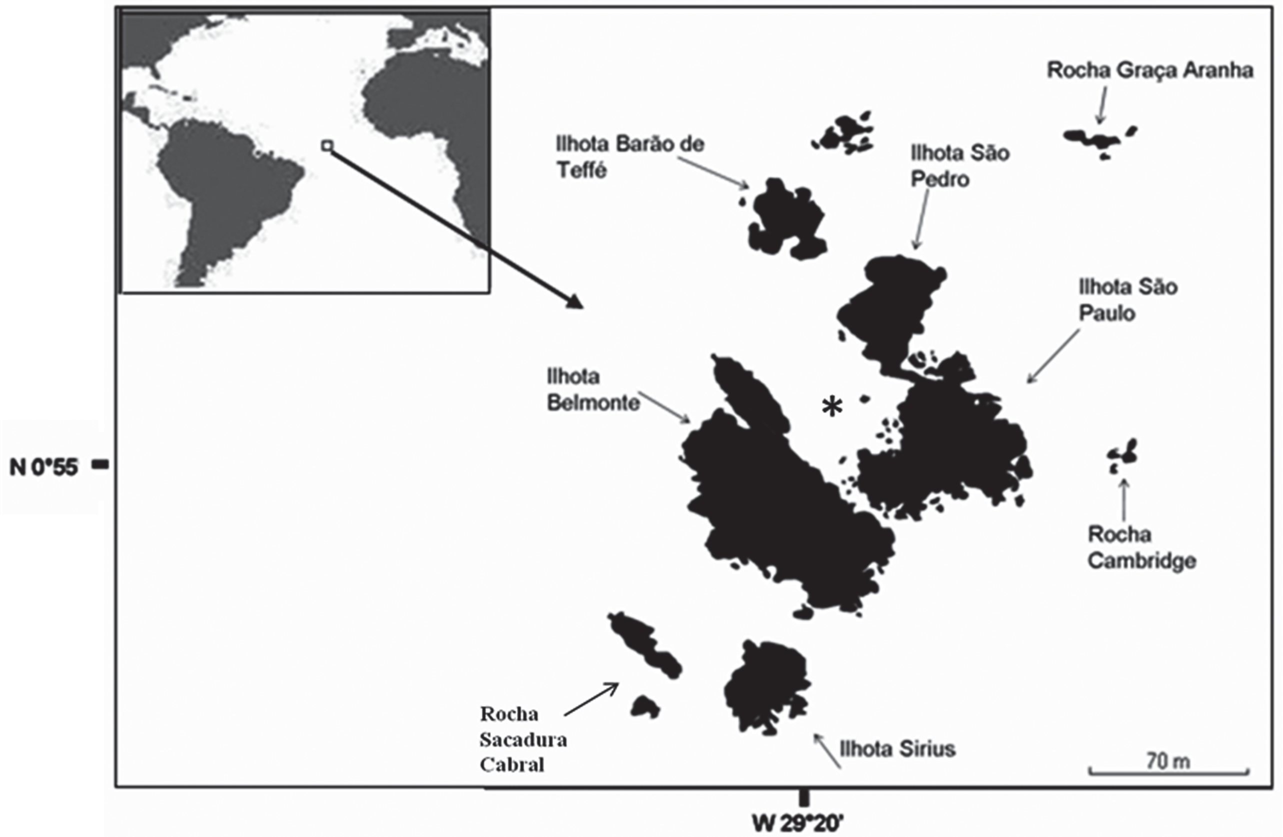

FIGURE 1. Location and detail of islands of SPSPA. The sampling location (cove) is indicated by *.

Results

CCA were observed occurring at depths between 3 and 70 m. Seven species were identified, namely: Corallinaceae sp. (RB 549687, RB 553190), *Hydrolithon rupestre* (Foslie) Penrose (1996: 265) (RB 549682, RB 553503), *Hydrolithon* sp. (RB 549684, RB 553180), *Lithophyllum johansenii* Woelkerling & Campbell (1992: 61–67) (RB 549692, RB 553493), *Titanoderma pustulatum* (J.V.Lamouroux) Nägeli in Nägeli & Cramer (1858: 532) (RB 549691, RB 553195), *Mesophyllum engelhartii* (Foslie) W.H. Adey (1970a: 23) (RB 549695, RB 553500), and *Lithothamnion muelleri* Lenormand ex Rosanoff (1866: 101) (RB 549694, RB 553497).

All CCA species are here reported for the first time from SPSPA. Details of carpogonial, carposporangial and tetrasporangial conceptacles of *Hydrolithon rupestre* are described for the first time from the Atlantic Ocean. An as yet undescribed species is also included, temporarily attributed to the genus *Hydrolithon*. A detailed taxonomic description for each species is presented below.

Species descriptions

Corallinaceae sp.

Figures 2 (A–D) and 3 (A–D).

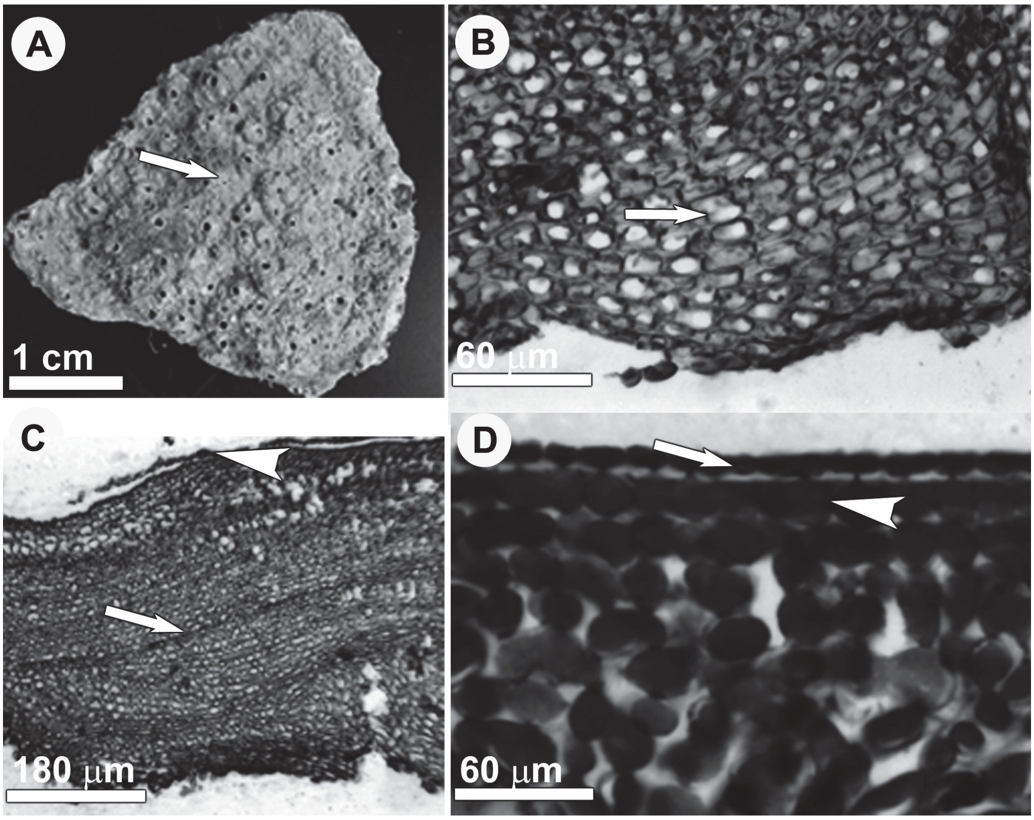

FIGURE 2 A–D. Vegetative anatomy of Corallinaceae sp. (A) Encrusting specimen firmly attached to the rocky substrate (arrow). (B) Section through the thallus showing the monomerous construction and cells of adjacent filaments joined by cell fusions (arrow). (C) Vertical section through the vegetative thallus showing the well-defined zoning patterns (arrow) and a layer of epithallial cells being shed (arrowhead). (D) Vertical section showing a single layer of rounded epithallial cells (arrow) and subepithallial initials as long as or longer than the cells imediately subtending them (arrowhead).

Thalli encrusting, 0.3–0.6 mm in thickness, pink to dark purple and firmly attached to the rocky substrate (Fig. 2A). The internal thallus construction is pseudoparenchymatous and monomerous with well-defined zoning patterns (Figs 2B, 2C). Cells of adjacent filaments are joined by cell fusions; secondary pit connections were not observed (Fig. 2B). Epithallial cells are rounded, measure 3–8 μm in length and 2–6 μm in diameter, and occur in a single layer; epithallial shedding is evident in some parts (Figs. 2C, 2D). Subepithallial initials are rounded, measure 5–8 μm in length and 4–6 μm in diameter, and are as long as or longer than the cells immediately subtending them (Fig.

2D). Tetrasporangial conceptacles are uniporate and are raised above the surrounding thallus surface (Fig. 3A). Their chambers are elliptical and measure 380–400 µm in height and 500–550 µm in diameter (Fig. 3B). Zonately divided tetrasporangia occur along the periphery of conceptacle chamber; central columella can be either present (Fig. 3C) or absent (Fig. 3B). The pore canal is surrounded by cells that are aligned more-or-less parallel or at a sharp angle to roof surface and that project into the pore canal as papillate (Figs. 3C, 3D). The conceptacle roof is located 10–15 cells below the surrounding thallus surface (Fig. 3C).

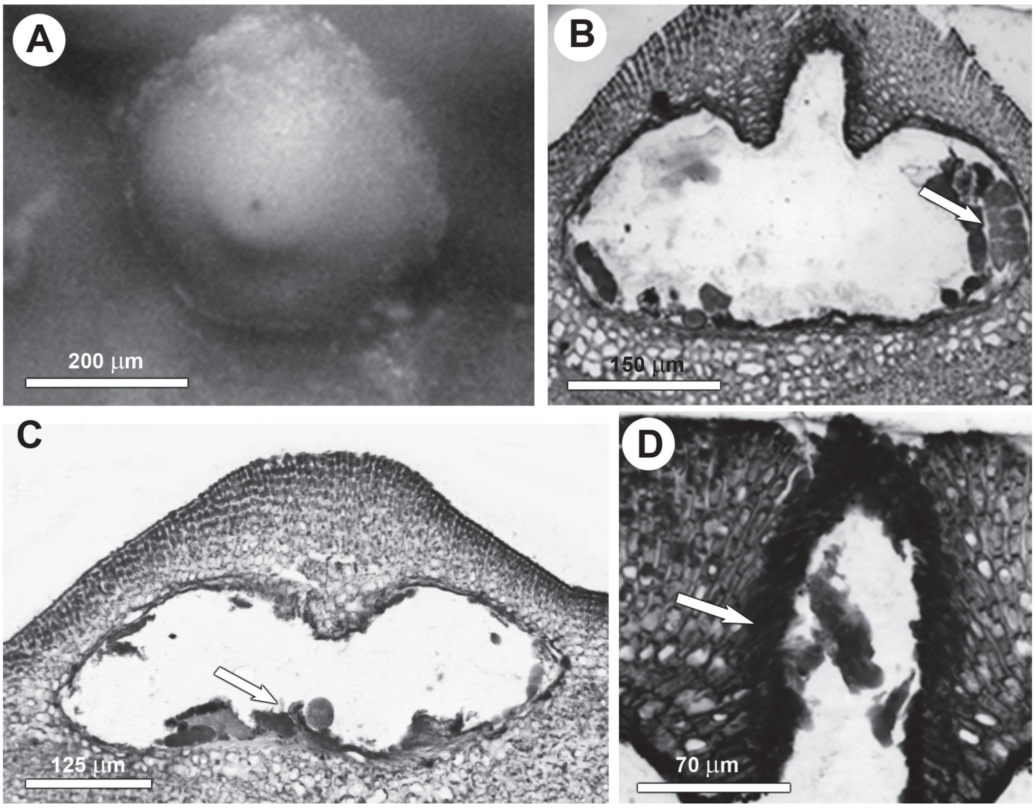

FIGURE 3 A-D. Tetrasporangial conceptacle anatomy of Corallinaceae sp. (A) Surface view of a uniporate conceptacle raised above the surrounding thallus surface. (B) Vertical section through a conceptacle showing an elliptical chamber with zonately divided tetrasporangia located along the periphery of the chamber (arrow). (C) Vertical section through a conceptacle showing remains of central columella (arrow). (D) Vertical sections showing the conceptacle pore canal lined by papillate cells orientated more or less parallel or at a sharp angle to the thallus surface (arrow).

***Hydrolithon* sp.**

Figures 4 (A–D) and 5 (A–D)

Thalli encrusting, 0.1–0.4 mm in thickness, pink to dark purple, firmly attached to the rocky substrate, and generally warty in appearance (Fig. 4A). The internal thallus construction is pseudoparenchymatous and monomerous (Fig.4B). Cells of adjacent filaments are joined by cell fusions; secondary pit connections were not observed (Fig. 4C). Subepithallial initials are square to rectangular, measure 4–10 µm in length and 6–8 µm in diameter, and are as long as or longer than the cells immediately subtending them (Fig. 4C). Epithallial cells are rounded to elliptical, measure 4–8 µm in length and 4–7 µm in diameter, and occur in a single layer (Figs. 4C). Solitary trichocytes occur only at the thallus surface (Fig. 4D). Tetrasporangial conceptacles are uniporate and are raised above the surrounding thallus surface (Fig. 5A). Their chambers are elliptical to spherical and measure 180–200 µm in diameter and 150–185 µm in height (Fig. 5B). The conceptacle pore canal is surrounded by a ring of 3–4 consecutive enlarged cells that are arranged more or less perpendicular to the thallus surface (Fig. 5C); these cells are formed from filaments interspersed amongst the tetrasporangia (Fig.5D). The conceptacle roof is 5–8 cells thick (Figs. 5B, 5C). The conceptacle floor is located 14–20 cells below the surrounding thallus surface. The conceptacle chamber lacks a central columella and zonately divided tetrasporangia measuring 35–80 µm in length and 18–30 µm in diameter, are scattered across the chamber floor.

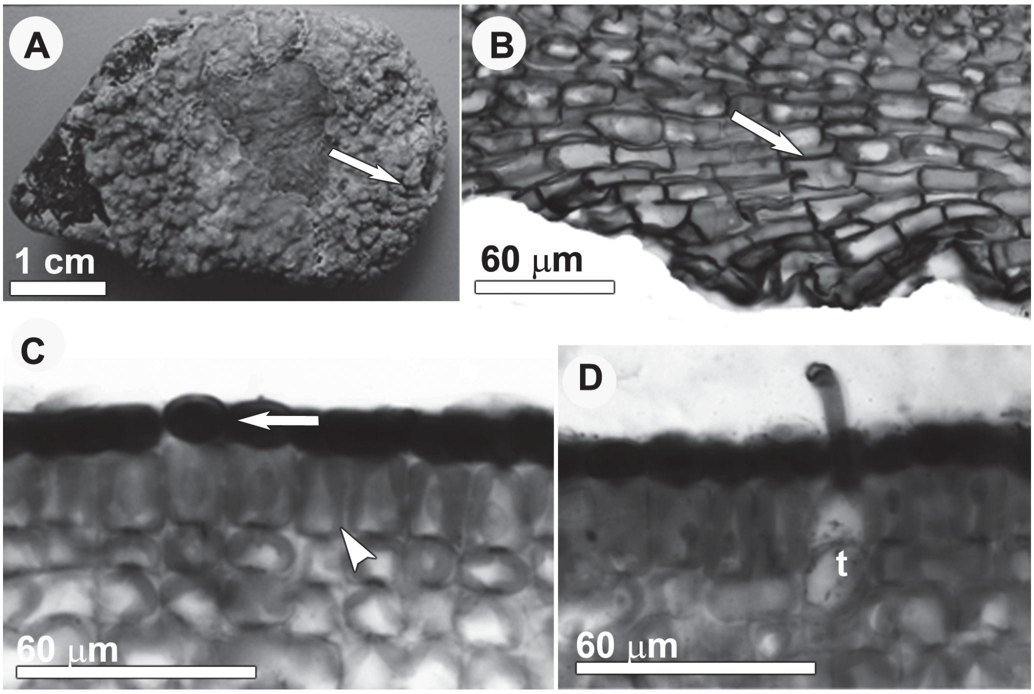

FIGURE 4 A-D. Vegetative anatomy of *Hydrolithon* sp. (A) Warty specimen attached to a rock (arrow). (B) Vertical section through the thallus showing a monomerous construction and cell fusions (arrow) between adjacent filaments. (C) Vertical section through the thallus surface showing a single layer of rounded epithallial cells (arrow) and square to rectangular subepithallial initials (arrowhead). (D) A solitary trichocyte (t) at the thallus surface.

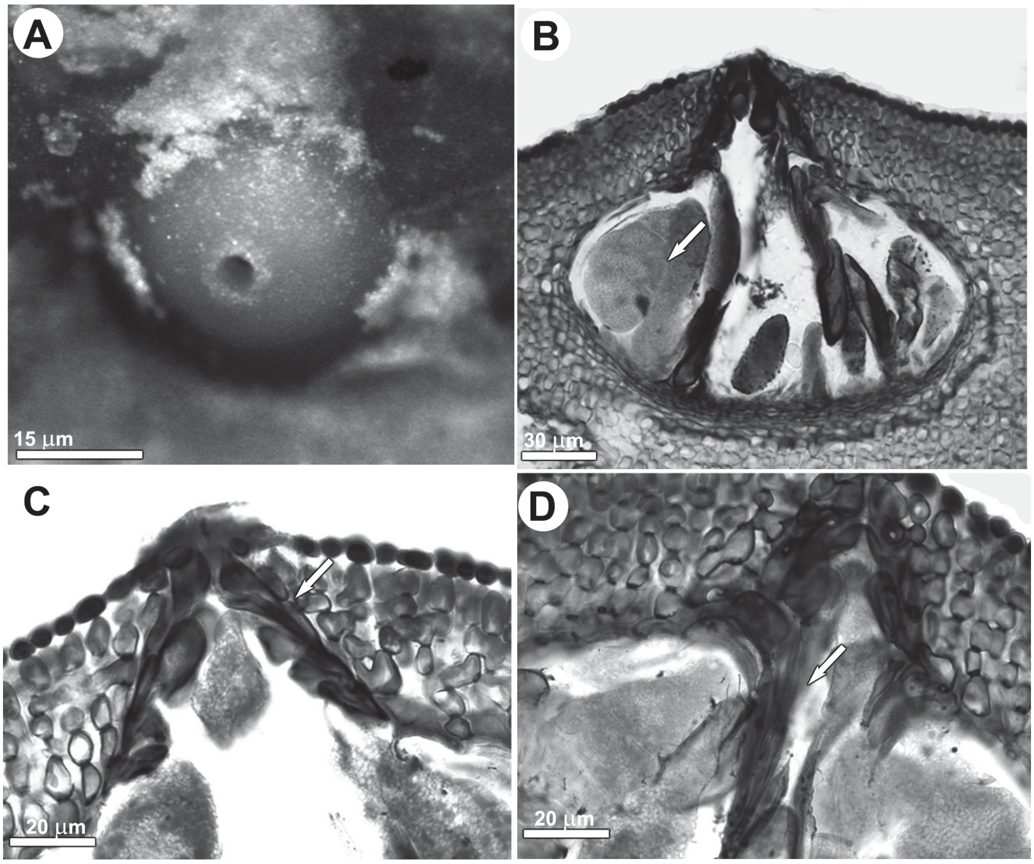

FIGURE 5 A-D Tetrasporangial conceptacle anatomy of *Hydrolithon* sp. (A) Surface view of a uniporate conceptacle. (B) Vertical section through a raised conceptacle containing zonately divided tetrasporangia (arrow). (C) Vertical section through the conceptacle pore canal showing the ring of 3–4 consecutive enlarged cells (arrow) lining the pore canal (arrow). (D) Magnified view of the conceptacle pore canal showing the interspersed filaments (arrow) that gave rise to the cells of the conceptacle pore canal.

Hydrolithon rupestre (Foslie) Penrose (1996: 265)
Figures 6 (A–C) and 7 (A–F)

Thalli encrusting, pink to dark purple and firmly attached to the rocky substrate (Fig. 6A). Thallus thickness ranges from 0.5–1.7 mm in the shallow (0–29 m depth) to 0.4–1.1 mm in deeper zones (30–49 m depth). The internal thallus construction is pseudoparenchymatous and monomerous (Fig. 6B). Cells of adjacent filaments are joined by cell fusions; secondary pit connections were not observed (Fig. 6B). Subepithallial initials are elliptical, measure 5–10 µm in length and 4–6 µm in diameter, and are as long as or longer than the cells immediately subtending them (Fig.6C). Epithallial cells are rounded, measure 3–7 µm in length and 4–6 µm in diameter, and occur in a single layer (Fig. 6C). Tetrasporangial conceptacles are uniporate and are raised above the surrounding thallus surface (Fig. 7A). Their chambers are elliptical to spherical and measure 204–217 µm in diameter and 160–180 µm in height (Fig.7B). Pore canals of tetrasporangial conceptacles are lined by a ring of conspicuously enlarged cells that arise from filaments interspersed among and surrounding sporangial initials; these cells do not protrude into the pore canal and are oriented more-or-less perpendicularly to the roof surface (Fig. 7C). Conceptacle roofs are 4–7 cell layers thick (Fig. 7C) and their floors are located 12–18 cells below the surrounding thallus surface (Fig. 7B). Spermatangial conceptacles are raised above the surrounding thallus surface, their chambers measure 70–74 µm in height and 95–102 µm in diameter, and contain simple (unbranched) spermatangial systems confined to the conceptacle floor (Fig. 7D). Mature female/carpogonial conceptacles are raised above the surrounding thallus surface and their roofs are 4–7 cells thick. Female conceptacle chambers are elliptical to flattened, measure 104–120 µm in height and 104–128 µm in diameter, and the chamber floor is located 14–18 cells below the thallus surface. Carpogonia are more or less bottle shaped, comprising a swollen base that extends into a trichogyne; an auxiliary cell is connected to the carpogonium (Fig. 7E). After presumed karyogamy, female conceptacles turn into carposporangial. Carposporangial conceptacles are large, measure 120–125 µm in height and 200–215 µm in diameter (Fig. 7F) and bear peripherally arranged gonimoblast filaments that arise from the margins of the central fusion cell.

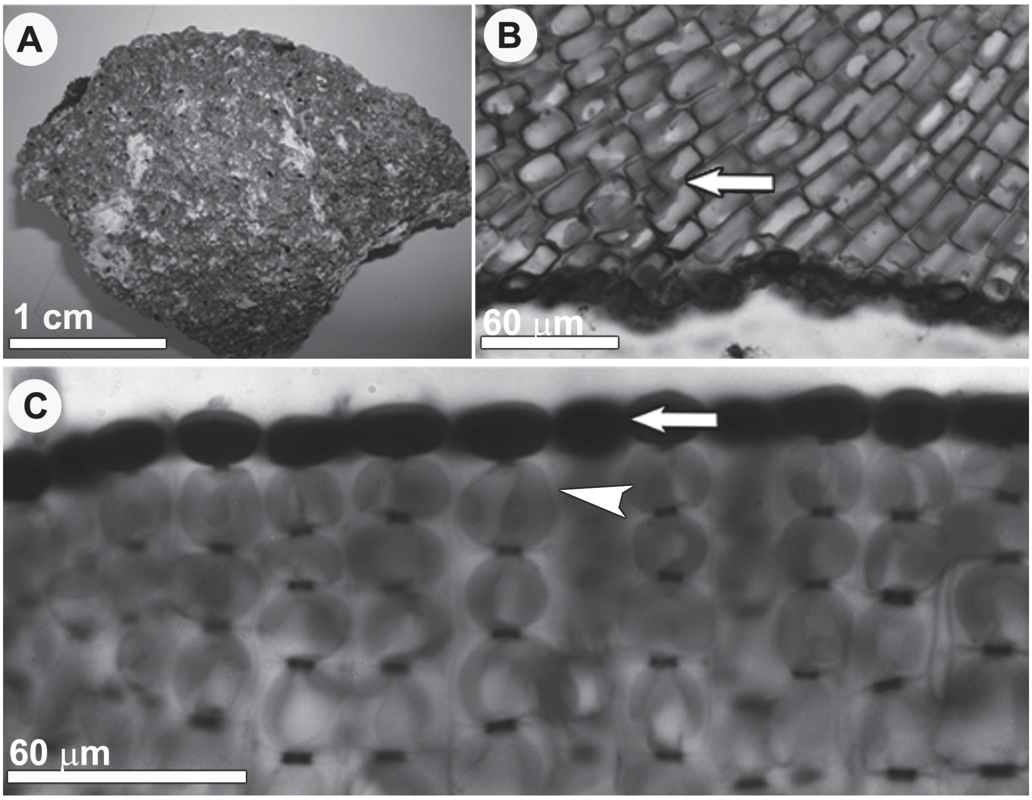

FIGURE 6 A–C. Vegetative anatomy of *H. rupestre* (A) External view of an encrusting specimen. (B) Vertical section through the thallus showing the monomerous construction and cells of adjacent filaments joined by cell fusions (arrow). (C) Vertical section through the thallus surface showing a single layer of rounded epithallial cells (arrow) and subepithelial initials (arrowhead) that are as long as or longer than the cells subtending them.

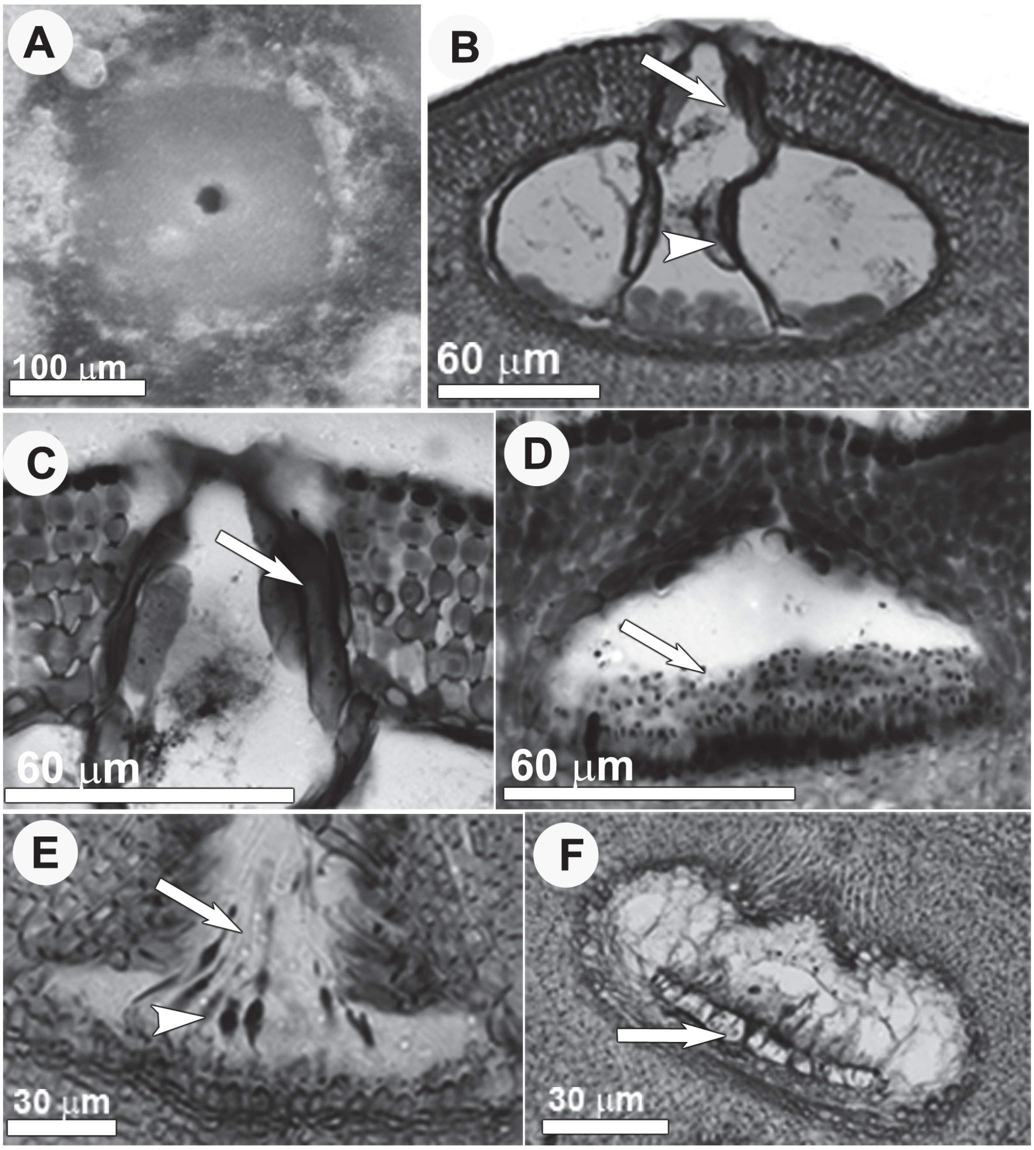

FIGURE 7 A–F. Reproductive anatomy of *H. rupestre* (A) Surface view showing a raised uniporate tetrasporangial conceptacle. (B) Section through a tetrasporangial conceptacle showing the pore canal surrounded by a ring of enlarged cells (arrow) orientated perpendicular to the thallus surface; note the remnants of filaments (arrowhead) from which these cells were derived. (C) Detail of a tetrasporangial conceptacle pore canal showing enlarged cells (arrow) lining the pore canal. (D) Spermatangial conceptacle bearing simple (unbranched) spermatangial systems restricted to the conceptacle floor. (E) Female conceptacle bearing carpogonial branches. Note the carpogonium (arrowhead) extended into a hair-like trichogyne (arrow). (F) A buried carposporangial conceptacle showing the remnants of a central fusion cell (arrow) and unfertilised carpogonial branches across its dorsal surface.

Lithophyllum johansenii Woelkerling & Campbell (1992: 61–67)
Figures 8 (A–D) and 9 (A–D)

Thalli encrusting, 0.5–1.0 mm in thickness, pink and firmly attached to the rocky substrate (Fig. 8A). The internal thallus construction is pseudoparenchymatous and dimerous (Fig. 8B). Cells of adjacent filaments are joined by secondary pit connections; cell fusions were not observed (Fig. 8C). Epithallial cells are rounded to flattened, measure 5–12 μm in length and 4–7 μm in diameter, and occur in a single layer (Fig. 8D). Subepithallial initials are square, measure 5–10 μm in length and 5–7 μm in diameter, and are as short as or shorter than the cells subtending them (Fig. 9A). Tetrasporangial conceptacles are uniporate and bear roofs that are flush with to raised above the surrounding thallus surface (Fig. 9A). Their chambers measure 190–210 μm in diameter and 90–115 μm in height (Fig. 9B). The pore canal of mature tetrasporangial conceptacle is completely occluded by a ring of enlarged and angular cells (Figs. 9C, 9D). The conceptacle roofs are 3–5 cells thick. The conceptacle floor is located 8–10 cells below the surrounding thallus surface. Chambers bear zonately divided tetrasporangia that measure 20–25 μm in length and 10–13 μm in diameter and occur peripherally around a central columella (Figs 9B, 9D).

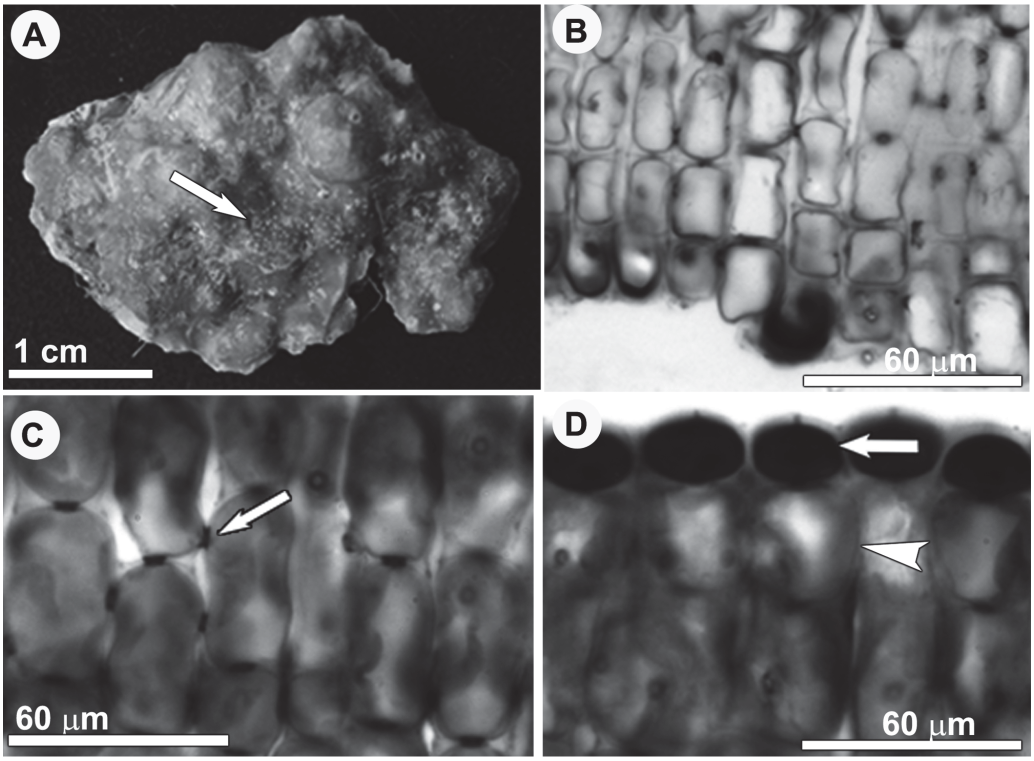

FIGURE 8 A–D. Vegetative anatomy of *L. johansenii* (A) An encrusting specimen (arrow) firmly attached to the rocky substrate. (B) Section through the thallus showing the dimerous internal construction. (C) Cells of adjacent filaments joined by secondary pit connections (arrow). (D) Vertical section through the thallus surface showing a single layer of rounded epithelial cells (arrow) and subepithelial initials (arrowhead).

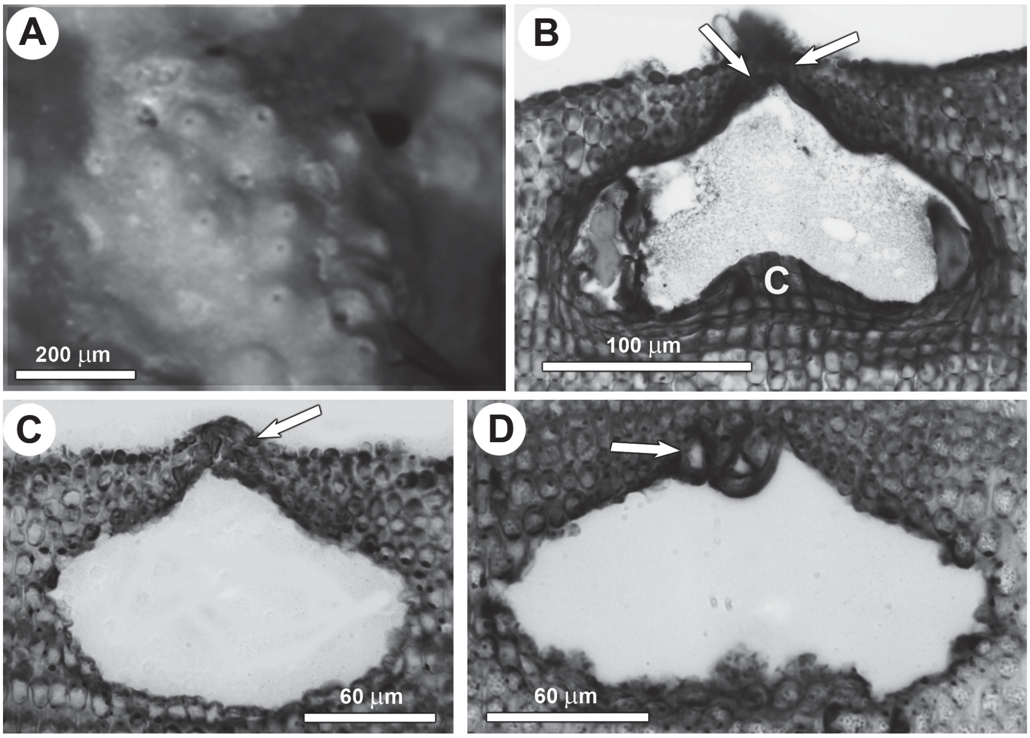

FIGURE 9 A–D. Tetrasporangial anatomy of *L. johansenii*. (A) Surface view showing uniporate conceptacles. (B) Longitudinal section through a conceptacle showing the roof (arrow) flush with the surrounding thallus surface, a central columella (c), and pore canal completely occluded by a ring of enlarged and angular cells (arrows). (C) Section through a empty conceptacle without central columella showing the ring of enlarged, angular cells (arrow) occluding the pore canal. (D) Longitudinal section through a buried conceptacle showing the ring of enlarged, angular cells (arrow) occluding the pore canal.

Titanoderma pustulatum (J.V.Lamouroux) Nägeli in Nägeli & Cramer (1858: 532)
Figures 10 (A–D) and 11 (A–D).

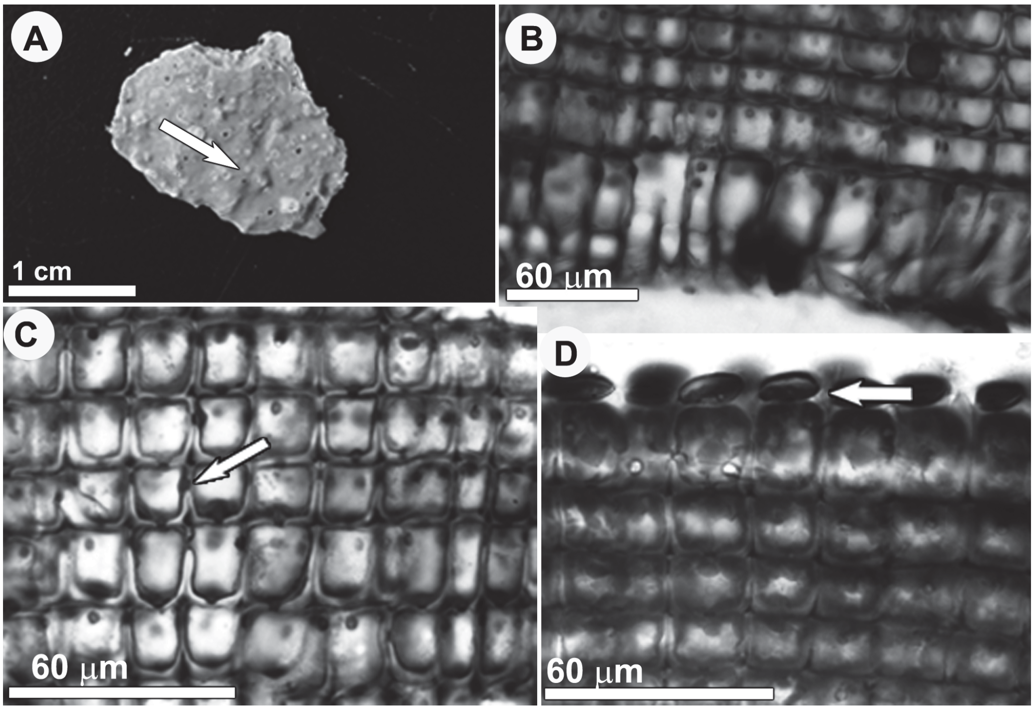

FIGURE 10 A–D. Vegetative anatomy of *T. pustulatum*. (A) Surface view of an encrusting specimen. (B) Section through the thallus showing the dimerous internal construction and the basal layer of palisade cells. (C) Vertical section of the thallus showing adjacent filaments joined by secondary pit connections (arrow). Vertical section through the thallus surface showing a single layer of rounded to flattened epithelial cells (arrow).

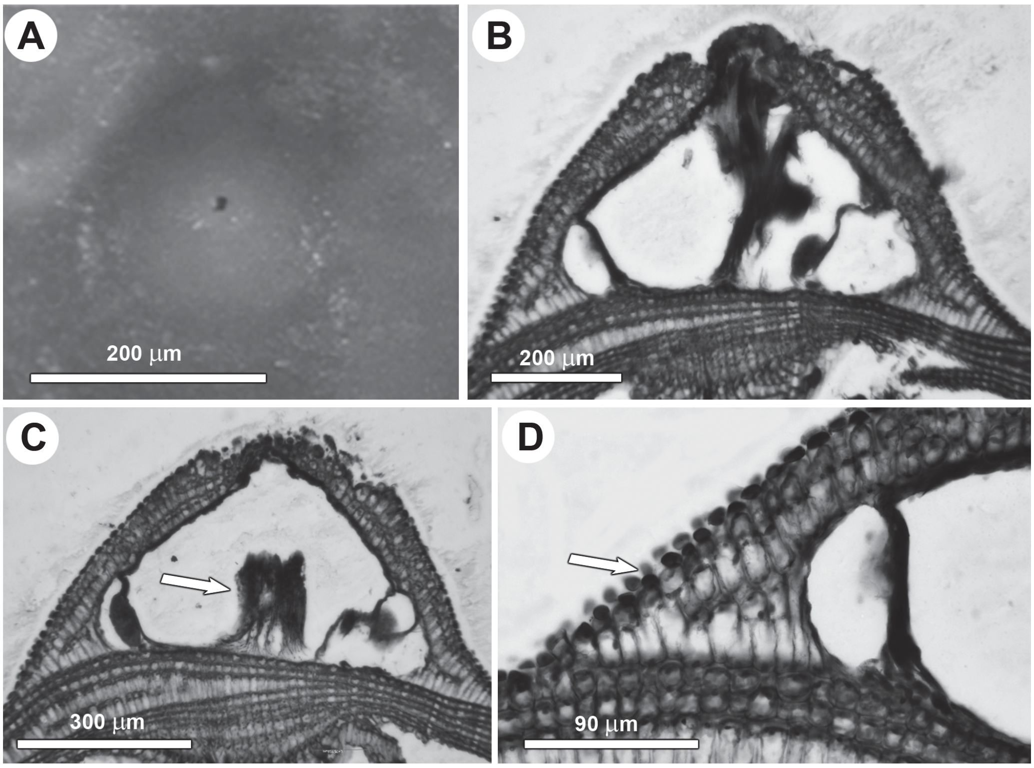

FIGURE 11 A–D. Tetrasporangial anatomy of *T. pustulatum*. (A) Surface view of a uniporate conceptacle. (B) Longitudinal section through a raised uniporate conceptacle. (C) Longitudinal section through a conceptacle showing a central columella (arrow). (D) Vertical section through the conceptacle periphery showing the conceptacle floor flush with the surrounding thallus surface.

Thalli encrusting, pink to dark purple, and firmly attached to the rocky substrate (Fig. 10A). Thallus thickness up to 0.1 mm. The internal thallus construction is pseudoparenchymatous and dimerous (Fig. 10B). The basal layer comprises predominantly palisade cells that measure 10–50 µm in diameter and 10–15 µm in length (Fig. 10B). Cells of adjacent filaments are joined by secondary pit connections; cell fusions were not observed (Fig. 10C). Epithallial cells are rounded to flattened, measure 4–8 µm in length and 10–15 µm in diameter and occur in a single layer (Fig. 10D). Tetrasporangial conceptacles are uniporate (Fig. 11A) and are raised above the surrounding thallus surface. Their chambers measure 420–465 µm in diameter and 300–320 µm in height (Fig. 11B). Roof filaments composed by 2–4 cells. Chambers bear zonately divided tetrasporangia that develop peripherally to a central columella (Fig. 11C). The conceptacle floor is flush located 1–3 cells below the surrounding thallus surface (Fig. 11D).

Mesophyllum engelhartii (Foslie) W.H. Adey (1970a: 23)
Figures 12 (A–D) and 13 (A–D).

Thalli encrusting to lumpy (Fig. 12A) with 0.1–0.2 mm in thickness. The internal thallus construction is monomerous and coaxial (Fig. 12B). Epithallial cells are rounded to flattened but without flared corners. Epithallial cells occur in a single layer and measure 4–8 µm in length and 3–5 µm in diameter (Fig. 12C). Subepithallial initials are as long as or longer than the cells immediately subtending them and measure 4–12 µm in length and 3–5 µm diameter (Fig. 12C). Adjacent filaments are joined by cell fusions; secondary pit connections were not observed (Fig. 12C). Solitary trichocytes are present at the thallus surface (Fig. 12D). Tetrasporangial conceptacles are multiporate and are raised above the surrounding thallus surface (Fig. 13A). Their chambers measure 130–170 µm in height and 190–235 µm in diameter (Fig. 13B). The conceptacle roof is composed of 4–6 cell layers. Tetrasporangia are zonately divided and bear apical plugs (Fig. 13C). Conceptacle pore canals are lined by cells that are similar in size and shape to other roof cells (Fig. 13D).

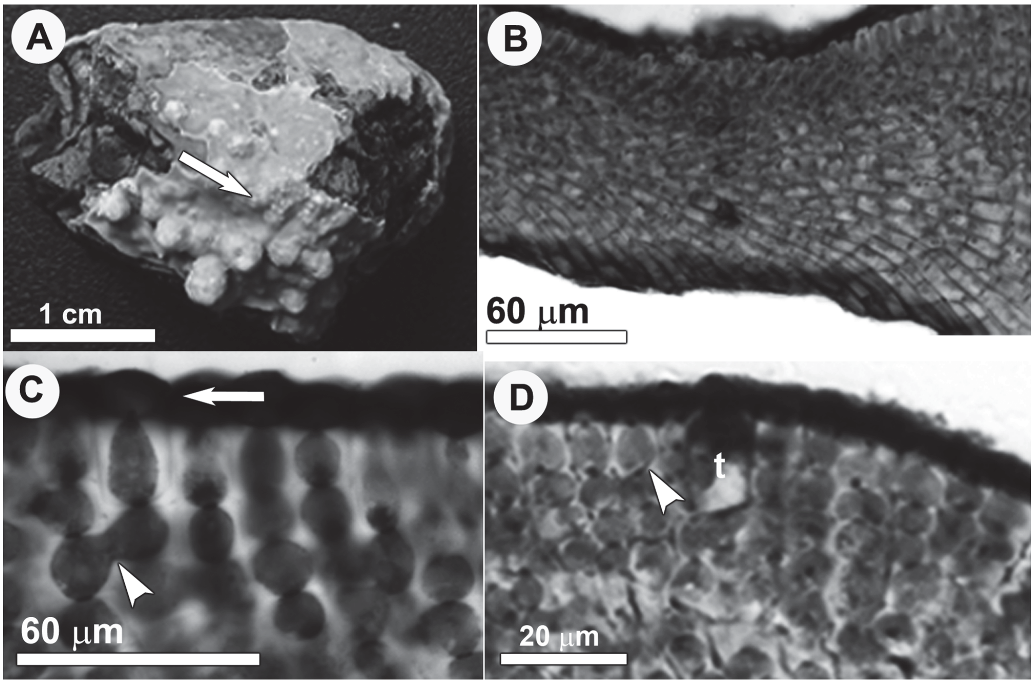

FIGURE 12 A–D. Vegetative anatomy *M. engelhartii.* (A) An encrusting to lumpy specimen (arrow). (B) Vertical section through the thallus showing the monomerous and coaxial internal construction. (C) Vertical section of the thallus showing a single layer of rounded epithallial cells (arrow) and adjacent filaments joined by cell fusions (arrowhead). (D) Vertical section of the thallus showing a solitary trichocyte (t) at the thallus surface and subepithallial initials that are as long as or longer than the cells immediately subtending them.

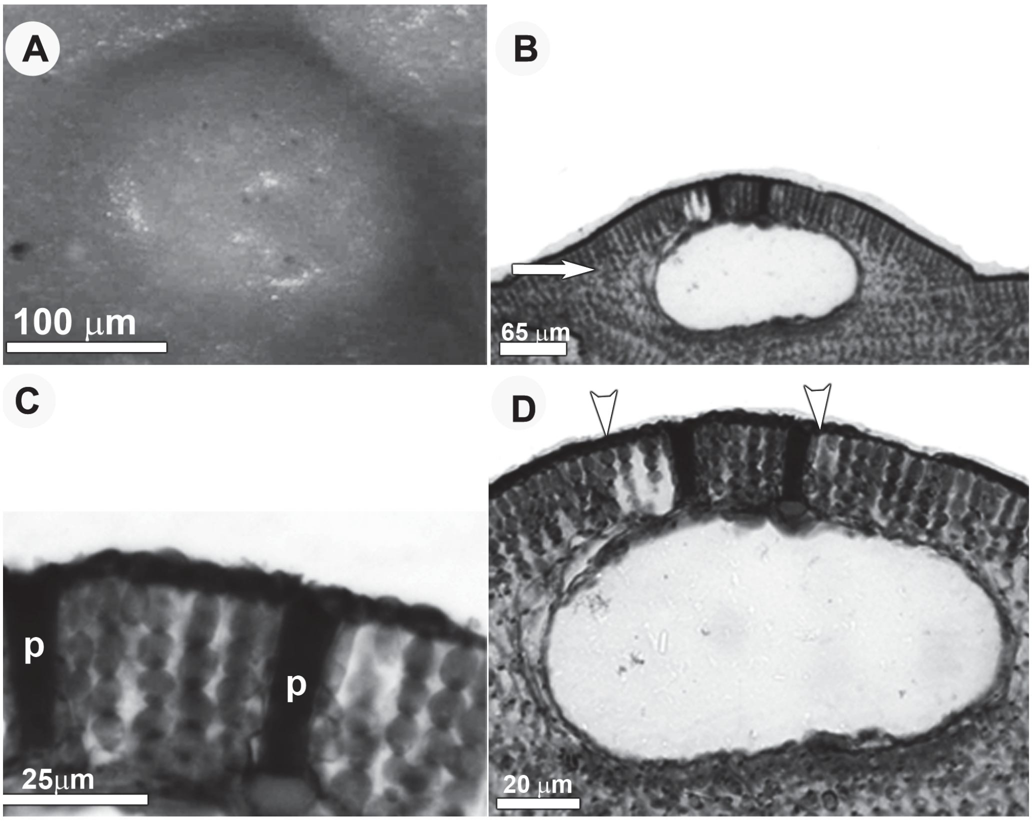

FIGURE 13 A–D. Tetrasporangial anatomy of *M. engelhartii* (A) Surface view of a multiporate conceptacle. (B) Vertical section showing a multiporate conceptacle raised above the surrounding thallus surface. (C) Vertical section through the conceptacle roof showing pore canals (p) lined by cells that are similar in size and shape to other roof cells. (D) Tetrasporangial conceptacle pore canals lined by cells that are similar in size and shape to other roof cells (arrowheads).

Lithothamnion muelleri Lenormand ex Rosanoff (1866: 101)
Figures 14 (A–D) and 15 (A–C).

Thalli encrusting, pink to dark purple, and firmly attached to the rocky substrate (Fig. 14A). Thallus thickness ranges from 0.3–0.4 mm at 0–49 m depth to 0.3 mm in deeper zones (50–70 m depth). The internal thallus construction is pseudoparenchymatous and monomerous (Fig. 14B). Epithallial cells occur in a single layer, are flared at their corners, and measure 4–6 µm in length and 5–8 µm in diameter (Fig. 14C). Subepithallial initials are square, measure 8–9 µm in length and 5–10 µm in diameter, and are as long or longer than the cells immediately subtending them (Fig. 14C). Cells of adjacent filaments are joined by cell fusions; secondary pit connections were not observed (Fig. 14D). Tetrasporangial conceptacles are multiporate and are raised above the surrounding thallus surface (Fig. 15A). Their chambers measure 200–350 µm in height and 400–650 µm in diameter and contain zonately divided tetrasporangia (Fig. 15B). Tetrasporangia bear apical pore plugs (Fig. 15C). Tetrasporangial conceptacle roofs are composed of 7–9 layers of cell. Cells of filaments bordering pore canals of tetrasporangial conceptacles do not differ in size and shape from other roof cells. The conceptacle floor is located 18–25 cells below the surrounding thallus surface.

Of the seven species recorded, only *L. muelleri* occurred along the entire depth range (Table 1). Four species (*Hydolithon* sp., Corallinaceae sp., *L. johansenii, M. engelhartii*) had their distribution confined to the shallower depth zone (0 to 29 m) while *T. pustulatum* was restricted to the deepest zone (60 to 70m).

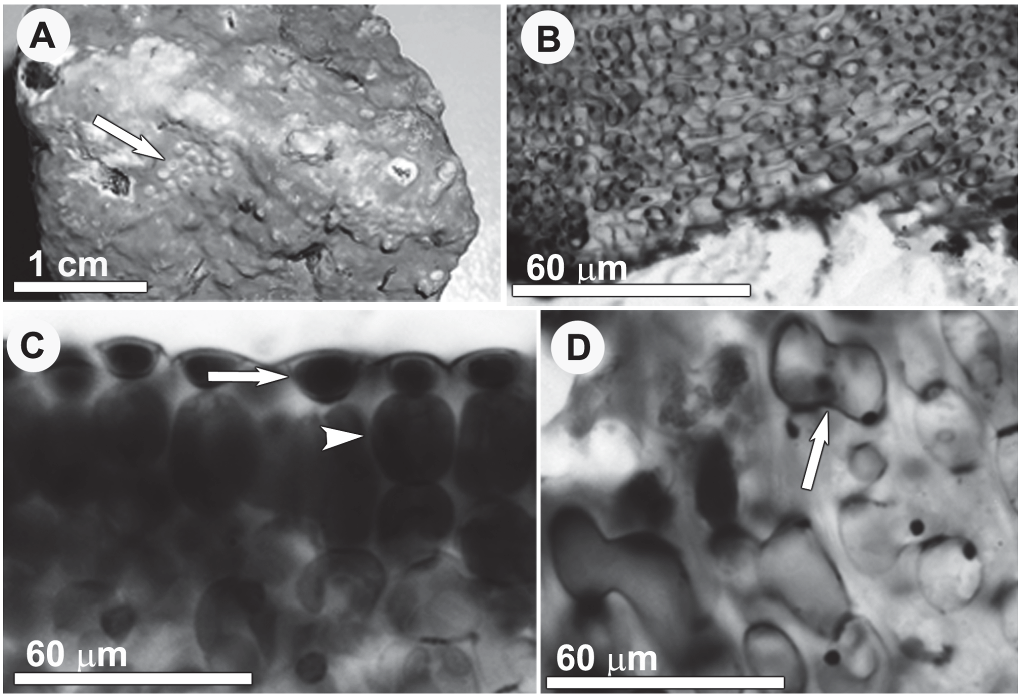

FIGURE 14 A–D. Vegetative anatomy of *L. muelleri* (A) An encrusting specimen (arrow) firmly attached to the rocky substrate. (B) Section through the vegetative thallus showing the monomerous internal construction. (C) Vertical section showing flared epithelial cells (arrow) and subepithelial initials that are as long as or longer (arrowhead) than the cells immediately subtending them. (D) Cells of adjacent filaments are joined by cell fusions (arrow).

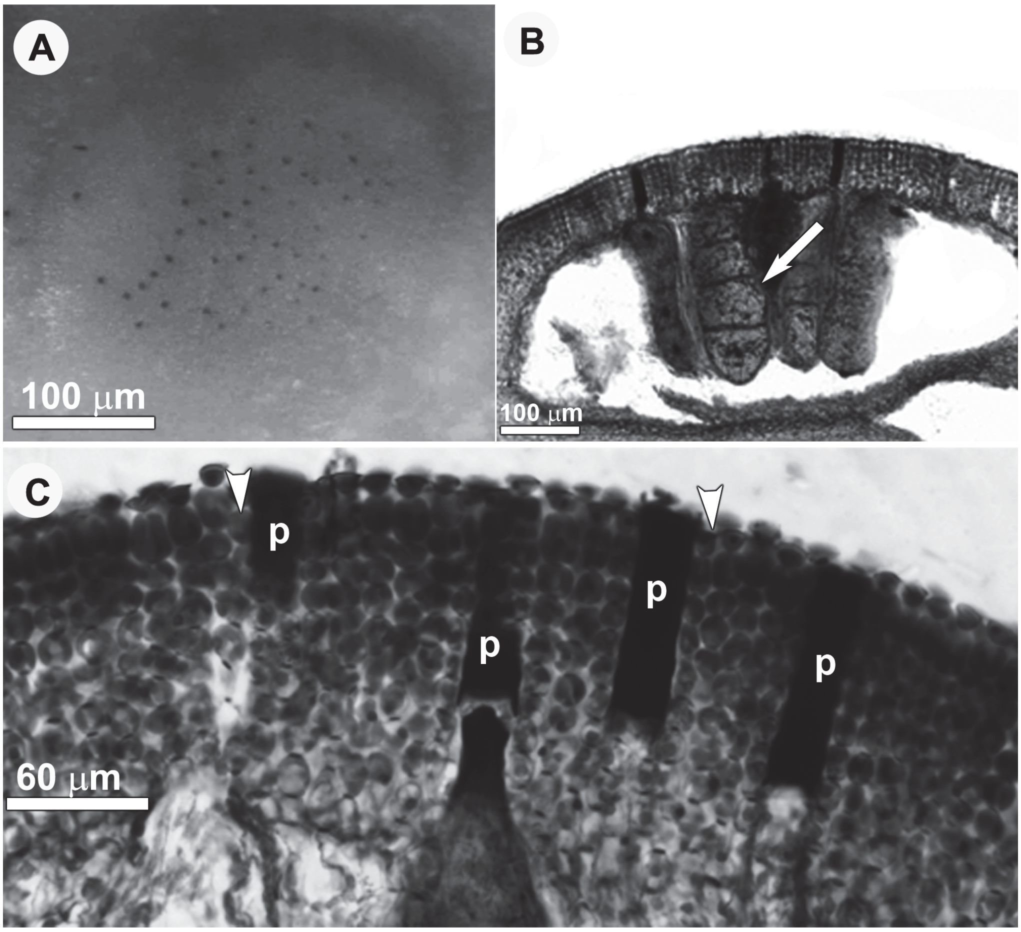

FIGURE 15 A–C. Tetrasporangial anatomy of *L. muelleri* (A) Surface view of a multiporate conceptacle. (B) Section through a raised multiporate conceptacle bearing zonately divided tetrasporangia (arrow). (C) Filaments (arrowheads) bordering pore canals (p) of a tetrasporangial conceptacle composed of cells that do not differ in size and shape from cells in other roof filaments.

TABLE 1. Species distribution by depth intervals.

Species	Depth Intervals 0–29m	30–49m	50–70m
Corallinaceae sp.	X	-	-
Hydrolithon rupestre	X	X	-
Hydrolithon sp.	X	-	-
Lithophyllum johansenii	X	-	-
Titanoderma pustulatum	-	-	X
Mesophyllum engelhartii	X	-	-
Lithothamnion muelleri	X	X	X

Temperature and light comparisons

Between 5 and 65 m depth, water temperature decreases according to depth, ranging from 28.9 ± 0.21 °C at 5 m to 19.7 ± 0.58 °C at 65 m (Fig. 16). At 15 m, 33 m and 45 m depth the average temperatures were 27.7 ± 0.32 °C, 26.8 ± 0.26 °C, and 21.7 ± 2.89 °C, respectively. The above data suggest the presence of a thermocline below 33 m with an abrupt change in temperature below this depth.

Photon irradiance decreased with depth and varied from 306 ± 26.52 µmol m^2 s^{-1} at 5 m depth to 3 ± 1.26 µmol m^2 s^{-1} at 65 m depht (Fig. 17). At 15 m, 33 m and 45 m depth, the average light intensities were 237 ± 17.54 µmol m^2 s^{-1}, 42 ± 1.08 µmol m^2 s^{-1} and 7 ± 252 µmol m^2 s^{-1}, respectively. Photon irradiance dropped significantly below 15 m depth, with a more dramatic reduction below the thermocline level (33 m depth).

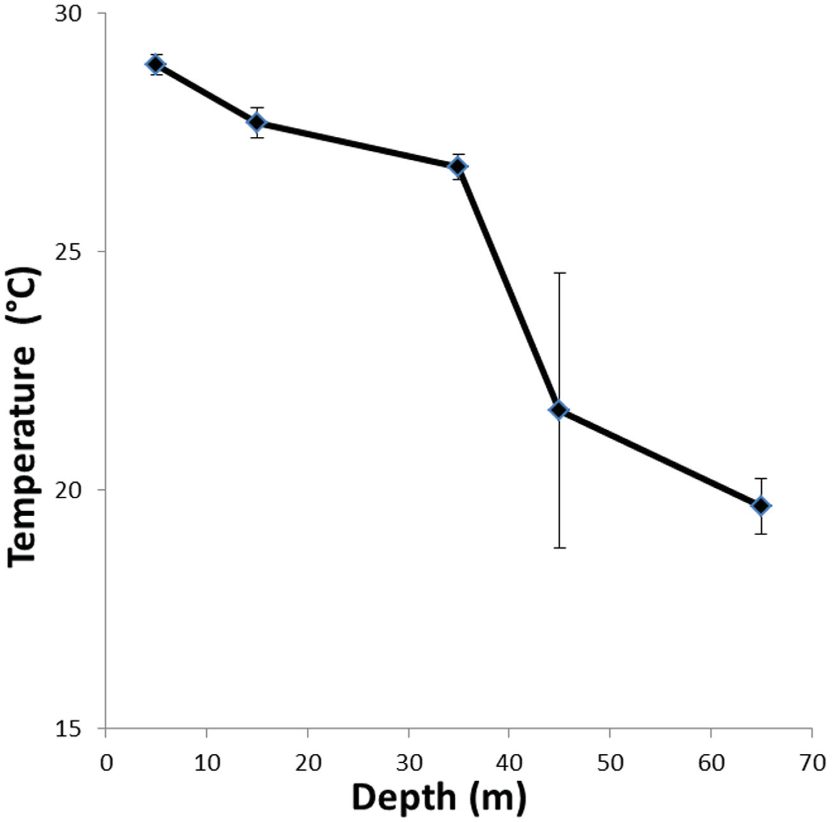

FIGURE 16. Graphical representation the variation of temperature (°C) according to the depth. Measurements were obtained at depths of 5, 15, 33, 45 and 65 m..

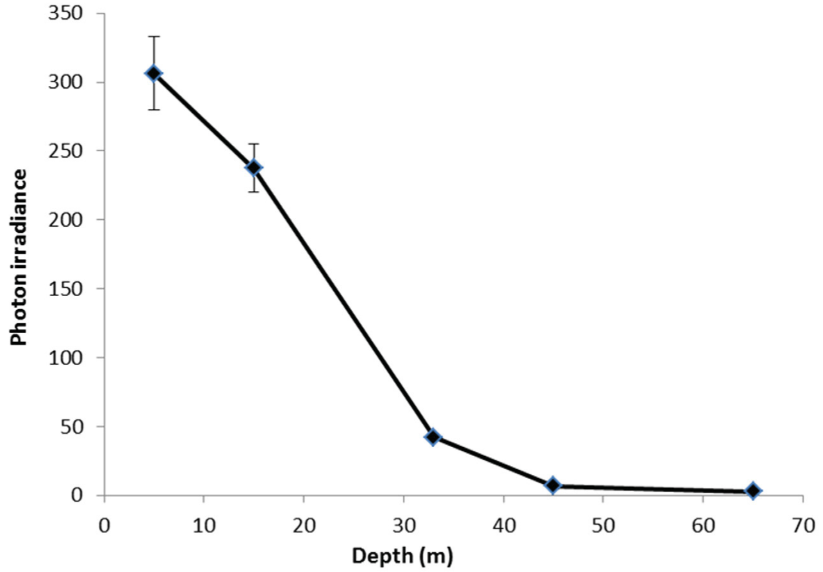

FIGURE 17. Graphical representation of the variation of photon irradiance (µmol m^2s^{-1}) according to the depth. Measurements were obtained at depths of 5, 15, 33, 45, 65 m.

Discussion

Till now there were no detailed taxonomic works on the CCA flora from the SPSPA. Hemsley (1885), in a botanical report on the Bermudas and different other islands of the Atlantic and southern oceans, recorded *Mesophyllum lichenoides* (J.Ellis) Me.Lemoine (1928: 252) and *Phymatolithon purpureum* (P.L.Crouan & H.M.Crouan) Woelkerling & L.M. Irvine (1986: 71) at shallow depths in SPSPA. However, there were no vouchers specimens of these species registered in herbaria nor were any descriptions of these records ever presented in his work, making it difficult to confirm the occurrence of these species for the SPSPA. In a recent survey, Burgos *et al.* (2009) identified the CCA species *Pneophyllum fragile* Kützing (1843: 385) for the SPSPA and recorded the species at 0–5m depth. This species is generally and commonly found worldwide (including Brazil) as an epiphyte on fleshy algae. As the present study examined only the epilithic CCA, we did not record *P. fragile*.

The tetrasporangial specimens of Corallinaceae sp. described herein can correspond to *Neogoniolithon* or *Spongites* genera, that are distinguished by gametangial and carposporophyte features (Penrose 1991). After an analysis in literature of well described species of both genera, the specimens here analyzed are in accordance with the modern description of the type and recently collected topotypes of *Spongites fruticulosus* Kützing (1841: 33) from the Mediterranean Sea (Penrose 1991, Basso & Rodondi 2000). The specimens exhibit all those vegetative and tetrasporangial features attributed to *S. fruticulosus* by Penrose (1991) and Basso & Rodondi (2006), among others: monomerous thallus, perithallium zoned by several growth lines, rounded epithallial cells covered by a thick cuticular layer, adjacent filaments connected laterally by cell fusions, tetrasporangial conceptacles chambers with 500–550 µm in diameter, roofs composed of 10–15 layers of cells, and pore canal surrounded by cells that are aligned more-or-less parallel to roof surface. *Spongites fruticulosus* can be distinguished from the another *Spongites* species previously reported for the Brazilian coast, i.e. *Spongites yendoi* (Foslie) Y.M.Chamberlain (1993: 102) (Henriques *et al.* 2012), mainly on the disparate size of mature tetrasporangial conceptacle chambers diameter (500–550 µm in *S. fruticulosus* vs < 280–290 µm in *S. yendoi*). The identification at family level is preferred until male or carposporophytes plants can be found.

Hydrolithon rupestre was first reported from the Atlantic Ocean by Pereira-Filho *et al.* (2012) who, however, gave no description of the species. Thus, our finding represents the first documented record of the species from that Ocean. Our material agrees with the description of the type and recent collections of *H. rupestre* from southern and southeastern Australia (Penrose,1996, Maneveldt, 2005 and Harvey *et al*., 2006). It also agrees with recent collections of *H. rupestre* from Fiji, South Africa, and Taiwan (Maneveldt 2005) . Some differences were observed in the range of dimensions of tetrasporangial and spermatangial conceptacles chambers, and number of cells of roof filaments in carpogonial conceptacles. As reinforced by Maneveldt (2005) and Harvey *et al.* (2006), the dimensions of tetrasporangial conceptacles chambers is a character variable within *Hydrolithon* species. Therefore, the observed difference (< 130 µm) in the tetrasporangial conceptacles chambers dimension should be considered an intraspecific variation within different *H. rupestre* populations (Table 2). The same criteria was adopted for observed differences in spermatangial, carpogonial and carposporangial dimensions. *Hydrolithon rupestre* is remarkably similar to *Hydrolithon munitum* (Foslie & M.A.Howe) Penrose (1996: 263). These two taxa can be distinguished mainly by the presence (in *H. munitum*) or absence (in *H. rupestre*) of a central columella within the sporangial conceptacle (Penrose 1996). A comparison of measured characters of *H. rupestre* from SPSPA with other *H. rupestre* populations and other *Hydrolithon* species recorded for the Brazilian coast is provided in Table 2.

The unidentified species of *Hydrolithon* reported in this study is similar to *H. rupestre*. However, the two species are different each other in the number of rings of enlarged cells lining the tetrasporangial conceptacle pore canal. Unlike all previously recorded species of *Hydrolithon* (incl. *H. rupestre*) in which the pore canals of tetrasporangial conceptacles are lined at their base by a single ring of enlarged cells, the new species has 3–4 rings of these enlarged cells, all of which have the typical *Hydrolithon*-type form of development. This feature (multiple layers of enlarged cells lining the tetrasporangial conceptacle pore canal) possibly supports the proposition of a new genus within the Corallinaceae. Further collections and molecular analyses of additional samples are, however, needed to confirm this suggestion. Comparisons of the main taxonomic characteristics of *Hydrolithon* species cited to Brazil are presented in table 2.

For most features, *Lithophyllum johansenii* found in this study agrees with the description of the type collection of this species from southern Australia (Woelkerling & Campbell 1992). Differences were observed in the tetrasporangial conceptacles chambers dimensions and in the presence or absence of central columella in tetrasporangial conceptacles. The specimens analyzed in this study have tetrasporangial chambers diameter with 190–210 µm (while in type specimens it is 130–196 µm) and their height is 90–115 µm (while in type specimens it is is 65–108 µm). These dimensions are, however, within the range presented by previously published record of *L. johansenii* for Brazil (Villas-Boas *et al*. 2009). Although central columella was not observed in the type specimens of *L. johansenii* (Woelkerling & Campbell 1992), such structure was observed in the specimens of *L. johansenii* collected both in SPSPA (this study) and Espírito Santo State, Brazil (Villas-Boas *et al*. 2009). These observations reveal that both characters (i.e. dimensions of tetrasporangial conceptacles and presence/absence of central columella) are variable and should not be used for separation of species of *Lithophyllum*. The main diagnostic feature of *L. johansenii* is the pore canals of tetrasporangial/bisporangial conceptacles normally completely occluded by enlarged angular cells which line the canal (Woelkerling & Campbell 1992), characteristic observed in our specimens (Fig. 9 B–D).

Titanoderma pustulatum here described matches the detailed description of the type collection of this species from France and representative specimens from southern Australia described by Woelkerling & Campbell (1992) (as *Lithophyllum pustulatum*). An important difference, however, was observed in the tetrasporangial conceptacle chamber height. It was practically twice higher in specimens from SPSPA (300–320 µm) than that observed by Woelkerling & Campbell (1992) (i.e. 110–180 µm). *Titanoderma pustulatum* can be distinguished from the other *Titanoderma* species recorded for Brazil, i.e. *Titanoderma prototypum* (Foslie) Woelkerling, Y.M.Chamberlain & P.C.Silva (1985: 333) (see Pereira-Filho *et al.* 2011, specimen RB 498282, as *Lithophyllum prototypum*), basically by having a vegetative thallus composed by more than two cell layers, and floors of sporangial conceptacles situated one to three cells below the thallus surface. According to Woelkerling & Campbell (1992) and personal observations on the specimen determined as *Lithophyllum prototypum* (= *Titanoderma prototypum*) for Brazil (RB 498282), the vegetative thallus is constituted by only two cell layers occurring as successive applanate branches, and floors of sporangial conceptacles situated only one cell below the thallus surface.

Mesophyllum engelhartii found in this study agrees with the type and recent collected samples of this species from southern Australia described in detail by Woelkerling & Harvey (1993). *Mesophyllum engelhartii* can be distinguished from the another *Mesophyllum* species previously reported for the Brazilian coast, i.e. *Mesophyllum erubescens* (Foslie) Me.Lemoine (1928: 252) (see Nunes *et al*. 2008, Horta *et al.* 2011), mainly by the cells bordering the tetrasporangial conceptacle pore canal. In *M. engelhartii* these cells are similar in size and shape than other roof cells whereas in *M. erubescens* they are more elongate, especially near the base of the pore, than other roof cells.

TABLE 2. Comparison of *Hydrolithon rupestre* and *Hydrolithon* sp. described in this study against previously published records of different populations of *Hydrolithon rupestre* and the other *Hydrolithon* species recorded for the Brazilian coast. Data from previously published records have been taken from both the descriptions and the figures. Unless otherwise stated, all measurements are in micrometres. ND = no data provided.

Character	*Hydrolithon* sp. (this study)	*Hydrolithon rupestre* (this study)	*Hydrolithon rupestre* (Penrose 1996)	*Hydrolithon rupestre* (Maneveldt 2005)	*Hydrolithon rupestre* (Harvey *et al*. 2006)	*Hydrolithon boergesenii* (Mendonza-González *et al*. 2009)*	*Hydrolithon samoënse* (Tâmega & Figueiredo, 2005)	*Hydrolithon farinosum* (Horta 2000 and Harvey *et al*. 2006)
Locality	Brazil	Brazil	Southern Australia	Fiji, South Africa, Southern Australia, and Taiwan	Southeastern Australia	Atlantic Mexico	Brazil	Brazil and southeastern Australia
Habit	epilithic	epilithic	epilithic	epilithic	epilithic	epilithic	epilithic	epiphytic
Thallus thickness (nº. of layers of cells)	>10	>10	>10	>10	>10	>10	>10	<10
Mature sporangial conceptacle chamber diameter	180–200	204–217	82–96	115–190	Up to 80	174–216 81–165	92–125	100–140
Mature sporangial conceptacle chamber height	150–185	160–180	77–82	75–105	Up to 55	81–96	65–70	85–105
No. of in mature sporangial conceptacle roof filaments	5–8	4–7	3–4	4–7	2–3	3 or more	2–3	2–3
Depth (nº. of cells) of mature sporangial conceptacle floor	14–20	12–18	~12	10–14	ND	ND	ND	ND
Nº. of rings of enlarged cells surrounding the tetrasporangial pore canal	3–4	1	1	1	1	1	1	1
Central columella	absent	absent	present	present	absent	absent	ND	present
Spermatangial conceptacle chamber diameter	ND	95–102	49–55	56	Up to 55	ND	ND	60–85
Spermatangial conceptacle chamber height	ND	70–74	41–49	16–21(taken from the holotype)	Up to 35	ND	ND	40–55
Carpogonial conceptacle chamber diameter	ND	104–128	77–104	31–74 (taken from the holotype)	ND	ND	ND	110–125
Carpogonial conceptacle chamber height	ND	104–120	63–90	12–37 (taken from the holotype)	ND	ND	ND	100–120
Carposporangial conceptacle chamber diameter	ND	200–2015	77–104	85–150 (taken from the holotype)	ND	ND	ND	ND
Carposporangial conceptacle chamber height	ND	120–125	63–90	50–85 (taken from the holotype)	ND	ND	ND	ND

*Although *H. boergesenii* has been recorded for the Brazilian coast by Figueiredo & Steneck (2002), no description of this species was provided by this study. Therefore, data presented on this species were obtained from Mendoza e González *et al*. (2009).

TABLE 3. Comparison of *Lithothamnion muelleri* described in this study against other *Lithothamnion* species from Brazil for which detailed descriptions are available. Data from previously published records have been taken from both the descriptions and the figures.

Character	***L. muelleri* (this study)**	***L. brasiliense* (Bahia *et al.* 2010**	***L. crispatum* (Bahia *et al.* 2010 and Farias *et al.* 2010**	***L. glaciale* (Henriques *et al.* 2012)**	***L. steneckii* (*Mariath et al.* 2012)**
Growth form	Encrusting	Encrusting to lumpy	Lumpy	Fruticose	Encrusting to fruticose
Tetrasporangial conceptacle chamber height	200-350 µm	100-180 µm	110-230 µm	160-280 µm	90-200 µm
Tetrasporangial conceptacle chamber diameter	400-650 µm	300-500 µm	220-525 µm	300-430 µm	195-330 µm
Tetrasporangial conceptacle roof surface	Flat	Sunken	Flat	Flat	Flat
Tetrasporangial conceptacle pores piited with depressions, resulting from the disintegration of the uppermost rosette cells surrounding the pore canal	Absent	Absent	Present	Absent	Absent
Position of tetrasporangial conceptacle pores in relation to the surrounding roof cells	Flush	Flush	Sunken	Flush	Sunken
Cells bordering the tetrasporangal pore canal	Similar in size and shape than other roof cells	Different in size and shape than other roof cells	Different in size and shape than other roof cells	Different in size and shape than other roof cells	Different in size and shape than other roof cells

The samples determined in this study as *Lithothamnion muelleri* are in accordance with the type and representative specimens of this species from southern Australia described in detail by Wilks & Woelkerling (1995). The only difference observed was the height of tetrasporangial conceptacle chamber (200–350 µm in specimens from SPSPA vs. 150–200 µm in specimens from southern Australia). *Lithothamnion muelleri* from SPSPA can be distinguished from other *Lithothamnion* species recorded for Brazil mainly by the following combination of features: 1) encrusting growth form; 2) roofs of mature tetrasporangial conceptacles not pitted with depressions around the pores; 3) tetrasporangial conceptacle roof filaments bordering pore canals composed of cells that do not differ in size and shape from cells in other roof filaments, and 4) tetrasporangial conceptacles raised above the surrounding thallus surface (Table 3). A comparison of *Lithothamnion muelleri* described in this study against other *Lithothamnion* species from Brazil for which detailed descriptions are available is provided in Table 3.

As stated by Littler & Littler (2000), many Coralline algae are widely distributed to great depths with species well adapted to low photon irradiance. For example, Adey (1970a) reported that *Phymatolithon lenormandii* (Areschoug) Adey (1966: 325) (as *Leptophytum laeve* W.H. Adey 1966) occurs at great depths in the North Atlantic subarctic, where it grows at 35 lux (1.1 µmol), which is about 0.1 % of the photon irradiance at the surface. At the SPSPA, we found *L. muelleri* and *T. pustulatum* at depths greater than 45 m at photon irradiance equal to 7 µmol. This value represents 0.8 % of the photon irradiance at the surface, which is also relatively low, but well above the range reported for *Phymatolithon lenormandii* (as *Leptophytum laeve*) by Adey (1970b). However, even though, as above mentioned, many Coralline algae are adapted to live at great depths, the vertical distribution of most of them is strongly influenced by both temperature and photon irradiance. In fact, we observed a dropping of CCA species composition below 30 m depth where a dramatic reduction in both the above abiotic factors there occurs.

In the present study, *L. muelleri* occurred throughout the depth range down to 65 m depth. This finding is consistent with the observations of Basso (1998) and Bressan (1974) that cites the ability of some species of Melobesioideae, including *Lithothamnion* species, to be present in a wide range of vertical distributions, being found in both shallow and deep water (184 m).

Conclusions

A total of seven species of CCA were identified for the SPSPA. *Titanoderma pustulatum* occurrence was restricted to the depth range of 50 to 70 m depth and *Lithothamnion muelleri* occurred throughout all sampled depth range. A decrease in CCA species richness and change in species composition was seen from shallow to deeper zones that can be explained by a significant reduction in measured temperature and photon irradiance observed bellow 30 m depth .

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