



Lithophylloideae and Mastophoroideae (Corallinales, Rhodophyta) from the Brazilian continental shelf

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Abstract

Brazilian continental shelf is rich in rhodolith beds and it has a relevant role as a critical ecosystem for conservation. However, we do not know the taxonomy of the rhodolith forming species and because of that we analysed samples from the REVIZEE project in which morpho-anatomical analysis was used to identify Lithophylloideae and Mastophoroideae species. We found *Titanoderma pustulatum*; *Lithophyllum stictaeforme*; *Lithophyllum corallinae*, *Hydrolithon breviclavium*, *Hydrolithon onkodes* and *Spongites fruticosus*. This is the first detailed description of *T. pustulatum* from Brazil and *S. fruticosus* from the Atlantic Ocean, the first record of *H. breviclavium* in the Atlantic Ocean and of *H. onkodes* in Brazilian water. *L. corallinae* was found 250 m deep—that is a new Coralline algae depth record for Brazilian waters. This study contributes to the understanding of the diversity in Brazilian continental shelf and indicates the importance of future systematic studies. This knowledge is relevant to guide conservation programs and evaluation of impacts.

Key words: Corallinophycidae, Red algal systematics, Rhodolith, Corallinaceae, Taxonomy

Introduction

Nongeniculate calcareous algae can form reefs or free-living structures called rhodoliths, which can be grouped to form the extensive rhodolith beds that are considered biodiversity hotspots (BIOMAERL Team 1998). It is widely distributed in several habitats around the world ranging from tropical to Polar Regions, from shallow to deep water (Steneck 1986). The Brazilian continental shelf is known for having the largest area covered by rhodolith beds in the world (Foster 2001; Amado-Filho & Pereira-Filho 2012).

Morphologically, coralline red algae are either geniculate (with branches consisting of alternating uncalcified and calcified segments) or non-geniculate (lacking alternating uncalcified and calcified segments) (Harvey *et al.* 2009). In this study, only non-geniculate Lithophylloideae Setchell (1943: 134) and Mastophoroideae Setchell (1943: 134) are described.

In 1997, the Brazilian government set up a Program for Evaluating the Sustainable Potential of Living Resources of the Brazilian Exclusive Economic Zone (REVIZEE). This program addressed potential fishery resources, with the objective to identify the main benthic taxonomic groups on the outer shelf and continental slope from 50 to 500 m depth. Today REVIZEE program is the most widespread marine project carried out on the Brazilian coast generating biological, geological, physical and chemical data (Lavrado 2006).

Four sites of REVIZEE were studied recently and three new occurrences of coralline red algae were observed in the continental shelf of Espírito Santo, Brazil, showing that Brazilian rhodolith beds have a big diversity not well known until the moment (Henriques *et al.* 2012). Therefore, the current study aims to contribute to the knowledge of this important habitat in some areas of the Brazilian central continental shelf, reporting the discovery of

previously unrecorded Coralline algae species in Brazilian waters, based on morphological and anatomical features and reporting a new algae depth record for Brazilian waters.

Material and methods

Fieldwork

Data were obtained from field trips conducted in 2001–2002 by REVIZEE aboard the supply boat N/RB Astro Garoupa of “Astronomia Navegação” (Lavrado 2006). The material was collected offshore at depths ranging from 54 to 250 m. The region is influenced by the Brazilian current that runs along the South Atlantic Ocean and is characterized by sea surface temperatures ranging from 21 to 27 °C (Lavrado 2006). At 50 m depth, the region is influenced by the South Atlantic Central Waters (SACW) and is characterized by temperatures from 6 to 20 °C (Silveira *et al.* 2000).

Laboratory work

Since 2001, the samples had been preserved in 4% formalin seawater (Yoneshigue-Valentin *et al.* 2006), decalcified in 10% nitric acid, dehydrated in alcohol series and embedded in hystoresin (Moura *et al.* 1997). As a consequence of this long preservation time, specimens were degraded, and it was difficult finding intact reproductive structures. The material was exhaustively sectioned with a microtome and stained for Optical Microscopy analysis. Type specimens were not examined. Identified samples were incorporated in the herbarium collection of the Botanical Garden of Rio de Janeiro (RB). The herbarium code follows the Index Herbariorum (Holmgren & Holmgren 2014, continuously updated). Conceptacle measurements follow Adey & Adey (1973), thallus anatomical terminology follows Woelkerling (1988), growth form terminology follows Woelkerling *et al.* (1993) and typification data follow Woelkerling (1993).

Results

Systematic treatment

Samples collected from different places of the Brazilian continental shelf were submitted to morpho-anatomical analysis to identify the species of Lithophylloideae and Mastophoroideae. We found *Titanoderma pustulatum* (J.V. Lamouroux) Nägeli (1858:532) (Fig. 1; Table 1); *Lithophyllum stictaeforme* (Areschoung in J. Agardh) Hauck (1877: 292) (Fig. 2; Table 2); *Lithophyllum corallinae* (Crouan et Crouan) Heydrich (1897a: 47) (Fig. 3; Table 2), *Hydrolithon breviclavium* (Foslie) Foslie (1909: 56) (Fig. 4; Table 3), *Hydrolithon onkodes* (Heydrich) D.Penrose & Woelkerling (1992: 83) (Fig 5; Table 3) and *Spongites fruticosus* Kützing (1841:33) (Fig. 6; Table 4). This is the first detailed description of *T. pustulatum* from Brazil and *S. fruticosus* from the Atlantic Ocean, the first record of *H. breviclavium* in the Atlantic Ocean and of *H. onkodes* in Brazilian water. *L. corallinae* was found 250 m deep, that is a new Coralline algae depth record for Brazilian waters. Detailed descriptions of these species are given below.

Titanoderma pustulatum (J.V. Lamouroux) Nägeli (1858: 532). (Fig. 1; Table 1)

Basionym:—*Melobesia pustulata* J.V.Lamouroux (1816: 315)

Lectotype:—CN (Herb. Lamouroux) unnumbered

Type Locality:—France

Further References:—Woelkerling & Campbell (1992); Woelkerling (1996a) e Harvey *et al.* (2009)

Description:—Plants non-geniculate, with encrusting growth form (Fig. 1A). Thallus pseudoparenchymatous with dorsiventral internal organization. One layer of flattened epithallial cells 4–6 µm in height and 7–11 µm in diameter (Fig. 1B). Dimerous thallus construction (Fig. 1C) consisting of a double system of branched filaments that forms a core running more or less vertical to the substratum terminating in the epithallial cells. The thallus is composed mainly of palisade rectangular cells (Fig. 1C) measuring 25–27 µm in height and 12–14 µm in diameter. Cells of adjacent filaments are linked by secondary pit connections (Fig. 1D); Cell fusions and trichocytes have not been observed.

TABLE 1: Comparison of *Titanoderma pustulatum* characters from Brazilian deep water and other areas.

	<i>T. pustulatum</i> British Isles ¹	<i>L. pustulatum</i> Australia ²	<i>T. pustulatum</i> Caribbean ³	<i>L. pustulatum</i> New Zealand ⁴	<i>T. pustulatum</i> Present study
Epithallial cells height (µm)	–	2–6 µm	–	–	3–4 µm
Epithallial cells diameter (µm)	–	4–12 µm	8–15 µm	–	7–10 µm
Number of cells in the tetrasporangial conceptacles roof	3	(2–) 3 (– 4)	4–5	1–2	4–5
Tetrasporangia conceptacle diameter (µm)	156–458 µm	(328 –) 390–500 (– 556) µm	500 µm	185–300 µm	415–500 µm
Tetrasporangia conceptacle height (µm)	78–234 µm	110–180 µm	100 µm	–	222–274 µm

¹ Chamberlain (1991) and Irvine & Chamberlain (1994); ² Woelkerling & Campbell (1992) as *Lithophyllum*. ³ Littler & Littler (2000); ⁴ Harvey et al. (2005) as *Lithophyllum*

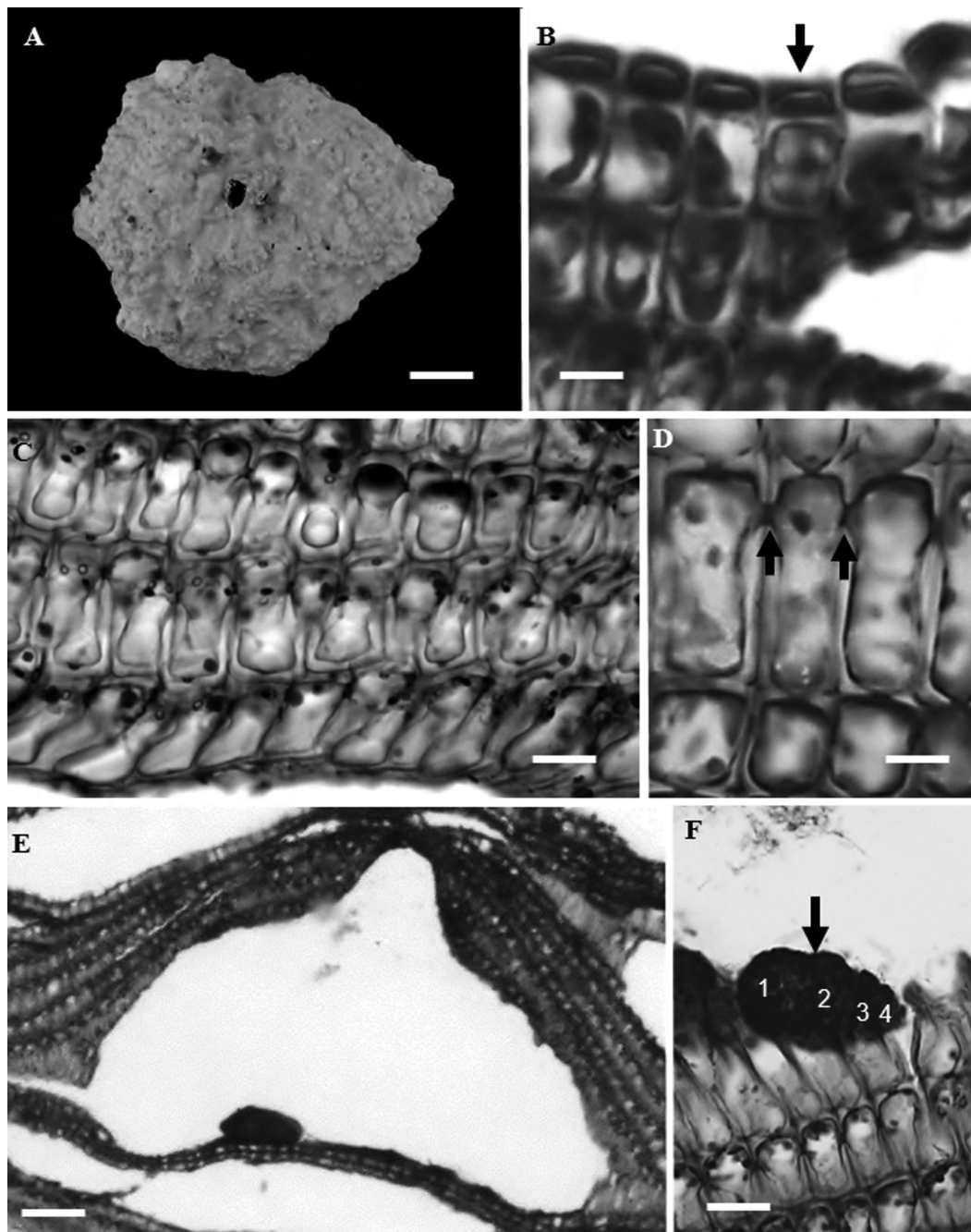


FIGURE 1 *Titanoderma pustulatum* A: encrusting growth form. Scale bar 1.0 cm; B: Flattened epithallial cells (arrow). Scale: 9 µm; C: Dimerous thallus construction with palisade rectangular cells. Scale: 25 µm; D: secondary pit connections (arrows). Scale: 14 µm; E: Tetrasporangia conceptacle. Scale 60 µm; F: Tetrasporangia (arrow). Scale 42 µm.

Tetrasporangial conceptacles uniporate with the roof more or less raised above the surrounding thallus surface. Conceptacle roofs 4–6 cells thick including the epithallial cells, pore without an apical plug (Fig. 1E). Conceptacle chambers 430–510 µm diameter and 220–275 µm in height, without a central columella with chamber floor usually situated 5 cell layers below the thallus surface. Pore canals of tetrasporangial conceptacles lined by cells do not protrude into the canal, and are oriented more or less perpendicularly to the roof surface (Fig. 1E). Tetrasporangia scattered across the chamber floor (Fig. 1F)

Material examined:—Espírito Santo, Brazil (19,520S–38,768W), 65 m deep, RB498379; (19,800S–37,773W), 58 m deep, RB 458702; R 210798; (19,813S–37,943W), 54 m deep, RB 458703; (20,614S–34,894W), 60 m deep, RB 458704; (20,767S–40,099W), 55 m deep, RB458705; (21,166S–40,283W) 82 m deep, RB 498380

Geographic distribution:—According to Woelkerling & Campbell (1992) it is not possible to discern the right distribution of this species since there are hundreds of publications recording *T. pustulatum* in all continents. This species was found in the São Paulo state, Brazil, but there is no detailed descriptions based on the modern diagnostic features (Taylor 1960).

Lithophyllum stictaeforme (Areschoung in J. Agardh) Hauck (1877: 292) (Fig. 2; Table 2)

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

Lectotype:—S (unnumbered); designated and illustrated in Athanasiadis (1999, p. 738, fig.1).

Type locality:—Mediterranean Sea.

Further references:—Furnari et al. (1996, pp.117–121, figs 1–11, as *L. frondosum*), Woelkerling (1996, pp. 233–237, figs 104–105, as *L. frondosum*), Ringeltaube & Harvey (2000, pp. 433–434, figs 2–4, as *L. frondosum*); Athanasiadis (1999, pp. 735–745, fig. 1–10); Harvey et al. (2005, pp. 94–95, fig. 12.5A–G); Villas-Boas et al. (2009).

Description:—Plants non-geniculate, forming free-living rhodoliths. With encrusting growth form (Fig.2A). Thallus pseudoparenchymatous with dorsiventral internal organization. Dimerous thallus construction (Fig. 2B, C) consisting of a double system of branched filaments that forms a core running more or less vertical to the substratum, terminating in one layer of flattened epithallial cells (Fig. 2B). The thallus is composed mainly of nonpalisade cells (Fig. 2C), measuring 11–26 µm in height and 5–18 µm in diameter. Epithallial cells 5–7 µm in height and 13–17 µm in diameter. Cells of adjacent filaments are linked by secondary pit connections (Fig. 2D). Cell fusions and trichocytes have not been observed.

Tetrasporangial conceptacles uniporate with the roof raised above the surrounding thallus surface (Fig. 2E). Conceptacle roofs 3–5 cells thick including the epithallial cells; pore channel narrowing toward the top configuring a conical shape; pore without an apical plug with cells surrounding somewhat elongate (papillate) and projecting to the pore canal but do not occlude it; mucilaginous material observed in the pore (Fig. 2E). Conceptacle chambers are somewhat elliptical and measure 292–310 µm in diameter and 160–187 µm in height. Without a central columella with chamber floor usually situated 14–16 cell layers below the thallus surface. Tetrasporangia present (Fig. 2F)

Material Examined:—Rio de Janeiro, Brazil (22,319S–40,826W), 59 m deep, RB 498381; R210797; RB588403

Geographic Distribution:—Australia (Woelkerling 1996; Ringeltaube & Harvey 2000), Brazil (Nunes *et al.* 2008, Villas-Boas *et al.* 2009), Mediterranean Sea (Furnari et al. 1996; Athanasiadis 1999) and central New Zealand (Harvey et al. 2005).

Lithophyllum corallinae (Crouan et Crouan) Heydrich (1897a:47) (Fig. 3; Table 2)

Basionym:—*Melobesia corallinae* Crouan et Crouan (1867: 150)

Lectotype:—CO (unnumbered); Chamberlain (1991: 67, Fig. 208 as *Titanoderma*); Woelkerling & Campbell (1992: 43, Fig. 22A as *Lithophyllum*).

Type Locality: Brest, France.

Further references:—Woelkerling & Campbell (1992); Woelkerling (1996a); Harvey et al. (2005); Villas-Boas et al. (2009)

Description:—Plants non-geniculate with encrusting to warty growth form (Fig. 3A). Thallus pseudoparenchymatous with dorsiventral internal organization. Dimerous thallus construction (Fig. 3B) consisting of a double

system of branched filaments that forms a core running more or less vertical to the substratum terminating in one layer of flattened epithallial cells (Fig. 3B). The thallus is composed mainly of nonpalisade cells measuring 10–20 μm in height and 7–12 μm in diameter. Epithallial cells 4–6 μm in height and 8–13 μm in diameter. Cells of adjacent filaments are linked by secondary pit connections (Fig. 3C); cell fusions and trichocytes have not been observed.

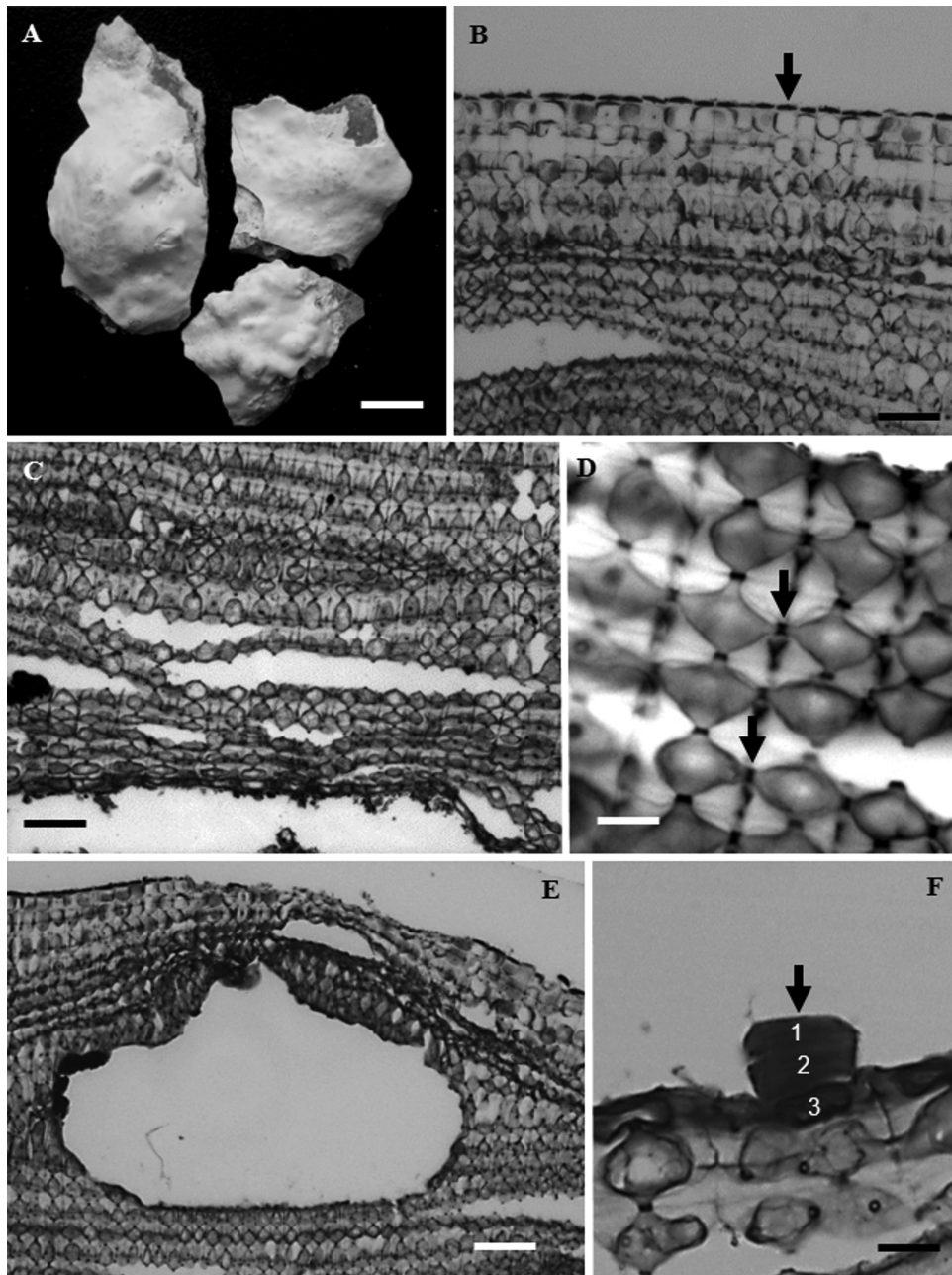


FIGURE 2 *Lithophyllum stictaeforme* A: encrusting growth form. Scale bar 1.0 cm; B: Flattened epithallial cells (arrow). Scale: 60 μm ; C: Dimerous thallus construction. Scale: 70 μm ; D: secondary pit connections (arrows). Scale: 14 μm ; E: Tetrasporangia conceptacle. Scale 65 μm ; F: Tetrasporangia (arrow). Scale 14 μm

Bisporangial conceptacles uniporate with the roof raised above the surrounding thallus surface (Fig. 3D). Conceptacle roofs 2–4 cells thick including the epithallial cells; pore channel narrowing toward the top configuring a conical shape; pore without an apical plug with mucilaginous material (Fig. 3E). Conceptacle chambers 228–271 μm in diameter and 166–168 μm in height, without a central columella with chamber floor usually situated 6–8 cell layers below the thallus surface. Bisporangia present (Fig. 3F)

Material Examined:—Bahia, Brazil (14,902S–38,860W), 250 m deep, RB 498382, RB588404, RB588405

Geographic Distribution:—Southern Australia (Woelkerling & Campbell 1992; Woelkerling 1996), British Isles (Irvine & Chamberlain 1994), central New Zealand (Harvey et al. 2005) and Brazil (Villas-Boas 2009).

TABLE 2: Comparison of *Lithophyllum stictaeforme* and *L. Corallinae* characters from Brazilian deep water and other areas.

	<i>Melobesia stictaeforme</i> ¹	<i>L. frondosum</i> ²	<i>L. stictaeforme</i> ^{3,4}	<i>L. stictaeforme</i> ⁵	<i>L. stictaeforme</i> ⁶	<i>L. stictaeforme</i>	<i>L. corallinae</i> ^{3,4,7}	<i>T. corallinae</i> ⁸	<i>L. corallinae</i> ⁵	<i>L. corallinae</i>
Type		Mediterranean	Australia, New Zealand	ES, Brazil	BA, Brazil	Present study	Australia, New Zealand	British Isles	ES, Brazil	Present study
Tetrasporangial conceptacle roof	Flush	Raised to Flush	Raised to Flush	Flush	Raised to Flush	Raised	Raised to Flush	Immersed to Raised	Flush	Raised
Number of cells in the tetrasporangial conceptacles roof	5–10	5–9	3–6	5	5–7	3–5	2–4	–	3–4	2–4
Differentiated cells lining tetrasporangial conceptacle pore canal	Present	Present	Present	Present	Absent	Present	Absent	Absent	Present	Present
Tetrasporangia conceptacle height (µm)	100–175	–	(65)90–125(160)	150–160	105–182	160–187	68–105(136)	75–117	125–135	166–198
Tetrasporangia conceptacle diameter (µm)	375–475	(200) 320–410 (450)	290–420(450)	230–275	202–262	292–310	(155)190–235(280)	160–235	220–230 (295)	228–271

¹Athanasiadis (1999); ²Fumari *et al.* (1996). ³Woelkerling (1996a); ⁴Harvey *et al.* (2005); ⁵Villas-Boas *et al.* (2009); ⁶Nunes *et al.* (2008); ⁷Woelkerling & Campbell (1992); ⁸Irvine & Chamberlain (1994) as *Titanoderma*.

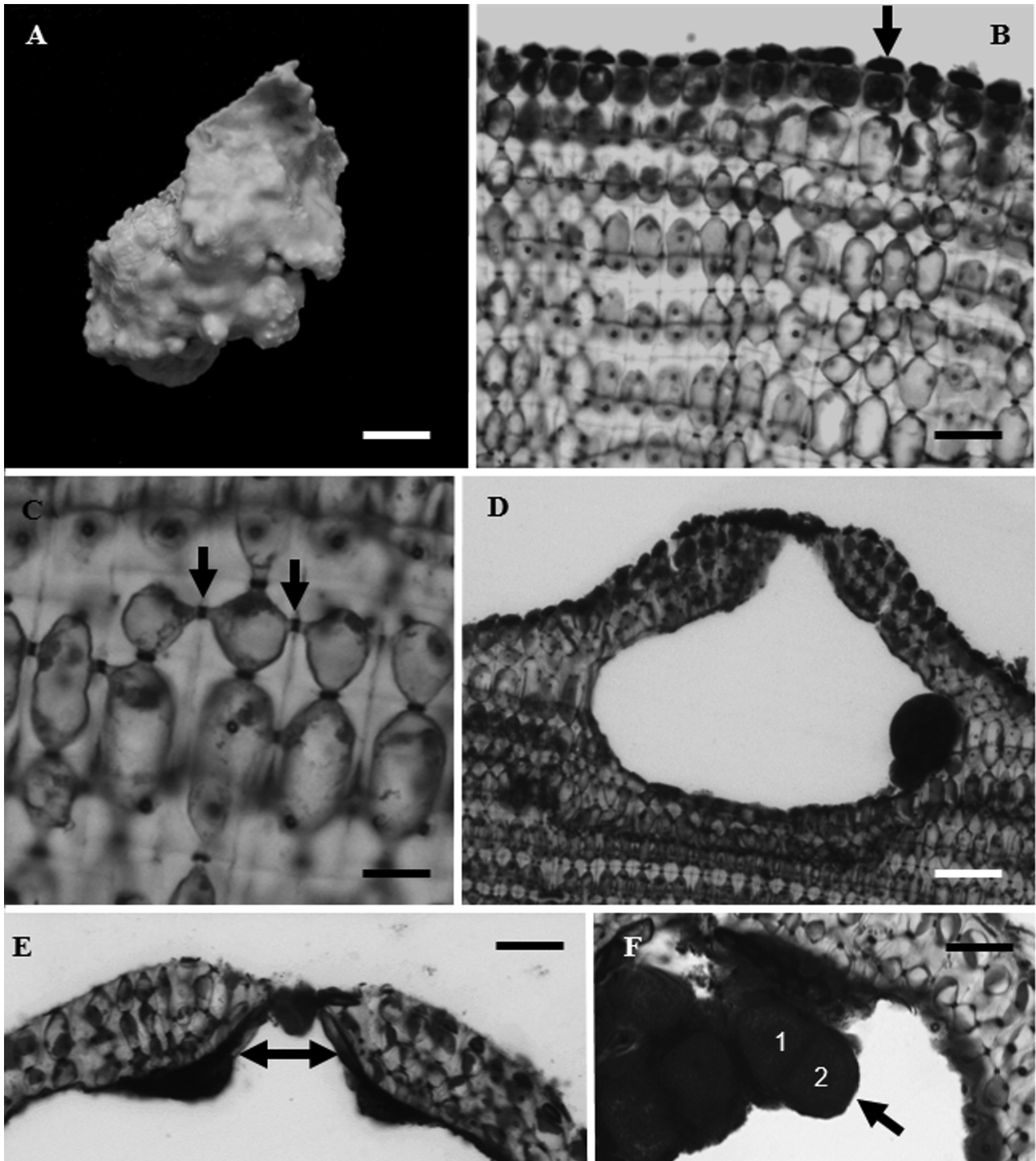


FIGURE 3 *Lithophyllum corallinae* A: encrusting growth form. Scale bar 1.0 cm; B: Flattened epithallial cells (arrow) and dimerous thallus construction. Scale: 18 µm; C: Secondary pit connections (arrows). Scale: 10 µm; D: Bisporangia conceptacle. Scale 60 µm; E: Bisporangial conceptacle pore cannal detailed (arrow). Scale 40 µm; F: Bisporangia (arrow). Scale 45 µm.

Hydrolithon breviclavium (Foslie) Foslie (1909: 56) (Fig. 4; Table 3)

Basionym:—*Goniolithon breviclavium* Foslie (1907: 20)

HOLOTYPE: Collected during *Eugenie* expedition, in herbarium of M. Foslie (TRH)

Isotype:—USNC

Type Locality:—Honolulu, Hawaii

Further References:—Magruder & Hunt (1979); Adey *et al.* (1982)

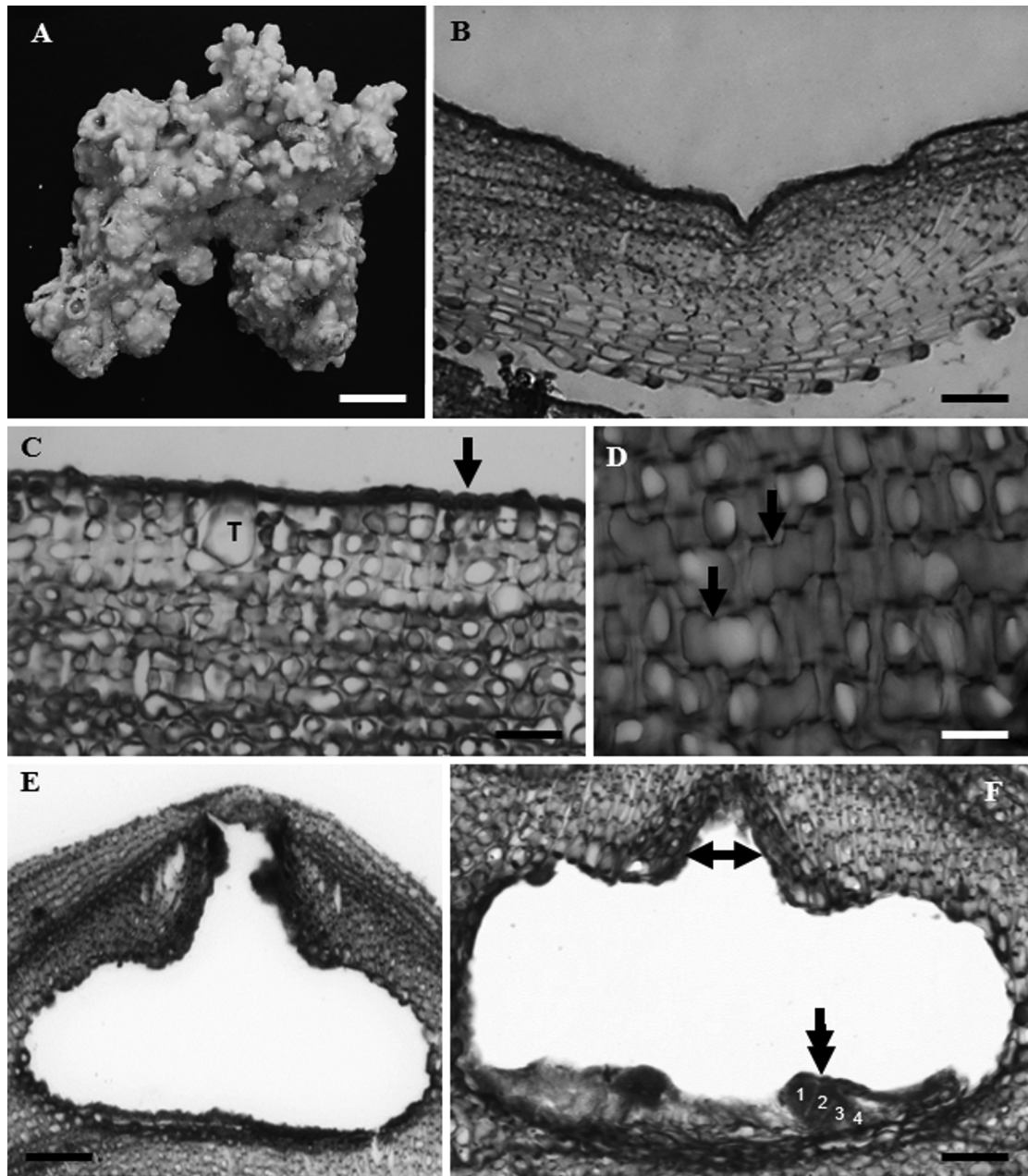


FIGURE 4 *Hydrolithon breviclavium* A: Warty growth form. Scale bar 1.5 cm; B: Monomerous thallus construction. Scale: 54 µm; C: Rounded epithallial cells (arrow) and isolated trichocytes (T). Scale: 16 µm; D: Lateral cell fusions (arrows). Scale 10 µm; E: Raised tetrasporangial conceptacle. Scale 64 µm; F: Elongated cells in pore cannal (arrow) and detailed tetrasporangia (double arrow). Scale 50 µm.

Description:—Plants non-geniculate, thallus-forming free-living rhodoliths with warty growth form with cylindrical protuberances (Fig. 4A). Rhodoliths consisting of several layers of plants overgrowing one another. *Hydrolithon breviclavium* compose the most external layer. Thallus pseudoparenchymatous with dorsiventral internal organization in encrusting portions and radial internal organization in protuberances. Monomerous thallus construction in encrusting portions (Fig. 4B) consisting of a single system of branched filaments that form a core running more or less parallel to the substratum and a more peripheral region in which portions of core filaments or their derivatives curve outwards toward the thallus, surface terminating in one layer of rounded epithallial cells (Fig. 4C). The core region is plumose (non-coaxial), comprises most of the thallus thickness and is composed mainly of rectangular cells measuring 18–22 µm in length and 5–9 µm in diameter. Cells of the peripheral region measure 5–7 µm in length and 6–11 µm in diameter. Epithallial cells measure 4–6 µm in length and 5–8 µm in diameter. Cells of adjacent filaments are linked by lateral cell fusions (Fig. 4D); isolated trichocytes (Fig. C) measure 15–19 µm in height and 9–12 µm in diameter.

TABLE 3: Comparison of *Hydroolithon breviclavium* and *H. onkodes* characters from Brazilian deep water and other areas.

	<i>H. breviclavium</i> present study	<i>H. breviclavium</i> Hawaiian Islands ¹	<i>H. onkodes</i> present study	<i>H. onkodes</i> Western Australia ²	<i>H. onkodes</i> Southern Australia ³	<i>H. onkodes</i> Caribbean coasts of Mexico ⁴	Lectotype of <i>H. onkodes</i> from TRH ⁴
Epithelial cells	Rounded	Rounded	Rounded	Rounded*	Rounded/ Flattened	Rounded	ND
Thallus construction	Monomerous	ND	Monomerous	ND	Dimerous/Monomerous	Monomerous	Monomerous
Trichocytes	Present	Present	Present	Present*	Present	Present	Present
Tetrasporangial conceptacle roof	Raised	Raised	Raised	Raised or flush	Flush	Raised or flush	Raised to flush
Number of cells in the tetrasporangial conceptacles roof	6–8	6–8	5–6	3–6	3–6	4–8	6–9
Tetrasporangia conceptacle diameter (µm)	270–325	190–450	130–170	ND	164–250	141–255	233
Tetrasporangia conceptacle height (µm)	145–225	65–180	100–140	ND	109–150	36–180	111

¹Adey et al (1982), ²Penrose and Woelkerling (1992) *see figs 4 and 5 p.84.; ³Penrose (1996); ⁴Mendoza-González et al (2009).

Tetrasporangial conceptacles uniporate with the roof raised above the surrounding thallus surface (Fig. 4E). Conceptacle roofs 6–8 cells thick including the epithallial cells, pore without an apical plug. Conceptacle chambers 270–325 µm in diameter and 145–225 µm in height, usually without a central columella and with chamber floors located 12–14 cell layers below the thallus surface. Tetrasporangia (Fig. 4F) measure 20–58 µm in length and 9–26 µm in diameter. Pore canals of tetrasporangial conceptacles lined by a ring of conspicuous, elongated cells that arise from filaments interspersed amongst sporangial initials, do not protrude into the canal, and are oriented more or less perpendicularly to the roof surface (Fig. 4E, F)

Material examined:—Brazil, Espírito Santo, Vitória-Trindade sea mountains, (20,478°S–37,193°W), 78 m depth, tetrasporangial, RB 514856, RB 588406, RB 588407

Geographic distribution:—Throughout Hawaiian Archipelago (Adey *et al.* 1982)

Hydrolithon onkodes (Heydrich) D.Penrose & Woelkerling (1992: 83) (Fig. 5; Table 3)

Basionym:—*Lithothamnion onkodes* Heydrich (1897b:6)

Lectotype:—TRH (Heydrich. No. 97) designated by Adey *et al.* (1982), illustrated by Penrose & Woelkerling (1988)

Type Locality:—Tami Island, Gulf of Huon, Papua New Guinea

Further References:—Penrose (1996); Harvey *et al.* (2006)

Description:—Plants non-geniculate, forming free- living rhodoliths with encrusting growth form (Fig. 5A). Thallus pseudoparenchymatous with dorsiventral internal organization. Monomerous thallus construction (Fig. 5B) consisting of a single system of branched filaments that form a core running more or less parallel to the substratum and a more peripheral region in which portions of core filaments or their derivatives curve outwards toward the thallus surface terminating in one layer of rounded epithallial cells (Fig. 5C). The core region is plumose (non-coaxial) and is composed mainly of rectangular cells measuring 15–20 µm in length and 8–11 µm in diameter. Cells of the peripheral region measure 5–10 µm in length and 4–7 µm in diameter. Rounded epithallial cells measure 4–7 µm in length and 5–8 µm in diameter. Cells of adjacent filaments are linked by lateral cell fusions (Fig. 5D); isolated trichocytes (Fig. 5C) measure 15 µm in height and 9 µm in diameter.

Tetrasporangial conceptacles uniporate with the roof raised to flush above the surrounding thallus surface (Fig. 5E). Conceptacle roofs 5–6 cells thick including the epithallial cells, pore without an apical plug. Conceptacle chambers 130–170 µm in diameter and 100–140 µm in height, with chamber floors located 10–17 cell layers below the thallus surface. Pore canals of tetrasporangial conceptacles lined by a ring of conspicuous, elongate cells that arise from filaments interspersed amongst sporangial initials, do not protrude into the canal, and are oriented more or less perpendicularly to the roof surface (Fig. 5F) Tetrasporangia (Fig. 5G, H) measure 40–63 µm in length and 15–21 µm in diameter.

Material examined:—Brazil, Espírito Santo, Vitória-Trindade sea mountains, (20,478°S – 37,193°W), 78 m deep, RB 514922, RB 588409, RB 588416

Geographic distribution:—Western Australia (Penrose & Woelkerling 1988), Great barrier Reef - Australia (Ringeltaube & Harvey 2000) and South-eastern Australia (Harvey *et al.* 2006); Bikini Atoll, Canary Islands, Chile, China, Costa Rica, Cuba, Ellice Islands, Hawaii, Kenya, New Guinea, Philippines, Red Sea, Solomon Islands, Sri Lanka, Tahiti and West Africa (Penrose 1996); French Polynesia (Payri *et al.* 2000), South Pacific Reefs (Littler & Littler 2003 as *porolithon onkodes*) and Indian Ocean (Silva *et al.* 1996).

Spongites fruticosus Kützing (1841: 33) (Fig. 6; Table 4)

Basionym:—*Lithothamnion fruticosum* (Kützing) Foslie (1895: 46)

Holotype:—L. 943..8..134 (Figs 1–3; see also Woelkerling 1985, figs 23–32).

Type Locality:—Mediterranean Sea

Further References:—Penrose (1991) and Basso & Rodondi (2006)

Description:—Plants non-geniculate, forming free- living rhodoliths with warty growth form (Fig. 6A). Thallus pseudoparenchymatous with dorsiventral internal organization. Thallus pseudoparenchymatous with dorsiventral internal organization in encrusting portions and radial internal organization in protuberances. Monomerous thallus

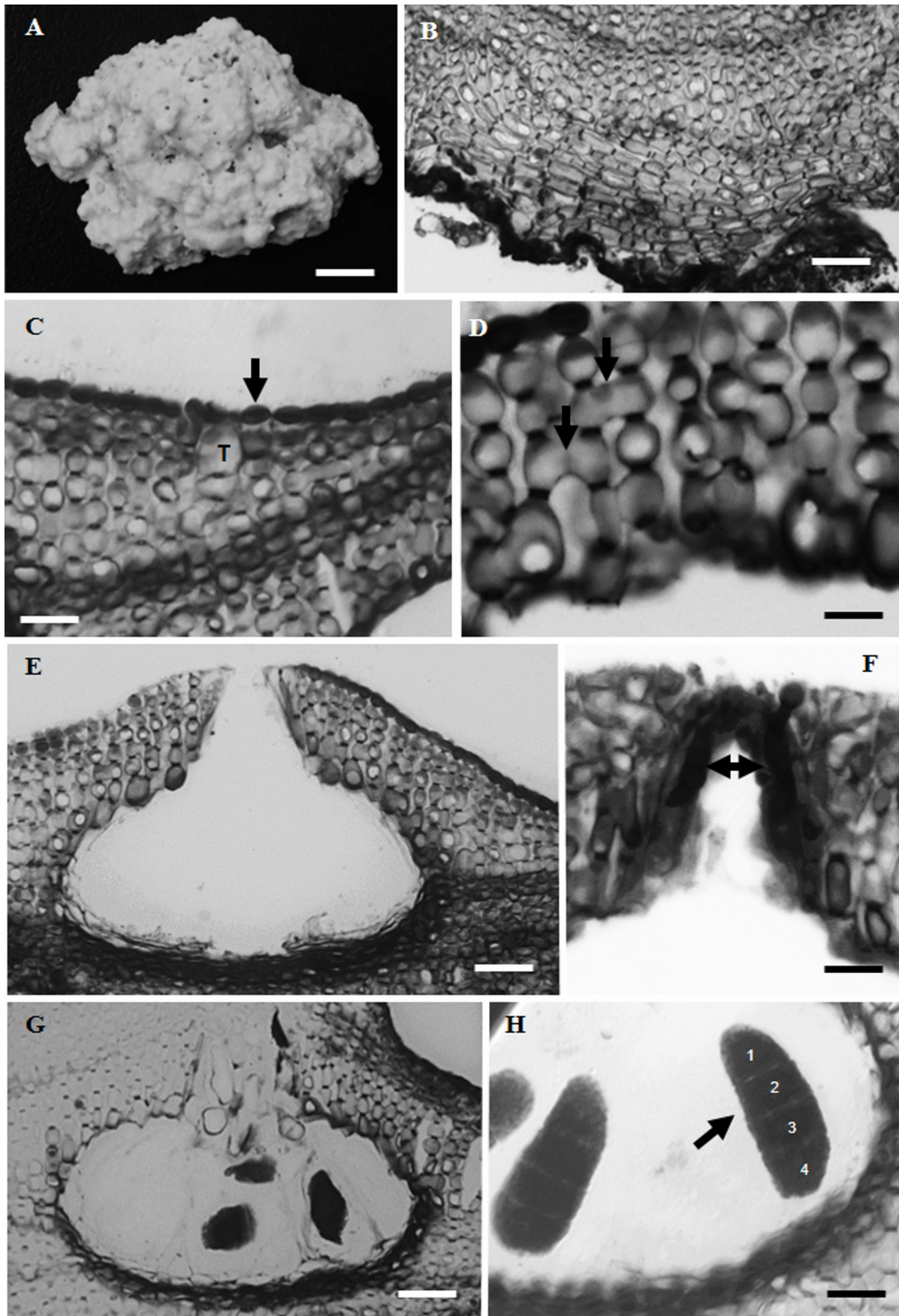


FIGURE 5 *Hydrolithon Onkodes* A: encrusting growth form. Scale bar 1.0 cm; B: Monomerous thallus construction. Scale: 50 μm ; C: Rounded epithallial cells (arrow) and isolated trichocytes (T). Scale: 22 μm ; D: Lateral cell fusions (arrows). Scale 9 μm ; E: Raised tetrasporangial conceptacle. Scale 27 μm ; F: Elongated cells in pore cannal (arrow). Scale 15 μm ; G: Conceptacle with tetrasporangia Scale 34 μm ; H: Detailed tetrasporangia (arrow). Scale 24 μm .

construction in encrusting portions (Fig. 6B) consisting of a single system of branched filaments that form a core running more or less parallel to the substratum and a more peripheral region in which portions of core filaments or their derivatives curve outwards toward the thallus surface terminating in one layer of flattened epithallial cells. The core region is plumose (non-coaxial) and is composed mainly of cells measuring 11–12 μm in length and 7–10 μm in diameter. Cells of the peripheral region measure 6–9 μm in length and 6–9 μm in diameter. Flattened epithallial cells measure 2–3 μm in length and 3–5 μm in diameter. Cells of adjacent filaments are linked by lateral cell fusions (Fig. 6C); trichocytes absent.

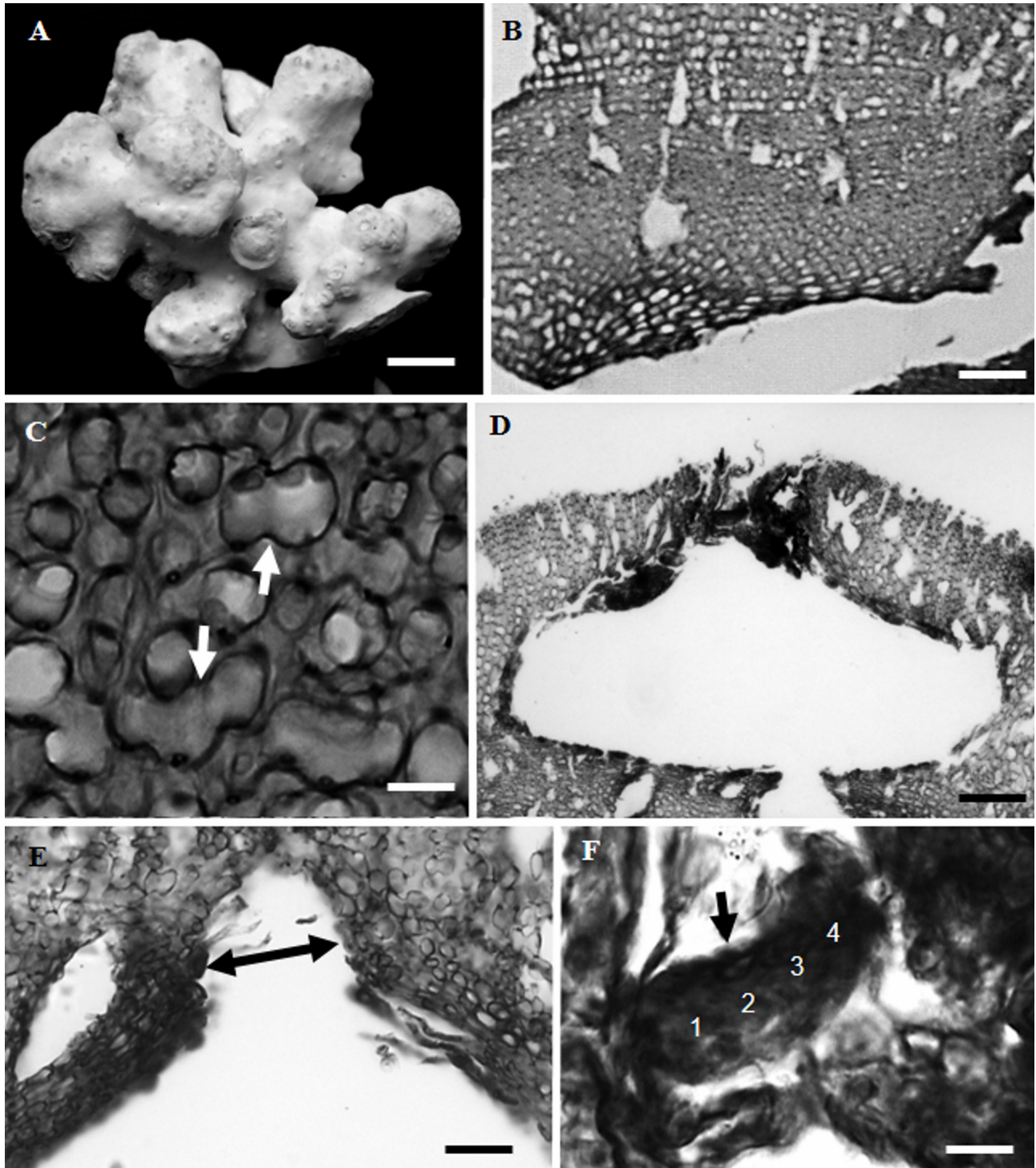


FIGURE 6 *Spongites fruticosus* A: Warty growth form. Scale bar 2,0 cm; B: Monomerous thallus construction. Scale: 30 μm ; C: Lateral cell fusions (arrows). Scale 10 μm ; D: Raised tetrasporangial conceptacle. Scale 50 μm ; E: Detailed pore cannal (arrow). Scale 27 μm .; F: Detailed tetrasporangia (arrow). Scale 10 μm .

Tetrasporangial conceptacles uniporate with the roof raised above the surrounding thallus surface (Fig. 6D). Conceptacle roofs 7–11 cells thick including the epithallial cells, pore without an apical plug. Conceptacle chambers 275–290 µm in diameter and 167–171 µm in height, usually without a central columella. Pore canals of tetrasporangial conceptacles lined cells that protrude into the canal, and are oriented more or less vertical to the roof surface (Fig. 6E). Tetrasporangia present (Fig. 6F)

Material Examined:—Espírito Santo, Brazil (21,166S–40,283W), 82 m deep, RB 498387, RB 588419, RB 588420

Geographic Distribution:—South Australia, Victoria, Western Australia and Mediterranean Sea (Penrose 1991).

TABLE 4: Comparison of *Spongites fruticosus* characters from Brazilian deep water and other areas.

	<i>S. fruticosus</i> Holotype ¹	<i>S. stalactitica</i> (= <i>Spongites</i> <i>fruticosus</i>) ² Lectotype	<i>S. fruticosus</i> ² Mediterranean	<i>S. fruticosus</i> ³ South Australia	<i>S. fruticosus</i> Present study
Thallus construction	Monomerous	–	–	Monomerous	Monomerous
Trichocytes	Present	Absent	Absent	Present	Absent
Number of cells in the tetrasporangial conceptacles roof	–	–	–	8 – 12	7–11
Tetrasporangia conceptacle height (µm)	222	410–595	25–480	145 – 245	168–170
Tetrasporangia conceptacle diameter (µm)	385	275–350	130–320	235 – 335	275–290

¹ Woelkerling (1985); ² Basso & Rodondi, 2006; ³ Penrose, 1991, 1996

Discussion

This study identified Lithophylloideae and Mastophoroideae species that are present in rhodolith beds along the Brazilian continental shelf. We found *Titanoderma pustulatum*; *Lithophyllum stictaeforme*; *Lithophyllum corallinae*, *Hydrolithon breviclavium*, *Hydrolithon onkodes* and *Spongites fruticosus*. This is the first detailed description of *T. pustulatum* from Brazil and *S. fruticosus* from Atlantic Ocean, the first record of *H. breviclavium* in the Atlantic Ocean and of *H. onkodes* in Brazilian water. *L. corallinae* was found at 250 m deep that is a new algae depth record for Brazilian water.

The genera *Lithophyllum* and *Titanoderma* have monomerous to dimerous cellular organization. Epithallial cells are rounded and subepithallial cells are squared. The cells are linked by secondary pit connections. The bi/tetrasporangial conceptacles are uniporate (Campbell & Woelkerling 1990; Woelkerling & Campbell 1992). For a long time *Titanoderma* have been distinguished from *Lithophyllum* on the basis of the size and shape of cells comprising basal filaments (Campbell & Woelkerling 1990). In *Titanoderma*, the basal cells are taller than broad, termed palisade cells (Chamberlain 1991), in contrast homologous cells in *Lithophyllum* typically are shorter and squarish. However some plants contain both palisade and squarish cells, therefore Campbell & Woelkerling (1990) subsumed *Titanoderma* in *Lithophyllum*. Others have chosen to maintain these genera as distinct (Chamberlain 1991, 1996; Athanasiadis 1999). Chamberlain (1991) suggested that the proportions of each cell type might be useful for placing species in one genus or the other. Despite morphological similarity, *Lithophyllum* and *Titanoderma* are phylogenetically distinct (Bailey 1999).

The characters that delimit *T. pustulatum* (Table 1) are the tetrasporangial conceptacle size and the number of cells in their roof. In comparative studies, Chamberlain (1991) concluded that at least 11 species are heterotypic synonyms of *T. pustulatum*. In Brazil this species was recorded from rocky shores (Taylor 1960), but not fully described and was found in this study at 82 m depth in Brazilian continental shelf. This is the first detailed description using modern taxonomy characters of *Titanoderma* in Brazilian water.

Woelkerling & Campbell (1992) suggested that bi/tetrasporangial conceptacles characters are useful to delimit *Lithophyllum* species. In this study *L. stictaeforme* has a bigger tetrasporangial conceptacle height when compared with the same species described from Espírito Santo, Brazil (Table 2) (Villas-Boas *et al.* 2009). This is justified by the fact that this species has great variation in their morphology and anatomical characters (Woelkerling 1996a). Villas-Boas *et al.* (2009) states that *L. stictaeforme* has elongated cells around the tetrasporangial conceptacle pore covering the entire conceptacle roof and has a mucilaginous material that can block the pore. These characters are present in the same species in our study. In Brazil this species was cited as *Titanoderma bermudense* (Foslie & M.A.Howe) Woelkerling, Y.M.Chamberlain & P.C.Silva (1985: 333) in Bahia state (Figueiredo & Steneck 2002). Our material agrees with the diagnostic features found in the type material of *L. stictaeforme*, described in Mediterranean as *Melobesia stictaeforme*. These features are pore channel narrowing toward the top configuring a conical shape (Athanasiadis 1999), associated with the chamber size and number of cells in the tetrasporangial conceptacle roof (Woelkerling & Campbell 1992).

Lithophyllum corallinae is similar to the same species described in Brazil (Villas-Boas *et al.* 2009) which presents strictly dimerous cellular construction (Table 2). Woelkerling & Campbell (1992) commented, however, that it is common for this species also occurs in the monomerous form.

L. corallinae and *L. stictaeforme* have similar characters in South Australia where *L. stictaeforme* was named *Lithophyllum bermudense* Foslie & M.A.Howe (1906: 132). These species are distinguished by *L. corallinae* possessing 2–4 cells on the roof of tetrasporangial conceptacle and containing differentiated subepithelial cells, unlike *L. bermudense* which has no differentiated subepithelial cells and has 3–7 cells in the tetrasporangial conceptacle roof (Woelkerling & Campbell 1992).

The characters that differentiate the two species are the tetrasporangial conceptacles dimensions combined with the number of cells on the roof of these conceptacles. According to Harvey *et al.* (2009), these conceptacles should comprise 260–390 µm in diameter and contain 4–7 cells in the tetrasporangial conceptacle roof in *L. stictaeforme* while *L. corallinae* should comprise 160–260 µm in diameter and 2–4 cells in the tetrasporangial conceptacle roof. It is often possible to find intermediate values between the two species as occurs in New Zealand. In this case, these species were treated as *L. stictaeforme*-*L. corallinae* complex (Harvey *et al.* 2005). In Brazil, we can differentiate consistently the species (Villas-Boas *et al.* 2009; present study). Woelkerling (1996a) concluded that more studies should be done to verify if these two species are actually two different taxa or whether they should be treated as one.

Penrose & Woelkerling (1992) provided stable basis for *Spongites* and *Hydrolithon* morpho-anatomical generic delimitation. The difference between these genera is that in *Spongites* the pore canals of tetrasporangial conceptacles are bordered by cells that arise from peripheral roof filaments, protrude into the canal and are oriented more or less parallel to the roof surface. In *Hydrolithon* the pore canals of tetrasporangial conceptacles are lined by a ring of conspicuous, elongate cells that arise from filaments interspersed amongst sporangial initials, do not protrude into the canal and are oriented more or less perpendicularly to the roof surface. *Hydrolithon* and *Porolithon* have the same patterns and because they were first recognized as genera in the same paper (Foslie 1909), it is possible to select either name to use. We choose to use *Hydrolithon* as Penrose & Woelkerling (1992) did. The name *Hydrolithon* had been chosen by them because it is slightly older as a name and because the pore canal anatomy is evident in the type specimen.

In the present study we describe for the first time the cells in pore canal of tetrasporangial conceptacle of *Hydrolithon breviclavium* confirming the genus of this species based in the characters adopted by Penrose & Woelkerling (1992). This species from Brazil have the same characters presented in Hawaiian Islands, although there were no description of the pore canal in this region (Adey *et al.* 1982). *H. breviclavium* from Hawaii was partially described by Adey *et al.* (1982) (Table 3). It is a mid to deep water species found 30–60 m deep in Hawaii (Adey *et al.* 1982) and 50 m deep in Brazil.

H. breviclavium differs from *H. onkodes* by having a bigger number of cells in the tetrasporangial conceptacles roof and a bigger tetrasporangia conceptacle diameter (Table 3). This is the first record of *H. onkodes* in Brazilian water where we found a different pattern of trichocytes distribution along the thallus. In other region, it has common horizontal rows/fields of trichocytes both at the thallus surface and buried within the thallus (Penrose & Woelkerling 1992; Penrose 1996; Harvey *et al.* 2006); In Brazil we mostly found singly in the thallus surface as occurs in Southern Australia (Penrose 1996).

Spongites fruticulosus was cited occurring in rhodolith beds in Espírito Santo state, Brazil, but it was not fully described (Villas-Boas *et al* 2013). So far, this is the first detailed description of this species in Atlantic Ocean. This species from Brazil differs from this species from South Australia not presenting trichocysts. According to Basso & Rodondi (2006) trichocysts are useless separating species in different localities. Comparing the material from the Mediterranean Sea and southern Australia, the Mediterranean species have smaller tetrasporangial conceptacles and don't present trichocysts while the species from Australia do (Basso & Rodondi 2006). Penrose (1991) described the anatomical and reproductive characters of the Australia population concluding that the tetrasporangial conceptacles diameters are close to those presented in Mediterranean, omitting extreme values. Most individuals of this locality seem not to present trichocysts.

In 1985, Woelkerling examined the type specimen of this species that classified in the genus *Lithothamnion* Heydrich, (1897c: 412). He found uniporate tetrasporangial conceptacles and changed the name to *Spongites fruticulosa* as the holotype. Many records of this species are currently multiporate conceptacles algae leading us to the conclusion that these classifications are wrong (Penrose 1991). So far, the identification of *S. fruticulosus* had only been confirmed, based on Corallinales modern taxonomy in South Australia (Penrose 1991; 1996), the Australia Great Barrier Reef (Ringeltaube & Harvey 2000) and Mediterranean Sea (Basso & Rodondi 2006).

The biodiversity of Corallinales in Brazil seems to be higher than previously known. It is evidenced by the description of new records in the Atlantic Ocean, increasing the recent reports for the order. This study contributes to the understanding of the diversity in this order and indicates that future systematic studies are important. This knowledge is relevant to guide conservation programs and evaluation of impacts.

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Referencias

- Adey, W. H. & Adey, P. J. (1973) Studies on the biosystematics and ecology of the epilithic crustose corallinaceae of the British Isles. *British Phycological Journal* 8: 343–407.
<http://dx.doi.org/10.1080/00071617300650381>
- Adey, W.H., Townsend, R.A. & Boykins, W.T. (1982) The crustose coralline algae (Rhodophyta: Corallinaceae) of the Hawaiian Islands. In: *Smithsonian Contributions to the Marine Sciences*. Vol. 15, pp. iv + 74.
<http://dx.doi.org/10.5479/si.01960768.15.1>
- Agardh, J.G. (1852) *Species genera et ordines algarum, seu descriptiones succinctae specierum, generum et ordinum, quibus algarum regnum constituitur*. Volumis secundi: Algas florideas complectens. Part 2, fasc. 2. Lundae [Lund]: C.W.K. Gleerup, pp. 577–700. [701–720, Addenda and Index]
<http://dx.doi.org/10.5962/bhl.title.1576>
- Amado-Filho, G.M. & Pereira-Filho, G.H. (2012) Rhodolith beds in Brazil: a new potential habitat for marine bioprospection. *Sociedade Brasileira de Farmacognosia* 22: 782–788.
<http://dx.doi.org/10.1590/s0102-695x2012005000066>
- Athanasiadis A. (1999) The taxonomic status of *Lithophyllum stictaeforme* (Rhodophyta, Corallinales) and its generic position in light of phylogenetic considerations. *Nordic Journal of Botany* 19(6): 735–745.
<http://dx.doi.org/10.1111/j.1756-1051.1999.tb00682.x>
- Bailey, J.C., (1999) Phylogenetic positions of *Lithophyllum incrustans* and *Titanoderma pustulatum* (Corallinaceae, Rhodophyta) based on 18S rRNA gene sequence analyses, with a revised classification of the Lithophylloideae. *Phycologia* 38: 208–216.
<http://dx.doi.org/10.2216/i0031-8884-38-3-208.1>
- Basso, D. & Rodondi, G. (2006) A Mediterranean population of *Spongites fruticulosus* (Rhodophyta, Corallinales), the type species of *Spongites*, and the taxonomic status of *S. stalactitica* and *S. racemosa*. *Phycologia* 45 (4): 403–416.
<http://dx.doi.org/10.2216/04-93.1>
- BIOMAERL Team (1998) Maerl grounds: habitats of high biodiversity in European waters. In: *Proceedings of the third European Marine Science and Technology Conference*, Project Synopses. Vol. I, Marine Ecosystems, Lisbon, pp.169–178.
- Campbell, S.J. & Woelkerling, W. J. (1990) Are *Titanoderma* and *Lithophyllum* (Corallinaceae, Rhodophyta) distinct genera?

- Phycologia* 29: 114–125.
<http://dx.doi.org/10.2216/i0031-8884-29-1-114.1>
- Chamberlain, Y.M. (1996) Lithophylloid Corallinaceae (Rhodophyta) of the genera *Lithophyllum* and *Titanoderma* from southern Africa. *Phycologia* 35: 204–221, 76.
<http://dx.doi.org/10.2216/i0031-8884-35-3-204.1>
- Chamberlain, Y.M. (1991) Historical and taxonomic studies in the genus *Titanoderma* (Rhodophyta, Corallinales) in the British Isles. [Bot. Ser.] *Bulletin of the British Museum* 21: 1–80.
- Crouan, P.L. & Crouan, H.M. (1867) *Florule du Finistère* contenant les descriptions de 360 espèces nouvelles de sporogames, de nombreuses observations et une synonymie des plantes cellulaires et vasculaires qui croissent spontanément dans ce département, accompagnées de trente-deux planches où est représentée l'organographie, faite sur l'état vif, des fruits et des tissus de 198 genres d'algues avec la plante grandeur naturelle ou réduite plus une planche supplémentaire où sont figures 24 champignons nouveaux. pp. [i]–x, [1]–262, frontisp., pi. 1–31, + 1 suppl. pl., coloured liths. by H. Crouan. Paris & Brest: Friedrich Klincksieck & J.B. et A. Lefournier.
- Figueiredo, M.A. de O. & Steneck, R.S. (2002) Floristic and ecological studies of crustose coralline algae on Brazil's Abrolhos reefs. *Proceedings of the 9th International Coral Reef Symposium* 1: 493–498.
- Foslie, M. & Howe, M.A. (1906) New American coralline algae. *Bulletin of the New York Botanical Gardens* 4: 128–136, Plates 80–93.
- Foslie, M. (1895) The Norwegian forms of *Lithothamnion*. *Kongelige Norske Videnskabers Selskabs Skrifter* 1894: 29–208, 23 pls.
- Foslie, M. (1907) Algologiske notiser III. *Det Kongelige Norske Videnskabers Selskabs Skrifter* 1906(8): 1–34.
- Foslie, M. (1909) Algologiske notiser VI. *Kongelige Norske Videnskabers Selskabs Skrifter* 1909(2): 1–63.
- Foster, M.S. (2001) Rhodoliths: between rocks and soft places. *Journal of Phycology* 37: 659–667.
<http://dx.doi.org/10.1046/j.1529-8817.2001.00195.x>
- Furnari, G., Cormaci, M. & Alongi, G. (1996) *Lithophyllum frondosum* (Dufour) comb. nov. (Corallinaceae, Rhodophyta): the species to which Mediterranean '*Pseudolithophyllum expansum*' should be referred. *European Journal of Phycology* 31: 117–122.
<http://dx.doi.org/10.1080/09670269600651281>
- Harvey, A.S., Phillips, L.E. Woelkerling, W.J. & Millar, J.K. (2006) The Corallinaceae, subfamily Mastophoroideae (Corallinales, Rhodophyta) in south-eastern Australia. *Australian of Systematic Botany* 19: 387–429.
<http://dx.doi.org/10.1080/09670269600651281>
- Harvey, A.S., Woelkerling, W.J. & Millar, J.K. (2009) The genus *Lithophyllum* (Lithophylloideae, Corallinaceae, Rhodophyta) in south-eastern Australia, with the description of *L. riosmenae* sp. nov. *Australian of Systematic Botany* 22: 296–317.
<http://dx.doi.org/10.1071/sb08051>
- Harvey, A.S., Woelkerling, W.J., Farr, T., Neill, K. & Nelson, W. (2005) *Coralline algae of central New Zealand: an identification guide to common 'crustose' species*, vol 57. NIWA Press, Wellington, 145 pp.
- Hauck, F. (1877) Beiträge zur Kenntnis der Adriatischen Algen. V. *Österreichische Botanische Zeitschrift* 27: 292–293.
<http://dx.doi.org/10.1007/bf01614779>
- Henriques, M.C., Villas-Boas, A., Riosmena-Rodriguez, R. & Figueiredo, M.A.O. (2012) New records of rhodolith-forming species (Corallinales, Rhodophyta) from deep water in Espírito Santo State, Brazil. *Helgoland Marine Research* 66: 219–231.
<http://dx.doi.org/10.1007/s10152-011-0264-1>
- Heydrich, F. (1897a) Corallinaceae, insbesondere Melobesieae. *Berichte der deutsche botanischen Gesellschaft* 15: 34–70, 3 figs, Plate III.
- Heydrich, F. (1897b) Neue Kalkalgen von Deutsch-Neu-Guinea (Kaiser Wilhelms-Land). *Bibliotheca Botanica* 7(41): 1–11 1 pl.
- Heydrich, F. (1897c) Melobesiae. *Berichte der deutsche botanischen Gesellschaft* 15: 403–420, Plate XVIII.
- Holmgren, P.K. & Holmgren N.H. (2014) [continuously updated electronic resource]. Index herbariorum: A global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. Available from: <http://sweetgum.nybg.org/ih/>. (accessed 6 January 2014)
- Irvine, L.M. & Chamberlain, Y.M. (1994) *Seaweeds of the British Isles*. Vol. I Rhodophyta, Part 2B Corallinales, Hildenbrandiales. St.Edmundsbury Press. The Natural History Museum London, 276 pp.
<http://dx.doi.org/10.1017/s0025315400044167>
- Kützing, F.T. (1841). Über die "Polypieres calcifères" des Lamouroux. In: *Zu der öffentlichen Prüfung sämtlicher Classen der Realschule zu Nordhausen*. (Kützing, F.T. Eds). Nordhausen: Realschule, pp. 3–34.
- Lamouroux, J.V.F. (1816) *Histoire des polypiers coralligènes flexibles*, vulgairement nommés zoophytes. pp. [i]–lxxxiv, chart, [1]–560, [560, err], pls I–XIX, uncol. by author. Caen: De l'imprimerie de F. Poisson.
<http://dx.doi.org/10.5962/bhl.title.11172>
- Lavrado, H.P. (2006) Capítulo 1. Caracterização do ambiente e da comunidade bentônica. In: Lavrado, H.P. & Ignácio, B.L. (Eds) *Biodiversidade bentônica da região central da Zona Econômica Exclusiva brasileira*. Museu Nacional. Rio de Janeiro, pp.19–64 .
- Littler, D.S. & Littler, Y.M. (2003) *South Pacific Reef Plants*. OffShore Graphics, Washington, 331 pp.

- Littler, M.M. & Littler, D.S. (2000) *Caribbean reef plants: an identification guide to the reef plants of the Caribbean, Bahamas, Florida and Gulf of Mexico*. Off Shore Graphics, Inc. Washington: 542 pp.
- Magruder, W.H. & Hunt, J.W. (1979) *Seaweeds of Hawaii*. Honolulu, Hawaii: Oriental Publ. Co., 116 pp.
- Mendoza-González, C., Pedroche, F.F. & Mateo-Cid, L.E. (2009) The genus *Hydrolithon* Foslie (Corallinales, Rhodophyta) along the Atlantic and Caribbean coasts of México. *Gayana Botánica* 66(2): 218–238.
<http://dx.doi.org/10.4067/s0717-66432009000200008>
- Moura, C.W.N., Kraus, J.E. & Cordeiro-Marino, M. (1997) Metodologia para obtenção de cortes histológicos com histo-resina e coloração com azul de toluidina O para algas coralíneas (Rhodophyta, Corallinales). *Hoehnea*, 24 (2): 17–27.
- Nägeli, C. & Cramer, C. (1858) *Die Stärkekörner*: Morphologische, physiologische, chemisch-physicalische und systematisch-botanische Monographie. Pflanzenphysiologische Untersuchungen. 2. Heft. Zürich: bei Friedrich Schulthess, pp. [i]–x, [1]–623, pls XI–XXVI.
- Nägeli, C. (1858) Die Stärkekörner. In: Nägeli, C. & Cramer, C. (Eds.) *Pflanzenphysiologische Untersuchungen*. Vol. 2 Zürich, pp. i–x, 1–623.
- Nunes, J.M.C., Guimarães, S.M.P.B., Donnangelo, A., Farias, J. & Horta, P.A. (2008) Aspectos taxonômicos de três espécies de Coralíneas não articuladas do litoral do estado da Bahia, Brasil. *Rodriguesia*, 59 (1): 075–086.
- Payri, C., N'Yeurt, A.D.R. & Orempuller, J. (2000). *Algae of French Polynesia. Algues de Polynésie française*. Tahiti: Au Vent des Iles Editions, 320 pp.
- Penrose, D. & Woelkerling, Wm.J. (1988) A taxonomic reassessment of *Hydrolithon* Foslie, *Porolithon* Foslie and *Pseudolithophyllum* Lemoine (Corallinales, Rhodophyta) and their relationships to *Spongites* Kützing. *Phycologia* 27: 159–176
<http://dx.doi.org/10.2216/i0031-8884-27-1-159.1>
- Penrose, D. & Woelkerling, W.J. (1992) A reappraisal of *Hydrolithon* and its relationship to *Spongites* (Corallinales, Rhodophyta). *Phycologia* 31: 81–88, 7 figs.
<http://dx.doi.org/10.2216/i0031-8884-31-1-81.1>
- Penrose, D. (1991) *Spongites fruticosus* (Corallinales, Rhodophyta), the type of *Spongites*, in southern Australia. *Phycologia*, 30 (5): 438–448.
<http://dx.doi.org/10.2216/i0031-8884-30-5-438.1>
- Penrose, D. (1996) "Subfamily Mastophoroideae (Spongites & Neogoniolithon)". In Womersley, H.B.S. *The marine Benthic Flora of Southern Australia - Part IIIB. Gracilariales, Rhodymeniales, Corallinales and Bonnemaisoniales*. Australian Biological Resources Study, Canberra, pp. 237–255.
- Philippi, R.A. (1837) Beweis, dass die Nulliporen Pflanzen sind. *Archiv für Naturgeschichte* 3: 387–393, figs 2–6, pl. IX.
- Ringeltaube, P. & Harvey, A. (2000) Non-geniculate coralline algae (Corallinales, Rhodophyta) on Heron Reef, Great Barrier Reef (Australia). *Botanica Marina* 43: 431–454.
<http://dx.doi.org/10.1515/bot.2000.045>
- Setchell, W.A. (1943) *Mastophora* and the Mastophoreae: genus and subfamily of Corallinales. *Proceedings of the National Academy of Science of the United States of America* 29: 127–135.
<http://dx.doi.org/10.1073/pnas.29.5.127>
- Silva, P.C., Basson, P.W. & Moe, R.L. (1996) *Catalogue of the benthic marine algae of the Indian Ocean*. University of California Publications in Botany 79: 1–1259.
- Silveira, I.C.A., Schmidt, A.C.K., Campos, E.J.D., Godoi, S.S., & Ikeda, Y. (2000) A corrente do Brasil ao largo da costa leste brasileira. *Revista Brasileira de Oceanografia* 48(2): 171–183.
<http://dx.doi.org/10.1590/s1413-77392000000200008>
- Steneck, R.S. (1986) The ecology of coralline algal crusts: convergent patterns and adaptative strategies. *Annal Review of Ecology and Systematics*, 17: 273–303.
<http://dx.doi.org/10.1146/annurev.es.17.110186.001421>
- Taylor, W.R. (1960) *Marine algae of the eastern tropical and subtropical coast of the Americas*. University of Michigan press, EUA, 870 pp.
- Villas-Boas, A.B., Riosmena-Rodriguez, R., Amado Filho G.M., Maneveldt, G.W. & Figueiredo, M.A.O. (2009) Rhodolith-forming species of *Lithophyllum* (Corallinales; Rhodophyta) from Espírito Santo State, Brazil, including the description of *L. depressum* sp. nov. *Phycologia*, 48 (4): 237–248.
<http://dx.doi.org/10.2216/08-35.1>
- Villas-Boas, A., Riosmena-Rodriguez, R. & Figueiredo, M.A. de O. (2013) Community structure of rhodolith-forming beds on the central Brazilian continental Shelf. *Helgoland Marine Research*
<http://dx.doi.org/10.1007/s10152-013-0366-z>
- Woelkerling, W.J. & Campbell, S.J. (1992) An account of southern Australian species of *Lithophyllum* (Corallinales, Rhodophyta). Bulletin of the British Museum (Natural History) *Botanical Series* 22(1): 1–107.
- Woelkerling, W.J. (1985) A taxonomic reassessment of *Spongites* (Corallinales, Rhodophyta) based on studies of Kützing's original collections. *British Phycological Journal* 20: 123–153.
<http://dx.doi.org/10.1080/00071618500650151>
- Woelkerling, W.J. (1988) *The coralline red algae: an analysis of the genera and sub-families of nongeniculate Corallinales*. British Museum Natural History and Oxford University Press, London.

- Woelkerling, W.J. (1993) Type collections of corallinales (Rhodophyta) in the Foslie Herbarium (TRH). *Gunneria* 67:1–289.
- Woelkerling, W.J. (1996) Subfamily Lithophylloideae. In: Womersley, H.B.S.W. (Ed.) *The Marine Benthic Flora of Southern Australia*. Part IIIB, Gracilariales, Rhodymeniales, Corallinales and Bonnemaisoniales. Australian Biological Resources Study, Canberra, pp. 214–237.
- Woelkerling, W.J., Irvine, L.M. & Harvey, A.S. (1993) Growthforms in non-geniculate coralline red algae (Corallinales, Rhodophyta). *Australian Systematic Botany* 6: 277–293.
<http://dx.doi.org/10.1071/sb9930277>
- Yoneshigue-Valentin, Y., Gestinari, L.M.S. & Fernández, D.R.P. (2006) Capítulo 2. Microalgas. In: Lavrado, H.P. & Ignacio, B.L. (Eds.) *Biodiversidade bentônica da região central da Zona Econômica Exclusiva brasileira*. Museu Nacional. Rio de Janeiro. pp. 67–105.