Phytotaxa 190 (1): 370–382
www.mapress.com/phytotaxa/

Article

ISSN 1179-3155 (print edition)
PHYTOTAXA
ISSN 1179-3163 (online edition)

http://dx.doi.org/10.11646/phytotaxa.190.1.22

Rhodolith forming coralline algae in the Upper Miocene of Santa Maria Island (Azores, NE Atlantic): a critical evaluation

ANA CRISTINA REBELO[1,2,3,4*], MICHAEL W. RASSER[4], RAFAEL RIOSMENA-RODRÍGUEZ[5], ANA ISABEL NETO[1,6,7] & SÉRGIO P. ÁVILA[1,2,3,8]

[1] *Departamento de Biologia, Universidade dos Açores, Campus de Ponta Delgada, Apartado 1422-801 Ponta Delgada, Açores, Portugal*

[2] *CIBIO - Centro de Investigação em Biodiversidade e Recursos Genéticos, InBIO Laboratório Associado, Pólo dos Açores - Departamento de Biologia da Universidade dos Açores, 9501-801, Ponta Delgada, Açores, Portugal*

[3] *MPB - Marine Palaeobiogeography Working group, University of Azores, Portugal*

[4] *SMNS - Staatliches Museum für Naturkunde Stuttgart, Rosenstein 1, D-70191 Stuttgart, Germany*

[5] *Programa de Investigación en Botánica Marina, Departamento de Biologia Marina, Universidad Autónoma de Baja California Sur, Km 5.5 Carretera al Sur, Col. Mezquitito, La Paz BCS 23080 México*

[6] *Interdisciplinary Centre of Marine and Environmental Research (CIIMAR/CIMAR), University of Porto, Rua dos Bragas 289, P 4050-123 Porto, Portugal*

[7] *CIRN - University of the Azores, Portugal*

[8] *Faculdade de Ciências da Universidade do Porto, Rua do Campo Alegre, s/n, 4169-007 Porto, Portugal*

* *Corresponding author, email: acfurtadorebelo@gmail.com*

ABSTRACT

The Late Miocene Malbusca outcrop is located in the southeastern coast of Santa Maria Island (Azores, NE Atlantic), interspersed in volcanic formations. At ~20 meters above present sea level, a prominent discontinuous layer of rhodoliths seizes with an extension of ~250 meters. This paper presents the first taxonomic record of fossil rhodolith forming coralline algae for the Miocene of the Azores. The preserved taxonomic features used were the following: (1) arrangement of basal filaments, (2) epithallial cells (when observable), (3) presence of cell fusions, (4) conceptacle type, (5) number of cells layers which conceptacle chamber floors are situated below the surrounding thallus surface and (6) for the sporangial pores, the orientation of the filaments around the conceptacle pores. Based on these characters, six taxa were identified encompassing three Corallinaceae (*Lithophyllum prototypum*, *Lithophyllum* sp., *Spongites* sp. and *Hydrolithon* sp.) and one Hapalidaceae (*Phymatolithon calcareum* and cf. *Phymatolithon* sp.). An unidentified coaxial thallus was also present, the coaxial construction ascribing the specimens to the genus *Mesophyllum* or *Neogoniolithon*. Taxonomic accounts for the identified taxa are described, illustrated and an identification key is provided. The report of *L. prototypum* represents the first Miocene record and the preservation of the specimens is very good. Miocene coralline algae seem very consistent among deposits but some species are relevant for particular areas, like in the Azores.

Key words: Fossil algae, Oceanic Islands, Rhodoliths, Corallinales (Rhodophyta)

INTRODUCTION

Rhodoliths are nodules of unattached nongeniculate coralline algae (Corallinales and Sporolithales, Rhodophyta). They are worldwide distributed and exist at variable depths and depositional environments. Their usual excellent fossil preservation state may provide important palaeoecological and palaeobiogeographical information (e.g., Bosellini & Ginsburg 1971, Adey & Macintyre 1973, Bosence 1983, Basso & Tomaselli 1994, Aguirre *et al*. 2000, 2012).

Reef and temperate carbonate units alternate in the upper Miocene–Pliocene stratigraphic record of Betic basins palaeogeographically connected to the Mediterranean. Shallow-water coralline algal assemblages in temperate units differ in taxonomic composition from those in reef carbonate units. The difference attains to the subfamily level

Accepted by Paulo Horta: 5 Dec. 2014; published: 24 Dec. 2014

since the temperate lithofacies are characterised by assemblages dominated by lithophylloids (*Lithophyllum*), whereas mastophoroids (*Spongites* and *Neogoniolithon*) predominate in the reef units. The proportion of lithophylloids, however, can be high in samples from shallow-reef palaeoenvironments. The distinction is less marked in deeper platform deposits since melobesioids (*Lithothamnion*, *Mesophyllum* and *Phymatolithon*) are the major elements in the assemblages from both reef and temperate units (Braga & Aguirre 2001).

Coralline algae are common components in Messinian reefs in the Sorbas Basin in SE Spain, with a species composition of *Neogoniolithon brassica-florida* and *Spongites fruticulosus*, dominating the shallow-water assemblages; *Lithophyllum* records peak at the base of reef-core and upper-slope deposits (around 20 m palaeodepth) and *Phymatolithon calcareum* and species of *Lithothamnion* are most abundant in deeper slope facies (Braga *et al*. 2009).

The main components of the Messinian Mediterranean reef coralline assemblages are extant species, common in the Mediterranean and along the north Atlantic coast from Morocco (and the Canary Islands) to the British Islands. A few, such as *Spongites fruticulosus* and *Phymatolithon calcareum*, have been living in the Mediterranean region for more than 25 Ma. Similar assemblages are present in Macaronesia, in the Miocene (Johnson *et al*. 2012), and younger limestone deposits enriched by rhodoliths and rhodolith-derived sediments are also known from the late Pleistocene (Amen *et al.* 2005). However their taxonomy in some areas are limited and need evaluation of species and genera present in the area.

In the literature, the fossil coralline algae from Santa Maria Island (Azores, NE Atlantic) have been described as "fragments de *Lithothamnium*" (Berthois 1950) or as "fragments d'algues calcaires" (Zbyszewski & Ferreira 1962), and the rhodoliths have been referred to as rolled debris ("Les *lithothamnium* s'observent aussi en debris roules" - Berthois 1950).

Rhodoliths are abundant at the Miocene of Malbusca in Santa Maria Island. Their maximum diameter ranges from 2 to 6 cm and they constitute the majority of the sediments (rhodolith rudstone). Malbusca is located in the southeastern coast of the island (Fig.1), and its sedimentary deposits occur interspersed in the volcanic formations, at approximately 20 m above present sea level, with a lateral extension of 250 m.

This work highlights the presence of Miocene fossil rhodoliths of the Azores. Due to scarcity of information about Miocene fossil records in the Atlantic (Amen *et al*. 2005), and their abundance and exposure along the outcrop. Herein it is also discussed the limitation and need for a better taxonomical access of the Azorean fossil coralline diversity.

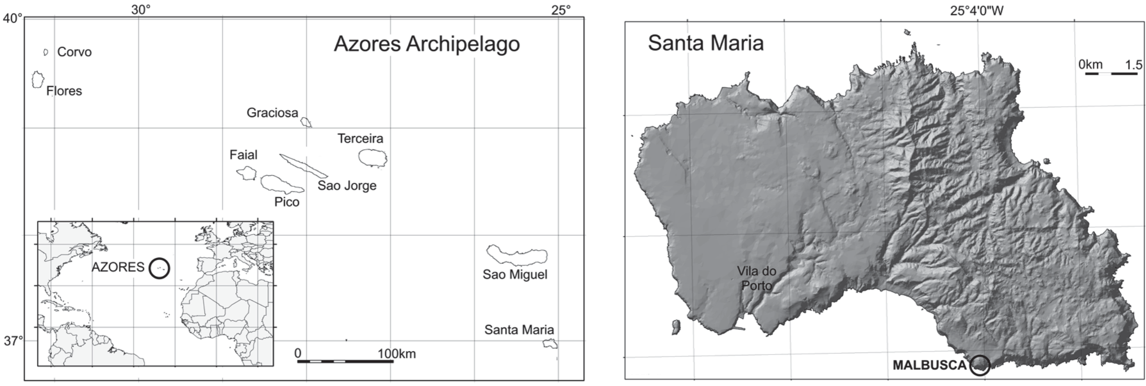

FIGURE 1. Geographical location of the Azores Archipelago, the island of Santa Maria and the studied Miocene outcrop of Malbus_ca, on the southeastern coast.

MATERIAL AND METHODS

Field work was carried out during the 9th workshop "Palaeontology in Atlantic islands", in July 2012 at the Miocene of Malbusca, Santa Maria Island (Azores) through the study of four stratigraphic logs. A total of nineteen bulk samples (each of 1–2 kg and containing several rhodoliths) were taken from each depositional bed in order to study the taxonomy.

Thirty eight rhodoliths were studied through petrographical thin sections under a digital microscope VHX-500F Keyence. Cell and conceptacle dimensions were measured according to Rasser & Piller (1999) directly under the microscope. Mean (M) and standard deviation (SD) were calculated for both cells and conceptacles, whenever the number of measurements allowed (Table 1).

Due to diagenetic overprint, cells of core and peripheral filaments were measured only for 3 genera. Whenever possible, a minimum of 4 measurements were made for the total lengths of peripheral and core filaments (Table 1). Anatomical and taxonomical terminologies follow the works by Braga *et al*. (1993) and Rasser & Piller (1999); growth form terminology follows Woelkerling *et al*. (1993).

TABLE 1. Anatomical and morphological features of the identified taxa: *Lithophyllum (Litho*.); *Spongites* (*Spon*.); *Hydrolithon* (*Hydro*.) and *Phymatolithon* (*Phyma*.) (all measurements are in µm).

	Litho. prototypum	*Litho.* sp.	*Spon.* sp.	*Hydro.* sp.	*Phyma. calcareum*	cf. *Phyma*. sp.
Growth form	Encrusting	Encrusting	Encrusting	Encrusting	Lumpy	Encrusting to layered
Thallus organisation	Dimerous	Dimerous	Monomerous non-coaxial	Dimerous	Monomerous non-coaxial	Monomerous non-coaxial
Thallus thickness	-	559–802 (n = 4)	324 (n =1)	253–351 (n = 4)	229–723 (n = 16)	82–160 (n = 26)
Core cells (L x D)	8–21 x 21–64 (n = 265)	-	-	14–19 x 30–37 (n = 3)	21–43 x 6–15 (n = 15)	-
Peripherall cells (L x D)	12–51 x 6–23 (n = 58)	-	-	8–15 x 15–21 (n = 11)	11–40 x 8–180 (n = 110)	-
Epithallial cells	-	-	-	-	Rounded and flat but not flared	-
Conceptacle shape	Flask-shape	Bean-shape	Lens to flask-shape	Bean-shape	Large rectangles with rounded corners to small round shapes	Lens-shape
Conceptacle elevation	Completely raised above thallus surface	Completely buried	Slightly to completely raised above thallus surface	Completely buried	Slightly raised above thallus surface	Nearly completely raised above thallus surface
Conceptacles (D x H)	125–431 x 36–136 (n = 9)	282–367 x 166–237 (n = 5)	335–404 x 161–191 (n = 3)	282 x 129 (n = 1)	194–582 x 103–236 (n = 140)	201–777 x 109–221 (n = 25)
Pore canal (D x H)	14–71 (n = 9) (D)	46–51 (n = 2) (D)	55–123 x 61–146 (n = 3)	61 x 76 (n =1)	7–48 (n = 297) (D)	8–22 (n = 46) (D)
Roof thickness	26–110 (n = 9)	-	-	-	24–63 (n = 145)	26–69 (n = 25)
Roof cell layers	Up to 3				4–6 (n = 45)	4–6 (n = 6)
Raised rims	No	No	No	No	Yes	No
Space left over conceptacles roof	No	No	No	No	Yes	Yes

All samples are stored at the fossil collection of the Department of Biology of the University of the Azores, under the acronym DBUA-F.

SYSTEMATIC PALAEONTOLOGY

The studied rhodoliths show a wide variety of growth forms from encrusting to warty, fruticose, and lumpy. The individual nuclei consisted either of bioclasts or volcanic pebbles. Rhodoliths range between 2 to 6 cm in diameter and are all multispecific (Fig. 2). Taxonomically they are composed of 6 identified taxa (*Lithophyllum prototypum*, *Lithophyllum* sp., *Spongites* sp., *Hydrolithon* sp., *Phymatolithon calcareum* and cf. *Phymatolithon* sp.).

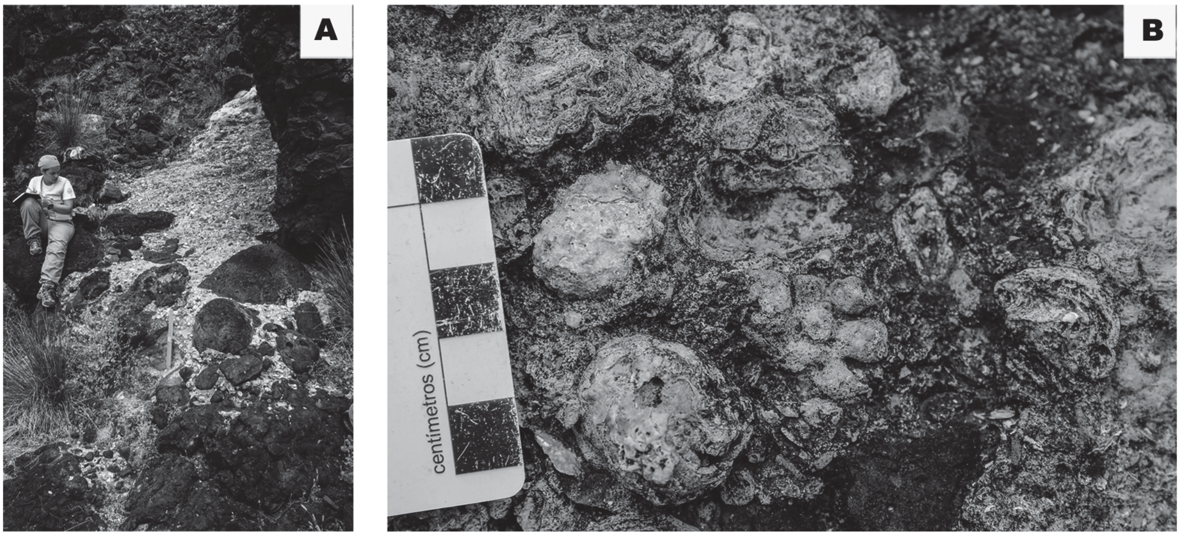

FIGURE 2. A. View of one of the 4 studied logs showing a rhodolith conglomerate, matrix is made up by volcanoclastic and bioclastic sandstone. The volcanic boulders at the base reach up to 1 m and the conglomerate is up to 3 m. Person for scale is ca 1.64 m tall. B. Detail of the rhodoliths different growth forms (Photos by M. W. Rasser).

Order Corallinales Silva & Johansen, 1986

Family CORALLINACEAE Lamouroux, 1812

Subfamily LITHOPHYLOIDEAE Setchell, 1943

Genus *Lithophyllum* Philippi, 1837

Lithophyllum prototypum (Foslie) Foslie, 1905
Figure 3: A–B

Synonyms: *Lithothamnion prototypum* Foslie 1897; *Melobesia prototypa* (Foslie) Foslie 1898; *Dermatolithon prototypum* (Foslie) Foslie 1900; *Goniolithon prototypum* (Foslie) Setchell & Mason 1943; *Tenarea prototypa* (Foslie) Adey 1970; *Titanoderma prototypum* (Foslie) Woelkerling, Y.M.Chamberlain & P.C.Silva 1985; *Lithophyllum tessellatum* Me.Lemoine 1930; *Goniolithon tessellatum* (M.Lemoine) Setchell & Mason 1943; *Dermatolithon tessellatum* (Me.Lemoine) Me.Lemoine 1971; *Tenarea tessellata* (Lemoine) M.M.Littler ex Adey *et al*. 1982; *Titanoderma tessellatum* (Me.Lemoine) Woelkerling, Y.M.Chamberlain & P.C.Silva 1985.

Growth form: encrusting, forming single thalli with multiple overgrowths.

Vegetative features: thallus dorsiventral and dimerous; unistratose basal filaments with large palisade cells, with a length of 8–21 µm (M = 14; SD = 3) and a diameter of 21–64 µm (M = 35; SD = 9) (Figure 3A). Postigenous filaments occur around the conceptacle chambers but also throughout all the vegetative thallus (Figure 3B), cell length 12–51 µm (M = 26; SD = 10), cell diameter 6–23 µm (M = 11; SD = 4). Secondary pit connections present. No epithallial cells were identified.

Reproductive features: tetra/bisporangial conceptacles are uniporate, flask-shaped and completely raised above thallus surface (Figure 3B). Tetra/bisporangial conceptacles measure 125–431 µm (M = 285; SD = 96) in diameter and 37–136 µm (M = 102; SD = 30) in height; pore length is 26–110 µm (M = 52; SD = 25) and 14–71 µm (M = 48; SD = 19) in diameter.

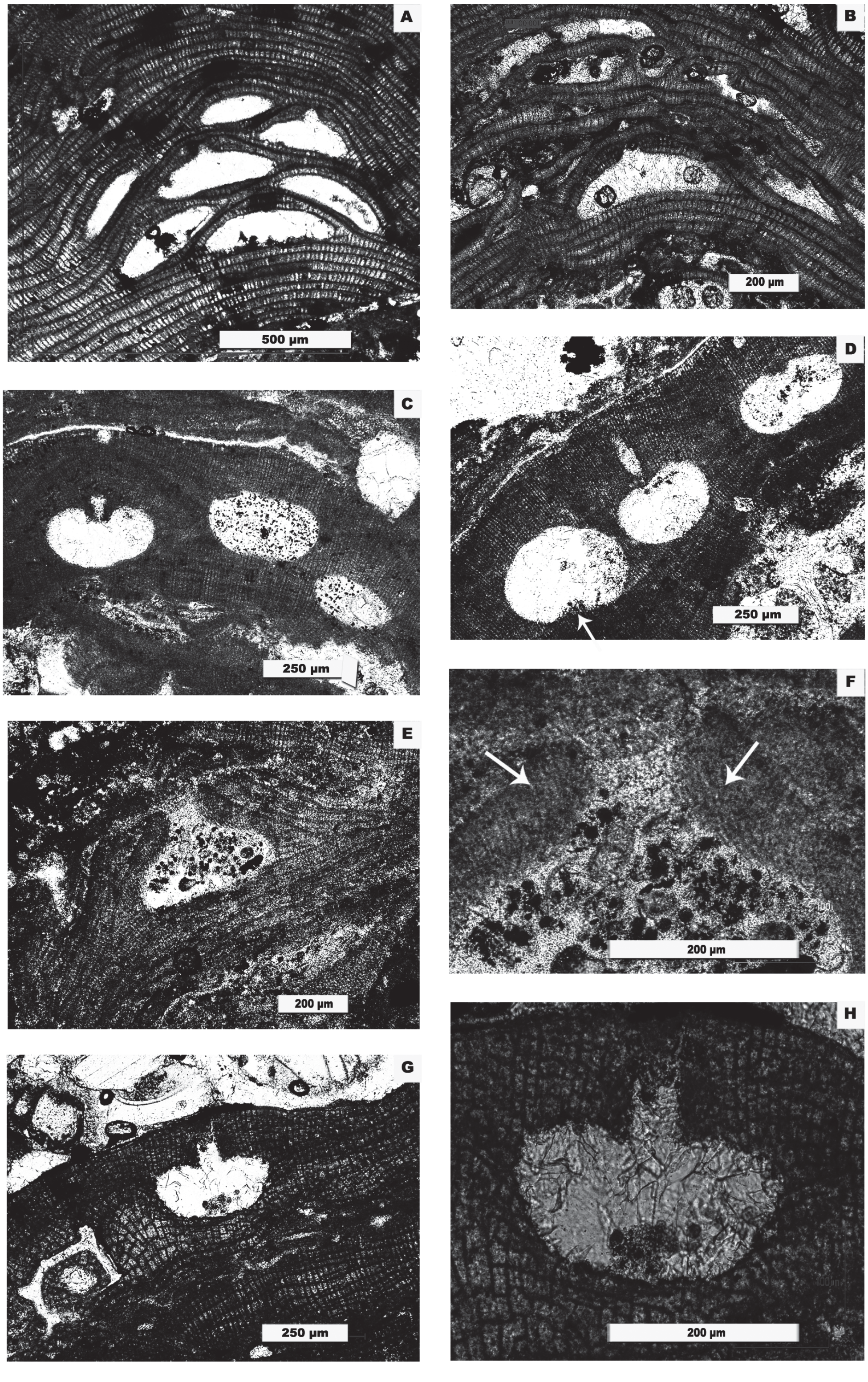

FIGURE 3. A and B. *Lihtophyllum prototypum*. A. Longitudinal view of dimerous thallus with palisade cells showing several uniporate conceptacles. Thin section DBUA-F 1106. B. Detail of uniporate conceptacle with postigenous filaments that occur around the conceptacles pore and throughout the vegetative thallus. Thin section DBUA-F 1103(1). C and D. *Lithophyllum* sp.. C. Longitudinal to oblique sections of uniporate conceptacles bean shaped with a central columella (arrow) (D). Thin section DBUA-F 1095_4a. E and F. *Spongites* sp.. E. Uniporate conceptacle with filaments around the pore canal oriented more or less subparallel to the roof surface (arrows). Thin section DBUA-F 1100(1). F. Higher magnification of E shows filaments around the pore. G and H. *Hydrolithon* sp.. G. Dimerous thallus and a uniporate conceptacle with filaments around the pore canal sub-parallel to the roof. H. Higher magnification of G shows filaments around the pore. Thin section DBUA-F 1087.

Remarks: Coralline algae belonging to the subfamily Lithophylloideae have uniporate tetra/bisporangial conceptacles and interfilamental cell connections made by secondary pits without cell fusions (Braga & Aguirre 1995). The *Lithophyllum-Titanoderma* complex represents distinct genera, but generic boundaries remain blurred on morphological grounds, having been treated as a complex using the oldest generic name *Lithophyllum* (Braga 2003, Iryu *et al*. 2009).

Studied thin sections: DBUA-F 1094(3), 1095(3), 1095(4)b, 1096(2), 1097(4), 1102(1), 1103(1), 1105(1)b and 1106(3).

Lithophyllum sp.
Figure 3: C–D

Growth form: encrusting.

Vegetative features: thallus organisation dorsiventral with a dimerous construction is from 559 to 802 µm in thickness. Cells rectangular in longitudinal section. No cell fusions present.

Reproductive features: sporangial uniporate conceptacles bean-shaped with a central columella, completely buried in the thallus (Figure 3C–D). Conceptacles 282–367 µm (M = 322; SD = 30) in diameter and 166–237 µm (M = 183; SD = 27) in height. The pore canal is particularly long and wide, measuring 46–51 µm in diameter and 90 µm in height.

Remarks: According to Irvine & Chamberlain (1994), the genus *Lithophyllum* is characterized by a thallus with single basal layer of mainly squarish non-palisade cells. Due to diagenesis, the basal cells are difficult to recognize; they appear to be rectangular to squarish, but this might be caused by the varying planes of the section. The non-palisade cells in the thallus, the uniporate conceptacle and absence of cells fusions indicate that the specimen belongs to the genus *Lithophyllum*.

Studied thin section: DBUA-F 1095(4)a.

Subfamily MASTOPHOROIDEAE Setchell, 1943

Genus *Spongites* Kützing, 1841

Spongites sp.
Figure 3: E–F

Growth form: encrusting.

Vegetative features: thallus organisation is dorsiventral and non-coaxial. The core filaments curve upwards to become perpendicular to the dorsal surface in the peripheral region. Cells of adjacent filaments are fused. The thallus is very irregular and has bryozoan encrustations but is ~324 µm in thickness. No epithallial cells were identified.

Reproductive features: one sporangial uniporate conceptacle, lens to flask-shaped, slightly to completely raised above thallus surface (Figure 3E), measuring 335–404 µm (M = 360; SD = 38) in diameter and 161–191 µm (M = 172; SD = 17) in height (excluding the pore canal length); the conceptacle pore is large, 55–123 µm (M= 85; SD = 34) in diameter and 61–146 µm (M = 94; SD = 45) in height. Filaments around the pore canal are oriented more or less subparallel to the roof surface (Figure 3F). No central columella was observed.

Remarks: The Mastophoroideae subfamily is poorly represented in the northern Atlantic (Irvine & Chamberlain 1994). The circumscription to the different genera is made according to the distribution and origin of the spermatangia in the conceptacle chamber, and the origin of the gonimoblast filaments (Penrose & Chamberlain 1993, Amen *et al.* 2005).

The combination of cell fusions and uniporate conceptacles allows the designation to the subfamily Mastophoroideae. The cell filaments surrounding the conceptacle pore canals subparallel to the conceptacle roof indicate that the genus is *Spongites*. Because it was not possible to observe trichocytes we could not define the species.

Studied thin sections: DBUA-F 1100(1) and 1101(3).

Genus *Hydrolithon* (Foslie) Foslie, 1909

Hydrolithon sp.
Figure 3: G–H

Growth form: encrusting.

Vegetative features: thallus arrangement dimerous, 253 to 351 µm in thickness. Cells of the ventral primigenous filaments are 14–19 µm (M = 16; SD = 3) in length and 30–37 µm (M = 33; SD = 4) in diameter. Postigenous filaments arise perpendicularly to the primigenous ones; cells are rectangular in longitudinal section and their size ranges from 8–15 µm (M = 12; SD = 3) in diameter and from 15–21 µm (M = 17; SD = 2) in length. Cell fusions are present.

Reproductive features: one sporangial uniporate conceptacle was found, measuring 282 µm in diameter and 129 µm in height. It is bean shaped and sunken into the thallus (Figure 3G). The pore canal is 61 µm in diameter and 76 µm in height. Filaments around the pore canal are subperpendicular to the roof (Figure 3H).

Remarks: The lack of palisade cells in the primigenous filaments and the cell filaments surrounding the pore canals more or less perpendicular to the roof surface indicate that the genus is *Hydrolithon*. The trichocytes in the basal filaments were not observed so we could not define the species.

Studied thin section: DBUA-F 1087.

Family HAPALIDACEAE Gray, 1864

Subfamily MELOBESIOIDEAE Bizzozero, 1885

Genus *Phymatolithon* Foslie, 1898

Phymatolithon calcareum (Pallas) Adey & McKibbin 1970
Figure 4: A–D

Synonyms: *Millepora calcarea* Pallas 1766; *Millepora polymorpha* Linnaeus 1767; *Melobesia calcarea* (Pallas) Harvey 1849; *Lithothamnion calcareum* (Pallas) Areschoug 1852; *Lithothamnion polymorphum* (Linnaeus) Areschoug 1852; *Lithothamnion corallioides* f. *subsimplex* Batters 1892; *Phymatolithon polymorphum* (Linnaeus) Foslie 1898; *Lithothamnion calcareum* f. *subsimplex* (Batters) Foslie 1905.

Growth form: lumpy protuberances.

Vegetative features: thallus dorsiventral and monomerous with a single system of filaments that are non-coaxial. Core filaments curve upwards to become perpendicular to the dorsal surface in the peripheral region. The thallus measures from 229 to 723 µm (M = 440; SD = 151) in thickness. The cells in the core are rectangular, measuring 21–43 µm (M = 31; SD = 6) in length and 6–15 µm (M = 11; SD = 3) in diameter; the core itself measures 41–126 µm, usually 70 µm in thickness and the peripheral filaments 197–610 µm (M = 332; SD = 117). New ventral core filaments arise from peripheral filaments and expand over the older portions of the thallus. Filaments in the protuberances become radially arranged and curve outwards. The alignment of cells of adjacent filaments is more or less well defined. Epithallial cells are rounded and flattened, but not flared (Figure 4D).

Reproductive features: there are several tetra/bisporangial multiporate conceptacles, irregularly distributed in the thallus. Their shape varies from more or less circular to large rectangles with rounded corners. Old conceptacles may be buried within the thallus (Figure 4A). In some conceptacles is not possible to observe the pore canals. Conceptacle size is variable in longitudinal section, measuring 194–582 µm (M = 381; SD = 83) in diameter and 103–236 µm (M = 170; SD = 26) in height. Conceptacle roofs are flattened to mound-like with rims (Figure 4A) and measure 24–63 µm (M = 42; SD = 9) in thickness. The roofs are composed of 4–6 cell layers. Pore tubes are cylindrical to conical and measure 7–48 µm (M = 17; SD = 6) in diameter. Some conceptacles fuse with one or more adjacent conceptacles measuring up to 894 µm in diameter (Figure 4B). Above some conceptacles there is a concavity void with a more or less triangular shape (Figure 4C) that is formed after spore release by the overgrowth of the perithallial filaments delimiting the conceptacles.

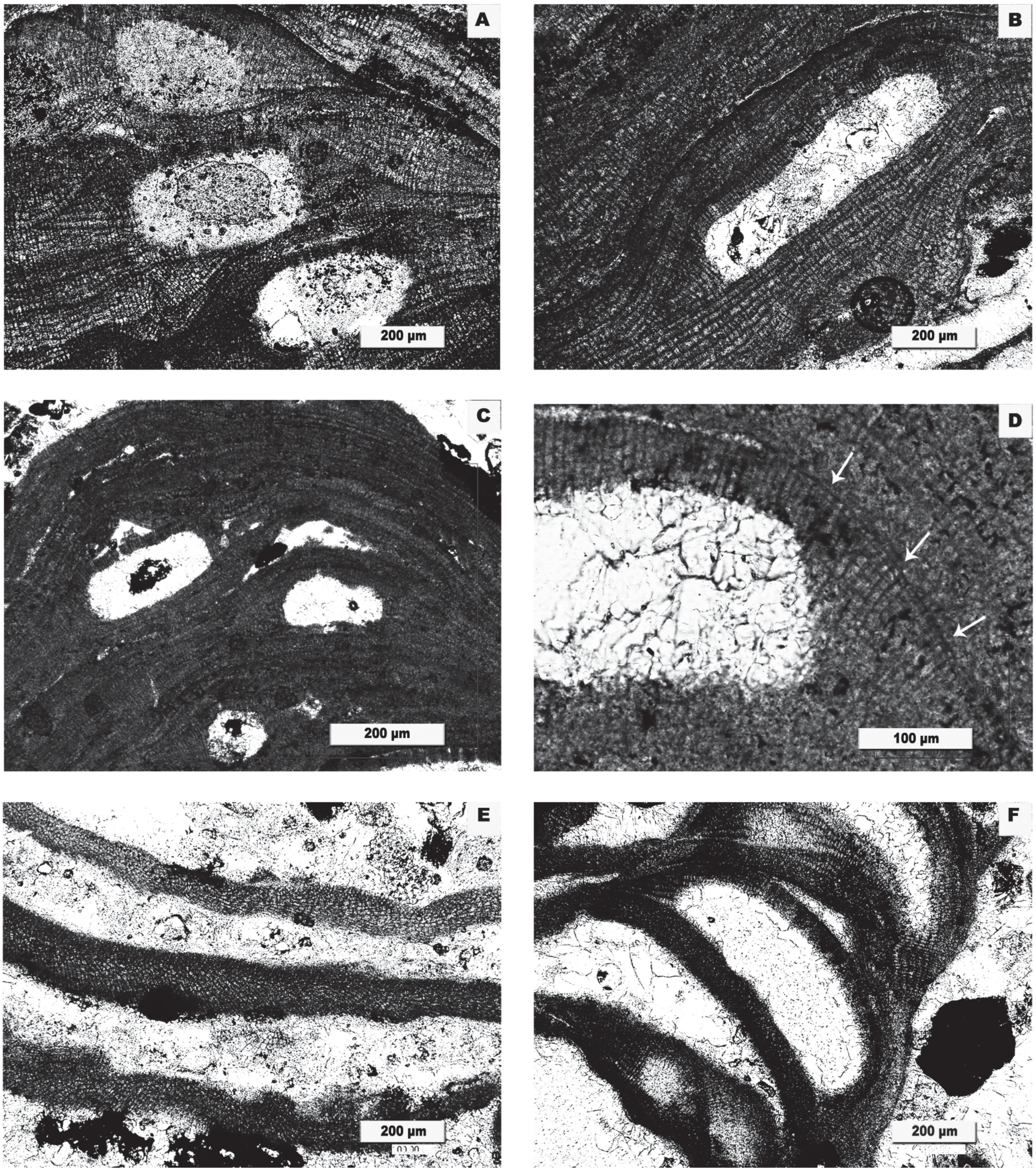

FIGURE 4. A–D. *Phymatolithon calcareum*. A. Multiporate conceptacles with raised rims, irregularly distributed in the thallus and slightly raised above thallus surface. Thin section DBUA-F 103(1). B. Conceptacles fused together. Thin section DBUA-F 1093(3). C. Concavity void formed by spore release and overgrowth of perithallial filaments, in a more or less triangular shape above conceptacle roof. Thin section DBUA-F 1096(4)a. D. Detail of conceptacle showing epithallial cells (arrows). Thin section DBUA-F 1096(4)a. E and F. cf. *Phymatolithon* sp.. E. Multiple growth of the thallus. Thin section DBUA-F 1098(2). F. Multiporate conceptacle, nearly completely raised above thallus surface; and concavity void, in a more or less triangular shape, formed by spore release and overgrowth of perithallial filaments above conceptacle roof. Thin section DBUA-F 1098(1).

Remarks: ten genera are recognized within the subfamily Melobesioideae (e.g., *Clathromorphum*, *Exilicrusta*, *Kvaleya*, *Leptophytum*, *Lithothamnion*, *Mastophoropsis*, *Melobesia*, *Mesophyllum*, *Phymatolithon* and *Synarthrophyton*). The distinction between the different genera is based mostly on the combination of anatomical characters, morphogenesis and the sexual reproduction (Mendoza & Cabioch 1998).

The shape of epithallial cells is used to separate the genus *Phymatolithon* from *Lithothamnion*. The epithallial cells should appear more or less convex rounded in *Phymatolithon*, flattened and "eared" in *Lithothamnion* (Woelkering & Irvine 1986, Basso 1994).

The conceptacle size, the rims above conceptacles and the flat rounded, but not flared or "eared" epithallial cells indicate *Phymatolithon calcareum* to be identified.

P. calcareum has been recorded since the Oligocene from the Mediterranean and Pannonian basins (Braga *et al*. 2009), it is also reported for the Pliocene of Spain (Braga & Aguirre 2001). This species is widely distributed (Guiry & Guiry 2014).

On present-day, *Phymatolithon calcareum* occurs in the Azores as a rhodolith forming species in a protected shallow (2 to 4 m depth) bay at Lajes do Pico, on Pico Island (Rosas-Alquicira *et al*. 2009).

Studied thin sections: DBUA-F 1093(1), 1093(2)a, 1093(2)b, 1093(3), 1093(4), 1094(1)a, 1094(1)b, 1094(2)a, 1094(4), 1095(3), 1096(4)a, 1096(4)b, 1100(1), 1101(3), 1103(1), 1105(1)a, 1105(4)a and 1106(3).

cf. ***Phymatolithon*** sp.
Figure 4: E–F

Growth form: encrusting to layered.

Vegetative features: thallus dorsiventral and monomerous with non-coaxial filaments. Thallus measures from 82 to 160 µm (M = 118; SD = 22) in thickness. Core filaments often curve towards the dorsal thallus surface. The core 32–106 µm (M = 70; SD = 34) is as thick, or even thicker as the perithallium 24–87 µm (M = 50; SD = 29) (Figure 4E). No epithallial cells were identified.

Reproductive features: tetra/bisporangial multiporate conceptacles lens-shaped, without a rim, nearly completely raised above thallus surface (Figure 4F), measuring 201–777 µm (M = 422; SD = 160) in diameter and 109–221 µm (M = 161; SD = 33) in height; the roofs of the conceptacles are 26–69 µm (M = 42; SD = 10) thick and composed of 4–6 cell layers. Some of the conceptacle roofs' are overgrown by peripheral cell filaments having a void.

Remarks: the monomerous non-coaxial thallus, the presence of cell fusions, the tetra/bisporangial multiporate conceptacles and the absence of columella indicate an Hapalidaceae, subfamily Melobesioideae. Because it was not possible to observe the epithallial cells, being this character the one that differentiates the genus *Phymatolithon* from *Lithothamnion* we could not reach the genus level, calling it cf. *Phymatolithon* sp.

This species differs from *Phymatolithon calcareum* in: (1) the lack of rims above the conceptacles and (2) in a thicker and more distinct core.

Studied thin sections: DBUA-F 1097(4), 1098(1), 1098(2), 1100(2) and 1103(1).

Undetermined coaxial thalli:

Two monomerous coaxial thalli without conceptacles were found. Cell fusions present both in the core and peripheral filaments. The core is well developed, 203–291 µm thick (M = 249; SD = 32), cell length 26–44 µm (M = 34; SD = 5) and cell diameter 9–23 µm (M = 15; SD = 3). The coaxial construction ascribes the specimens to the genus *Mesophyllum* Lemoine, 1928 or *Neogoniolithon* Setchell & Mason, 1943.

Studied thin section: DBUA-F 1101(3).

DISCUSSION AND CONCLUSION

This paper describes three Corallinaceae and one Hapalidaceae red algal genera comprising six taxa (*Lithophyllum prototypum*, *Lithophyllum* sp., *Spongite*s sp., *Hydrolithon* sp., *Phymatolithon calcareum* and cf. *Phymatolithon* sp.) from the Late Miocene of Malbusca, at Santa Maria Island (NE Atlantic). *Phymatolithon calcareum* was the most abundant species in the sections studied. Furthermore, two coaxial thalli ascribed to *Mesophyllum* sp. or *Neogoniolithon* sp., both rhodolith-forming species, were also found. The record of *L. prototypum* is the first one for the Miocene deposits.

Identifications were based on the following preserved taxonomic features: (1) arrangement of basal filaments (palisade dimeric, non palisade dimeric, monomeric), (2) epithallial cells (flared vs. non flared), (3) presence/absence of cell fusions or secondary pit connections, (4) conceptacle type (uni vs. multiporate), (5) number of cells layers which conceptacle chamber floors are situated below the surrounding thallus surface and (6) for sporangial pores, the orientation of filaments around conceptacle pores. Still, several species could not be identified, a situation that may be overcome in the future with the documentation of the present-day taxa (work in progress). The identification of fossil corallines suffers from the necessity to focus on calcified characters, such as reproductive organs and vegetative features. This has led to taxonomic confusion in the history of palaeoalgology and resulted in the study of Braga *et al*. (1993), who aimed to unify extant and fossil taxonomy. Since then, remarkable progress has been made, and our results confirm that an approximation between extant and fossil taxonomy is possible, even though uncertainties remain.

Albeit meagre in number of taxa, the geographical distribution of the identified Miocene algal species is consistent with the biogeographical relationships' pattern of both the modern (Tittley & Neto 1995, 2006, Santos *et al*. 1997, Ávila 2000, Almada *et al*. 2001, Ávila & Albergaria 2002, Ávila *et al*. 2012a, Micael *et al*. 2012, Xavier & Soest 2012, Ávila & Sigwart 2013, Meireles *et al*. 2014) and the fossil marine fauna and flora of the Azores (Ávila *et al*. 2002, 2009, 2010, 2012b, Madeira *et al*. 2011, Meireles *et al*. 2012, Ávila 2013).

IDENTIFICATION KEY TO THE GENERA OF CORALLINALES FROM THE LATE MIOCENE OF MALBUSCA OUTCROP, SANTA MARIA ILSAND (AZORES, NE ATLANTIC)

A. Family Corallinaceae

Tetra/bisporangial conceptacles uniporate.

1. Subfamily Lithophylloideae

I. Thallus dorsiventral:

1.1. Thallus dimerous with palisade cells; interfilamental cells connected by secondary pit connections; postigenous filaments around conceptacles and throughout all the vegetative thallus; tetra/bisporangial conceptacles completely raised above thallus surface. .... ***Lithophyllum prototypum***

1.2. Thallus dimerous, non-palisade cells; absence of cell fusions; sporangial conceptacle uniporate...... ***Lithophyllum* sp.**

2. Subfamily Mastophoroideae

I. Thallus composed of numerous layers of cells; cells of contiguous filaments connected by cell fusions:

2.1. Thallus monomerous and non-coaxial. Sporangial conceptacle slightly to completely raised above thallus surface. Filaments around conceptacle pore canals subparallel to the roof surface. .... ***Spongites* sp.**

2.2. Thallus dimerous. Sporangial conceptacle sunken into the thallus. Filaments around conceptacle pore canals subperpendicular to the roof surface .... ***Hydrolithon* sp.**

B. Family Hapalidaceae

Tetra/bisporangial conceptacles multiporate.

3. Subfamily Melobesioideae

I. Thallus monomerous, composed of numerous layers of cells; cells of contiguous filaments connected by cell fusions:

3.1. Tetra/bisporangial conceptacles completely raised above thallus surface, and with a distinct raised rim. Epithallial cells flat and rounded, but not flared .... ***Phymatolithon calcareum***

3.2. Tetra/bisporangial conceptacles completely raised above thallus surface without a rim .... cf. ***Phymatolithon* sp.**

ACKNOWLEDGEMENTS

This research was partially supported by the European Regional Development Fund (ERDF) through the COMPETE Programme - Operational Competitiveness Programme and national funds through FCT – PEst-C/MAR/LA0015/2011. This research was also funded by the SYNTHESYS Project (GB-TAF-3394), with support to A.C. Rebelo to study the rhodolith specimens at the Natural History Museum of London (NHM).

A.C. Rebelo was supported by a grant SFRH/BD/77310/2011 from FCT (Fundação para Ciência e Tecnologia), Portugal. S.P. Ávila was supported by FCT Ciência 2008 contract.

We thank Direcção Regional da Ciência e Tecnologia (Regional Government of the Azores), Clube Naval de Santa Maria and Câmara Municipal de Vila do Porto for field assistance on the International Workshops "Palaeontology in Atlantic Islands".

Sincere thanks to C. Wimmer-Pfeil (Staatliches Museum für Naturkunde Stutgart, Germany) for thin sections preparation and to A.R. Mendes, V. Zanon and J. Pacheco (CVARG, Universidade dos Açores) for laboratory assistance and helpful suggestions.

REFERENCES

Adey, W.H. & Macintyre, I.G. (1973) Crustose coralline algae: a re-evaluation in the Geological Sciences. *Geological Society of America Bulletin* 84(3): 883–904.

Afonso-Carrillo, J. (1988) Structure and reproduction of *Spongites widpretii* sp. nov. (Corallinaceae, Rhodophyta) from the Canary Islands, with observations and comments on *Spongites absimile* comb. nov.. *British Phycological Journal* 23: 89–102.

Aguirre, J., Braga, J.C. & Martín, J.M. (1993) Algal nodules in the Upper Pliocene deposits at the coast of Cadiz (S Spain), *In:* Barattolo, F., De Castro, P. & Parente, M. (Eds.) *Studies on Fossil Benthic Algae, Boll. Soc. Paleontol. Ital.* Spec. Vol. 1. Mucchi, Modena, Italy, pp. 1–7.

Aguirre, J., Riding, R. & Braga, J.C. (2000) Diversity of coralline red algae: origination and extinction patterns from the Early Cretaceous to the Pleistocene. *Paleobiology* 26(4): 651–667.

Aguirre, J., Braga, J.C., Martín, J.M. & Betzler, C. (2012) Palaeoenvironmental and stratigraphic significance of Pliocene rhodolith beds and coralline algal bioconstructions from the Carboneras Basin (SE Spain). *Geodiversitas* 34(1): 115–136.

Almada, V.C., Oliveira, R.F., Gonçalves, E.J., Almeida, A.J., Santos, R.S. & Wirtz, P. (2001) Patterns of diversity of the north-eastern Atlantic blenniid fish faun (Pisces: Blenniidae). *Global Ecology & Biogeography* 10: 41–422.

Amen, R.G., Neto, A.I. & Azevedo, J.M.N. (2005) Coralline-algal framework in the Quaternary of Prainha (Santa Maria island, Azores). *Revista Española de Micropaleontología* 37(1): 63–70.

Ávila, S.P. (2000) Shallow-water marine molluscs of the Azores: biogeographical relationships. *Arquipélago*. Life of marine Sciences. Supplement 2 (Part A): 99–131.

Ávila, S.P. (2013) Unravelling the patterns and processes of evolution of marine life in oceanic islands: a global framework. *In:* Fernández-Palacios, J.M., Nascimento, L., Hernández, J.C. Clemente, S. González, A. & Díaz-González, J.P. (Eds.) *Climate Change perspectives from the Atlantic: past, present and future*. Universidad de La Laguna, Tenerife, pp. 95–125.

Ávila, S.P. & Albergaria, A. (2002) The shallow-water Polyplacophora of the Azores and some comments on the biogeographical relationships of the Azorean malacofauna. *Bollettino Malacologico* 38 (1–4): 41–44.

Ávila, S.P. & Sigwart, J. (2013) New records for the shallow-water chiton fauna (Mollusca, Polyplacophora) of the Azores (NE Atlantic). *Zookeys* 312: 23–38.

Ávila, S.P., Amen, R. Azevedo, J.M.N., Cachão, M. & García-Talavera, F. (2002) Checklist of the Pleistocene marine molluscs of Prainha and Lagoinhas (Santa Maria Island, Azores). *Açoreana* 9: 343–370.

Ávila, S.P., Goud, J. & Martins, A.M.F. (2012a) Patterns of diversity of the Rissoidae (Mollusca: Gastropoda) in the Atlantic and the Mediterranean Region. *The Scientific World Journal* 2012(164890): 1–30.

Ávila, S.P., Ramalho, R. & Vullo, R. (2012b) Systematics, palaeoecology and palaeobiogeography of the Neogene fossil sharks fom the Azores (Northeast Atlantic). *Annales de Paléontologie* 98: 167–189.

Ávila, S.P. Silva, C.M, Schiebel, R., Ceca, F., Backeljau, T. & Martins, A.M.F. (2009) How did they get here? Palaeobiogeography of the Pleistocene marine molluscs of the Azores. *Bulletin of the Geological Society of France* 180: 201–213.

Ávila, S.P., Rebelo, A.C., Medeiros, A., Melo, C., Gomes, C., Bagaço, L., Madeira, P., Borges, P.A., Monteiro, P., Cordeiro, R., Meireles, R. & Ramalho, R. (2010) *Os fósseis de Santa Maria (Açores). 1. A jazida da Prainha*, 103 pp. OVGA – Observatório Vulcanológico e Geotérmico dos Açores, Lagoa.

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.

Bassi, D., Braga, J.C. & Iryu, Y. (2009) Palaeobiogeographic patterns of a persistent monophyletic lineage: *Lithophyllum pustulatum* species group (Corallinaceae, Corallinales, Rhodophyta). *Palaeogeography, Palaeoclimatology, Palaeoecology* 284: 237–245.

Basso, D. (1994) Study of living calcareous algae by a paleontological approach: the non-geniculate Corallinaceae (Rhodophyta) of the soft bottoms of the Tyrrhenian Sea (Western Mediterranean). The genera *Phymatolithon* Foslie and *Mesophyllum* Lemoine. *Riv. It. Paleont. Strat.* 100(4): 575–596.

Basso, D. & Tomaselli, V. (1994) Palaeoecological potentiality of rhodoliths: A Mediterranean case history. *Bolletino-Societa Paleontologica Italiana* 33: 17–28.

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: 403–416.

Berthois, L. (1950) Sur la présence d'une microfaune dans le calcaire de Santa Maria (Açores). *Açoreana* 4(4): 277–287.

Bosellini, A. & Ginsburg, R.N. (1971) Form and internal structure of recent algal nodules (rhodolites) from Bermuda. *The Journal of Geology* 79(6): 669–682.

Bosence, D.W.J. (1983) Description and Classification of Rhodoliths (Rhodoids, Rhodolites). *In* Peryt, T.M. (Ed.) *Coated Grains*. Springer-Verlag, Berlin, pp. 218–224.

Braga, J.C. (2003) Application of botanical taxonomy to fossil coralline algae (Corallines, Rhodophyta). *Acta Micropaleontologica Sinica* 20: 47–56.

Braga, J.C. & Aguirre, J. (1995) Taxonomy of fossil coralline algal species: Neogene Lithophylloideae (Rhodophyta, Corallinaceae) from southern Spain. *Review of Palaeobotany and Palynology* 86: 265–285.

Braga, J.C. & Aguirre, J. (2001) Coralline algal assemblages in upper Neogene reef and temperate carbonates in Southern Spain. *Palaeogeography, Palaeoclimatology, Palaeoecology* 175: 27–41.

Braga, J.C., Bosence, D.W.J. & Steneck, R.S. (1993) New anatomical characters in fossil coralline algae and their taxonomic implications. *Palaeontology* 36: 535–547.

Braga, J.C., Vescogni, A., Bosellini, F.R. & J. Aguirre (2009) Coralline algae (Corallinales, Rhodophyta) in western and central Mediterranean Messinian reefs. *Palaeogeography, Palaeoclimatology, Palaeoecology* 275: 113–128.

Guiry, M.D. & Guiry, G.M. (2014) *AlgaeBase*. World-wide electronic publication, National University of Ireland, Galway. Available from http://www.algaebase.org (accessed 11 January 2014).

Irvine, L.M. & Chamberlain, M. (1994) *Seaweeds of the British Isles*. Vol. 1 Rhodophyta, PArt 2B Corallinales, Hildenbrandiales. London (HMSO), 276 pp.

Iryu, Y., Bassi, D. & Woelkerling, W.J. (1999) Re-assessment of the type collections of fourteen corallinacean species (Corallinales, Rhodophyta) described by W. Ishijima (1942–1960). *Palaeontology* 52(2): 401–427.

Johnson, M.E., Baarli, B.G., Cachão, M., da Silva, C.M., Ledesma-Vázquez, J., Mayoral, E.J., Ramalho, R.S. & Santos, A. (2012) Rhodoliths, uniformitarianism, and Darwin: Pleistocene and recent carbonate deposits in the Cape Verde and Canary archipelagos. *Palaeogeogry, Palaeoclimatoly, Palaeoecology* 329–330: 83–100.

Madeira, P., Kroh, A., Cordeiro, R., Meireles, R. & Ávila, S.P. (2011) The fossil echinoids of Santa Maria Island, Azores (Northern Atlantic Ocean). *Acta Geologica Polonica* 61(3): 243–264.

Meireles, R.P., Faranda, C., Gliozzi E., Pimentel, A., Zanon, V. & Ávila, S.P. (2012) Late Miocene marine ostracods from Santa Maria Island, Azores (NE Atlantic): Systematics, palaeoecology and palaeobiogeography. *Révue de Micropaléontologie* 55: 133–148.

Meireles, R.P., Keyser, D. & Ávila, S.P. (2014) The Holocene to Recent ostracods of the Azores (NE Atlantic): systematics and biogeography. *Marine Micropaleontology* 112: 13–26.

Mendoza, M.L. & Cabioch, J. (1998) Étude comparée de la reproduction de *Phymatolithon calcareum* (Pallas) Adey & McKibbin et *Lithothamnion corallioides* (P. & H. Crouan) P. & H. Crouan (Corallinales, Rhodophyta), et reconsidérations sur la définition des genres. *Canadian Journal of Botany* 76: 1433–1445.

Micael, J., Alves, M.J., Jones, M.B. & Costa, A.C. (2012) Diversity of shallow-water asteroids (Echinodermata) in the Azorean archipelago. *Marine Biodiversity Records* 5
http://dx.doi.org/10.1017/S1755267211000534

Penrose, D. (1991) *Spongites fruticulosus* (Corallinaceae, Rhodophyta), the type species of *Spongites*, in southern Asutralia. *Phycologia* 30(5): 438–448.

Penrose, D. & Chamberlain, Y.M. (1993) *Hydrolithon farinosum* (Lamouroux) comb. nov.: implications for generic concepts in the Mastophoroideae (Corallinaceae, Rhodophyta). *Phycologia* 32(4): 295–303.

Rasser, M.P. & Piller, W.E. (1999) Application of neontological taxonomic concepts to Late Eocene coralline algae (Rhodophyta) of the Austrian Molasse Zone. *Journal of Micropalaeontology* 18: 67–80.

Rosas-Alquicira, E.F., Riosmena-Rodríguez, R., Couto, R.P. & Neto, A.I. (2009) New additions to the Azorean algal flora, with ecological observations on rhodolith formations. *Cah. Biol. Mar.* 50: 143–151.

Santos, R.S., Porteiro, F.M. & Barreiros, J.P. (1997) *Marine Fishes of the Azores: An annoted checklist and bibliography. Arquipélago.* Lifes and Marine Sciences. Supplement 1, XXVIII + 244 pp.

Tittley, I. & Neto, A.I. (1995) The marine algal flora of the Azores and its biogeographical affinities. *Boletim do Museu Municipal do Funchal* 4: 747–766.

Tittley, I. & Neto, A.I. (2006) The marine algal flora of the Azores: island isolation or Atlantic stepping-stones). *In*: Hayden, T.J., Murray, D.A. & O'Connor, J.P. (Eds.) Proceedings of the 5th international symposium on the fauna and flora of

Atlantic Islands. Dublin, 24–27 August 2004. *Occasional Publication of the Irish Biogeographical Society* 9: 40–51.

Verheij, E. (1994) Nongeniculate Corallinaceae (Corallinales, Rhodophyta) from the Spermonde Archipelago, SW Sulawesi, Indonesia. *Blumea* 39: 95–137.

Wilks, K.M. & Woelkerling, W.J. (1994) An account of Southern Australian species of *Phymatolithon* (Corallinaceae, Rhodophyta) with comments on *Leptophytum*. *Australian Sytematic Botany* 7: 183–223.

Woelkerling, W.J. (1985) A taxonomic reassessment of *Spongites* (Corallinales, Rhodophyta) based on studies of Kützing original collections. *British Phycological Journal* 20: 123–153.

Woelkerling, W.J. (1988) *The coralline red algae: an analysis of the genera and subfamilies of nongeniculate Corallinaceae.* Oxford University Press, Oxford, 268 pp.

Woelkerling, W.J. & Irvine, L.M. (1986) The typification and status of *Phymatolithon* (Corallinaceae, Rhodophyta). *British Phycological Journal* 21:55–88.

Woelkerling, W.J., Irvine, L.M. & Harvey, A.S. (1993) Growth-forms in non-geniculate coralline red algae (Corallinales, Rhodophyta). *Australian Systematical Botany* 6: 277–293.

Xavier, J.R. & Van Soest, R.W.M. (2012) Diversity patterns and zoogeography of the Northeast Atlantic and Mediterranean shallow-water sponge fauna. *Hydrobiologia* 687: 107–125.

Zbyszewski, G. & Ferreira, O. (1962) Étude géologique de l'île de Santa Maria (Açores). *Com. Serv. Geol. Portugal* 45: 467–478.