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CORALLINE-ALGAL FRAMEWORK IN THE QUATERNARY OF PRAINHA (SANTA MARIA ISLAND, AZORES)

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Abstract

At the south coast of the island of Santa Maria (Azores, Portugal) a coralline-algal framework emerges near the base of a Quaternary succession. It is located about 2 m above the present mean sea level, extends for near 200 m along the littoral zone, and has a maximum thickness of 60 cm. The main framework builders are coralline red algae (Corallinaceae, Rhodophyta). Mollusc shells, vermetid tubes and bryozoans are the secondary framework builders. The coralline assemblage is composed of *Spongites fruticulosus,* with some *Neogoniolithon brassica-florida, Lithophyllum incrustans* and *Titanoderma pustulatum*. The morphological network and taxonomic composition show close analogies with the coralline algal assemblages of the Mediterranean and west Atlantic, formed at sea level in narrow tide amplitudes and moderate hydrodynamics.

Key words: Coralline red algae, coralline framework, Quaternary, Azores.

Resumen

En la costa Sur de la isla de Santa Maria (Azores, Portugal) queda expuesto un arrecife calcáreo atribuido al Cuaternario, situado 2 m sobre el nivel del mar, extendiéndose 200 m a lo largo del litoral, con un espesor máximo de 60 cm. Las algas coralinas rojas (Corallinaceae, Rhodophyta), son los constructores primordiales de esta bioconstrucción. Conchas de moluscos, tubos de vermétidos y briozoos son los constructores secundarios. La asociación coralina está compuesta por *Spongites fruticulosus*, junto con algún *Neogoniolithon brassica-florida*, *Lithophyllum incrustans* y *Titanoderma pustulatum*. Estructuras de algas coralinas de composición taxonómica y morfológica similares existen cerca del nivel del mar en el Mediterráneo y Atlántico occidental en condiciones hidrodinámicas moderadas y con poca amplitud de marea.

Palabras clave: Algas coralinas rojas, *framework* coralino, Cuaternario, Azores.

INTRODUCTION

Santa Maria is the oldest (around 5,2-8,12 Ma, see Abdel-Monem *et al.*, 1975; Ferraud *et al.*, 1984) and easternmost island of the Azores, situated 430 km east of the Mid-Atlantic Ridge (Fig. 1a, b). The island has two distinct morphologic areas: the western part is flat and exhibits extensive wave-cut platforms reaching altitudes of 250 m above sea level, whereas the eastern part is irregular, the highest point exceeding 450 m. The shoreline is rugged with high steep cliffs reaching 342 m. There are some bays but only one relatively long sand beach, Praia Formosa.

There are no indications of recent volcanism, the last eruptions having occurred during the Upper Pliocene (Serralheiro & Madeira, 1993). It is the only island of the archipelago where marine fossiliferous deposits are known (Mitchell-Thomé, 1981; Ferraud *et* *al.*, 1984). The marine fossils of Santa Maria have been studied since the 19th century (see revision in Mitchell-Thomé, 1976). Most of the older work concentrated on Miocene-Pliocene successions. More recently, however, attention has been given to the Quaternary deposits (Zbyszewski & Ferreira, 1961; Garcia-Talavera, 1990; Callapez & Soares, 2000; Ávila *et al.*, 2002).

At Prainha, situated on the South coast of the island (Fig. 1c), a small fossiliferous cliff emerges at about 2 m above sea level, and extends for 200 m along the shore (Fig. 3a). Although no absolute dating has been made, all authors agree that it represents a Quaternary deposit, with Garcia-Talavera (1990) placing it as Tyrrhenian or Neotyrrhenian. According to Zbyszewski *et al.* (1961), a contemporary sequence to this fossil deposit can be found in several other parts of the island, and indeed Callapez & Soares (2000) established a direct association between Prainha and Lagoinhas, another Pleistocene shore deposit.

All the stratigraphic descriptions of the outcrop of Prainha mention the occurrence of a level of calcareous algae, named by Berthois (1953a, b) and Zbyszewski & Ferreira (1961) as "Lithothamnium". No detailed studies of this specific level are known.

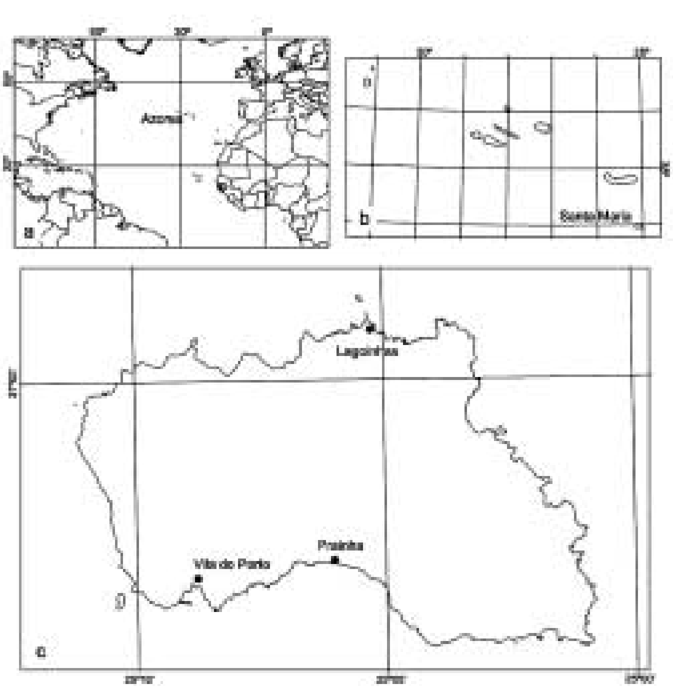

FIGURE 1–The Azores in the North Atlantic (a, b) and the location of Prainha in Santa Maria Island (c).

This is the first phycological study of the outcrop of Prainha. Therefore, the present paper aims to identify and describe the algal components of the fossil framework of Prainha and to compare the algal association with similar modern frameworks elsewhere.

MATERIAL AND METHODS

Fieldwork was done in February 2001 and June 2002. Eight vertical profiles were selected along the outcrop. For each profile, the different layers were identified and measured, panoramic and detailed photographs were taken, and a lithologic description was produced. The collections made were numbered and deposited in the Department of Biology at the University of the Azores, Ponta Delgada.

For microscopic analysis, thin sections and electron microscopy preparations were made. The diagnosis of the algal components was based on morphological and anatomical characters and reproductive structures, following Woelkerling (1988), Braga *et al*. (1993), Irvine & Chamberlain (1994), Braga & Aguirre (1995), Womersley (1996) and Braga (2003). The relative abundance of each species was determined on the thin section slides using a transparent overlay with a grid of dots. Nomenclature and synonymy follow Guiry & Nic Dhonncha (2004).

RESULTS

Lithology

The outcrop of Prainha is located over an irregular platform of ankaramnitic basalts (Fig. 2, A), belonging to the Anjos complex that dates from the origin of the island (Upper Miocene, probably Tortonian, Serralheiro & Madeira, 1993). Basaltic veins often intersect the bedding surface.

Above the basalt platform is an extremely cemented fossiliferous marine conglomerate, with a maximum thickness of 40 cm (Fig. 2, B).

Overlying the conglomerate is a coralline-algal framework (Fig. 2, C) that incorporates some pebbles and a large quantity of mollusc shells.

Above the coralline-algal framework is a layer of sands, up to 130 cm thick (Fig. 2, D) and rich in microfauna such as *Cantharus variegatus*, *Lucinella divaricata*, *Polynices lacteus*, *Conus ermineus* and *Ensis minor* (more information in Ávila *et al.*, 2002). This unit varies in colour from grey to yellow. It shows in the lower part an alternation of sand grains and small rounded pebbles (to 10 cm in diameter) deposited by wave action. These sand and pebble deposits form in some places cemented lenses. The top layer in unit D is characterised by cross-laminated eolic sediment with roots of non-identified plants.

Torrential and landslide deposits (Fig. 2, E) cover the sequence.

This lithologic succession is in agreement with descriptions made by Berthois (1953a) and Zbyszewski & Ferreira (1961).

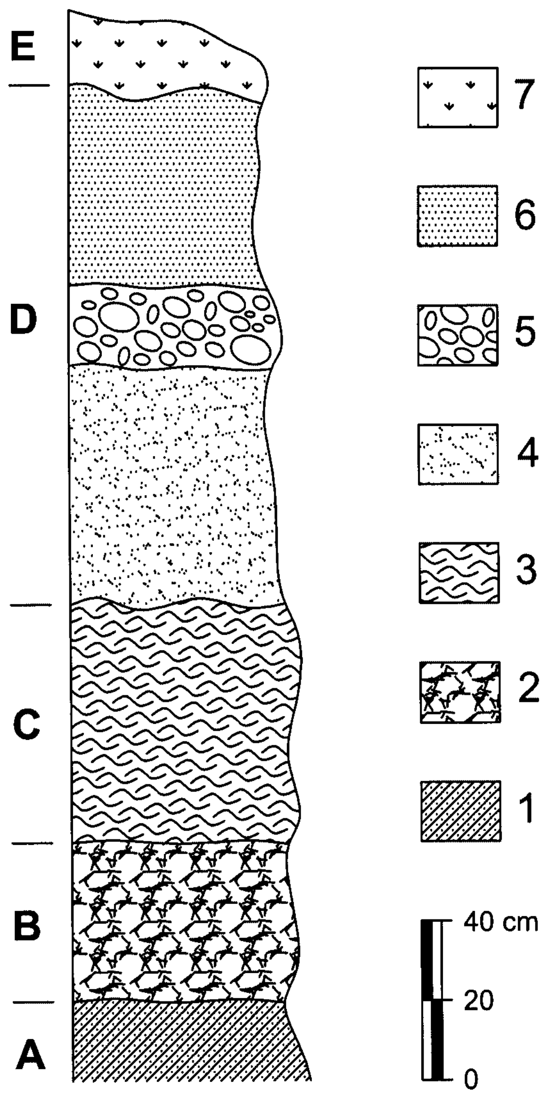

FIGURE 2–Schematic profile of the Prainha outcrop: 1) basaltic bedrock; 2) cemented fossiliferous conglomerate; 3) coralline-algal framework; 4) biogenic sands; 5) small rounded pebbles; 6) cross-laminated eolic sands; 7) torrential and landslide deposits.

Coralline-algal framework

Macroscopically, the coralline-algal framework (Fig. 2, C) appears as a flattened bed (Fig. 3a). It varies in colour from light to dark yellow and shows oxidation signs. The surface is mostly uneven, but in some areas may be smooth and shiny. It shows multiple fissures filled with sand from unit D.

The primary framework building are non-geniculate, attached, Corallinaceae that overgrow each other, as intimate adherent layers with warty to lumpy growth forms (*sensu* Woelkerling *et al.*, 1993, Fig. 3b, c). In many places these growth forms form a less compact structure, with an intricate net of tunnels and small chambers filled with sediment, mollusc shells, bryozoans, and vermetid tubes. These are accessory components of the framework. It is also possible to see landings colonized by borers that are enclosed inside the framework by the coralline growth.

Four species of Corallinaceae (see descriptions below) were identified in the samples (SMAf-02-05; SMAf-02-07; SMAf-02-09) collected on algal framework. Intergrowth between taxa is common, but it was not possible to evaluate the encrusting successions. *Spongites fruticulosus* had the highest relative abundance (77%) in the samples studied, followed by *Lithophyllum incrustans* (12%), *Neogoniolithon brassica-florida* (10%) and *Titanoderma pustulatum* (1%).

TAXONOMY

Division RHODOPHYTA Wettstein, 1901
Class RHODOPHYCEAE Rabenhorst, 1863
Order CORALLINALES Silva and Johansen, 1986
Family CORALLINACEAE Lamouroux, 1812
Subfamily MASTOPHOROIDEAE Setchell, 1943
Genus *Spongites* Kützing, 1841
Spongites fruticulosus Kützing, 1841

Synomyms.–*Lithothamnion ramulosum* Philippi 1837; *Melobesia fruticulosa* (Kützing) Decaisne 1842; *Spongites ramulosa* (Philippi) Kützing 1869; *Lithothamnion fasciculatum f. fruticulosum* (Kützing) Hauck 1883; *Lithothamnion meneghianum* Vinassa 1892; *Lithothamnion fruticulosum* (Kützing) Foslie 1895; *Paraspora fruticulosa* (Kützing) Heydrich 1900; *Goniolithon verrucosum* Foslie 1900; *Lithophyllum verrucosum* (Foslie) Foslie 1901; *Neogoniolithon verrucosum* (Foslie) Adey 1970.

Description.–Thallus pseudoparenchymatous, 2-3 mm thick with dorsiventral organization. Monomerous construction, consisting of a plumose ventral region (Fig. 4a) and a peripheral region where portions of core filaments curve outwards towards the thallus surface. Cells of adjacent filaments connected laterally by cell-fusions (Fig. 4b). Secondary pit-connections not observed. Cells more or less quadrangular, 15-18 µm in diameter and 23-25 µm long. A single layer of non-flared epithallial cells (15-20 µm in diameter, 10-13 µm long), distal walls rounded, was observed. Trichocytes in horizontal arrangement or single were observed on the thallus surface (Fig. 4c).

Uniporate sporangial conceptacles (Fig. 4d) are, in average, 515-750 µm in diameter and 316-450 µm long. Central columella was not observed. Pore canal cylindrical to slightly bulbous, lined by protruding cells. Conceptacle roof protruding the thallus surface. 9-30 cells above the sporangial chamber. No male conceptacles were recognized.

Genus *Neogoniolithon* Setchell & Mason, 1943
Neogoniolithon brassica-florida (Harvey) Setchell & Mason, 1943

Synomyms.–*Melobesia brassica-florida* Harvey 1849; *Lithothamnion brassica-florida* (Harvey) Areschoug 1852; *Melobesia notarisii* L. Dufour 1861; *Lithophyllum insidiosum* Solms-Laubach 1881; *Lithophyllum fosliei* (Heydrich) Heydrich 1897; *Melobesia insidiosa* (Solms-Laubach) Heydrich 1897; *Lithothamnion fosliei* Heydrich 1897b; *Choreonema notarisii* (Dufour) Foslie 1898; *Goniolithon brassica-florida* (Harvey) Foslie 1898; *Lithophyllum chalonii* Heydrich 1899; *Goniolithon notarisii* (Dufour) Foslie 1900; *Goniolithon frutescens* Foslie 1900c; *Goniolithon fosliei (Heydrich)* Foslie 1903; *Goniolithon laccadivicum* (Foslie) Foslie 1904; *Lithophyllum frutescens* (Foslie) M. Lemoine 1911; *Lithophyllum notarisii* (L. Dufour) Lemoine 1912; *Lithothamnion notarisii (*Dufour) Lemoine 1915; *Neogoniolithon fosliei*

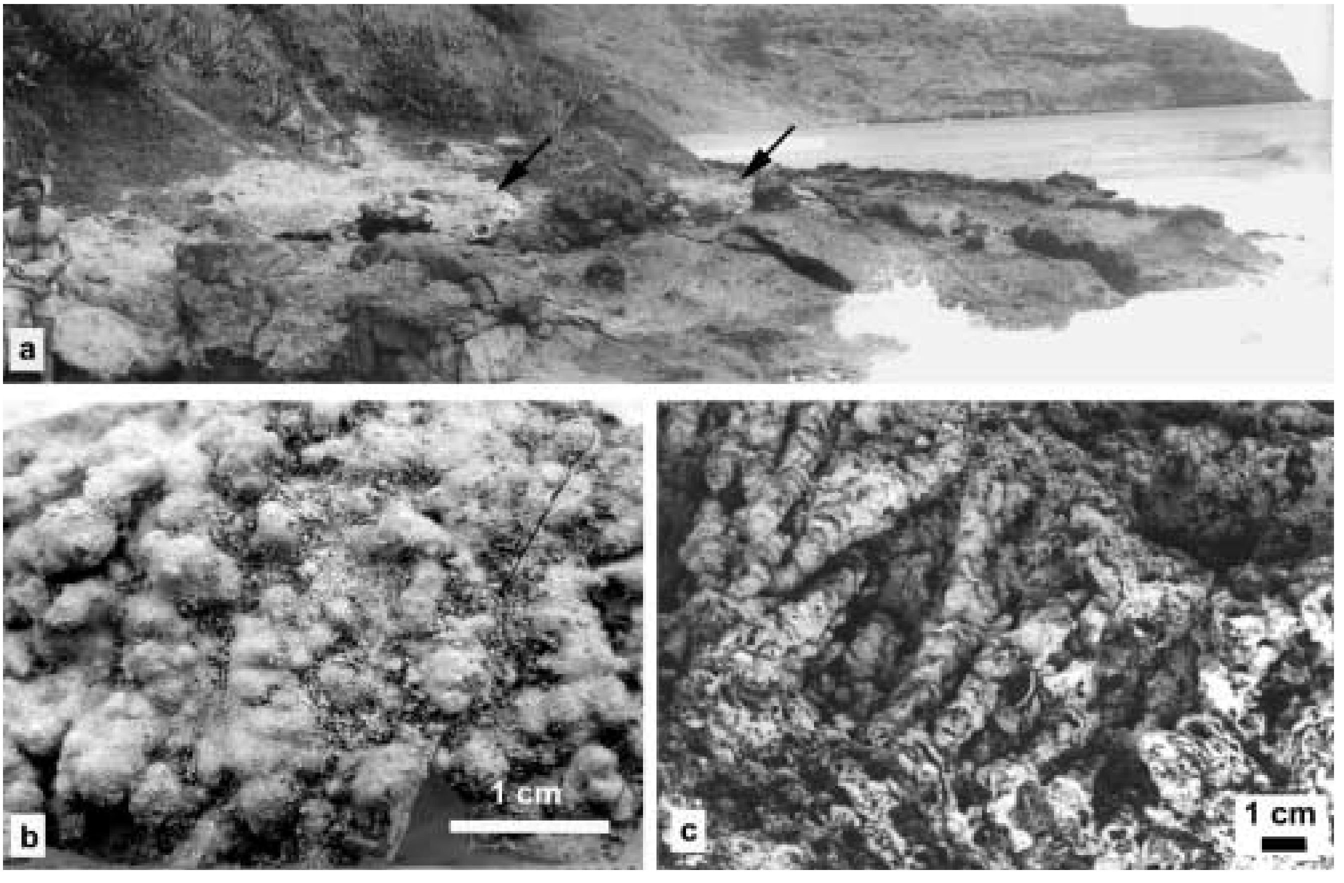

FIGURE 3–Field view of Prainha coralline-algal framework (a) and warty to lumpy growth-form of the crustose algae, unbranched (b) and branched (c).

(Heydrich) Setchell & Mason 1943; *Neogoniolithon frutescens* (Foslie) Setchell & Mason 1943; *Neogoniolithon laccadivicum* (Foslie) Setchell & Mason 1943; *Neogoniolithon notarisii* (Dufour) G. Hamel & M. Lemoine 1953; *Spongites notarisii* (L. Dufour) Athanasiadis 1987.

Description.–The plants exhibit a pseudoparenchymatous thallus 2.4 mm thick with dorsiventral organization. Monomerous construction, cells of the ventral region arranged in coaxial filaments (Fig. 4e) that curve outwards towards the thallus surface. Cells of adjacent filaments connected laterally by cell-fusions. Secondary pit-connections not observed. Cells of the peripheral region 13-15 µm in diameter and 20-23 µm long. Epithallial cells not observed. Trichocytes arranged in horizontal and vertical rows within the thallus.

Sporangial conceptacles (Fig. 4f), elliptical in shape, are uniporate and lacking a central columella. Chambers are, in average, 724 µm in diameter and 332 µm long. The pore canal is cylindrical with gentle curved sides in longitudinal section, and lined by cells oriented more or less parallel to the thallus surface. Conceptacle roof protrudes conspicuously above surrounding thallus surface. Over 20 cells above the sporangial chamber. No male conceptacles have been found.

Subfamily LITHOPHYLLOIDEAE Setchell, 1943
Genus *Lithophyllum* Philippi, 1837
Lithophyllum incrustans Philippi, 1837

Synomyms.–*Corallium cretaceum-lichenoides* Ellis 1755; *Spongites confluens* Kützing 1841; *Melobesia polymorpha* Harvey 1843; *Lithothamnion depressum* P. L. Crouan & H. M. Crouan 1867; *Lithothamnion incrustans* (Philippi) Foslie 1895; *Crodelia incrustans* (Philippi) Heydrich 1911.

Description.–plants with dimerous thallus, 1-3 mm thick. The filaments appear as continuous aligned rows of cells clearly delimited from adjacent ones. Cells of contiguous filaments joined by secondary pit-connections. No epithallial cells have been found in the samples studied. In surface view, the cells are irregularly arranged, rectangular to polygonal, almost rhomboedric in shape. Cells of primigenous filaments are 8-10 µm in diameter and 13-15 µm high. Cells of postigenous filaments are clearly distinct and measure 18-23 µm high and 10-13 µm in diameter.

Uniporate sporangial conceptacles (Fig. 4g) are bean-shaped in section and exhibit the remains of a columella. Chambers are, in average, 214-230 µm in diameter and 112-117 µm high. The pore canal is cylindrical, with gentle curved sides in longitudinal section. There were 13-21 cells above the sporangial chamber. No male conceptacles were recognized.

Genus *Titanoderma* Nägeli, 1858
Titanoderma pustulatum (J. V. Lamouroux) Nägeli, 1858

Synomyms.–*Titanoderma litorale* (P. L. Crouan & H. M. Crouan) Boudouresque & Perret; *Melobesia pustulata* J. V. Lamouroux 1816; *Melobesia verrucata* J. V. Lamouroux 1816; *Melobesia macrocarpa* Rosanoff 1866; *Melobesia simulans* P. L. Crouan & H. M. Crouan 1867; *Melobesia hapalidioides* P. L. Crouan & H. M. Crouan 1867; *Lithophyllum hapalidioides* (P. L. Crouan & H. M. Crouan) Hariot 1889; *Lithothamnion adplicitum* Foslie 1897; *Dermatolithon hapalidiodes* (P. L. Crouan & H. M. Crouan) Foslie 1898; *Dermatolithon pustulatum* (J. V. Lamouroux) Foslie 1898; *Dermatolithon macrocarpum* (Rosanoff) Foslie 1899; *Melobesia caspica* Foslie 1899; *Dermatolithon adplicitum* (Foslie) Foslie 1900; *Lithophyllum pustulatum* (J. V. Lamouroux) Foslie 1904; *Lithophyllum macrocarpum* (Rosanoff) Foslie 1904; *Litholepis caspica* (Foslie) Foslie 1905; *Epilithon pustulatum* (J. V. Lamouroux) Lemoine 1921; *Lithophyllum adplicitum* (Foslie) Lily Newton 1931; *Fosliella ascripticia* (Foslie) G. M. Smith 1944; *Dermatolithon caspica* (Foslie) Zaberzhinskaya ex Zinova 1967; *Tenarea ascripticia* (Foslie) Adey 1970; *Tenarea caspica* (Foslie) Adey 1970; *Tenarea hapalidioides* (P. L. Crouan & H. M. Crouan) Adey & P. J. Adey 1973; *Tenarea pustulata* (J. V. Lamouroux) Shameel, nom. inval 1983; *Titanoderma ascripticia* (Foslie) Woelkerling, Y. M. Chamberlain & P. C. Silva 1985; *Titanoderma hapalidioides* (P. L. Crouan & H. M. Crouan) J. H. Price *et al.* 1986; *Titanoderma verrucatum* (J. V. Lamouroux) Y. M. Chamberlain 1986; *Titanoderma macrocarpum* (Rosanoff) Y. M. Chamberlain 1986; *Titanoderma caspica* (Foslie) Woelkerling 1986.

Description.–Thallus pseudoparenchymatous with dorsiventral organization, 265 µm thick. Dimerous construction with a single layer of palisade cells. Cells of contiguous filaments joined by secondary pit-connections (Fig. 4h). Epithallial cells not observed. Primigenous cells are 18-20 µm in diameter and 24-25 µm high. Postigenous cells, rectangular in shape, are 23-25 µm in diameter and 15-18 µm long.

Sporangial conceptacles are uniporate, hemispherical in longitudinal section and lack a central columella. Chambers are, in average, 321 µm in diameter and 122 µm high. The pore canal is wide and cylindrical. 4-6 cells thick above the sporangial chamber. No male conceptacles were recognized.

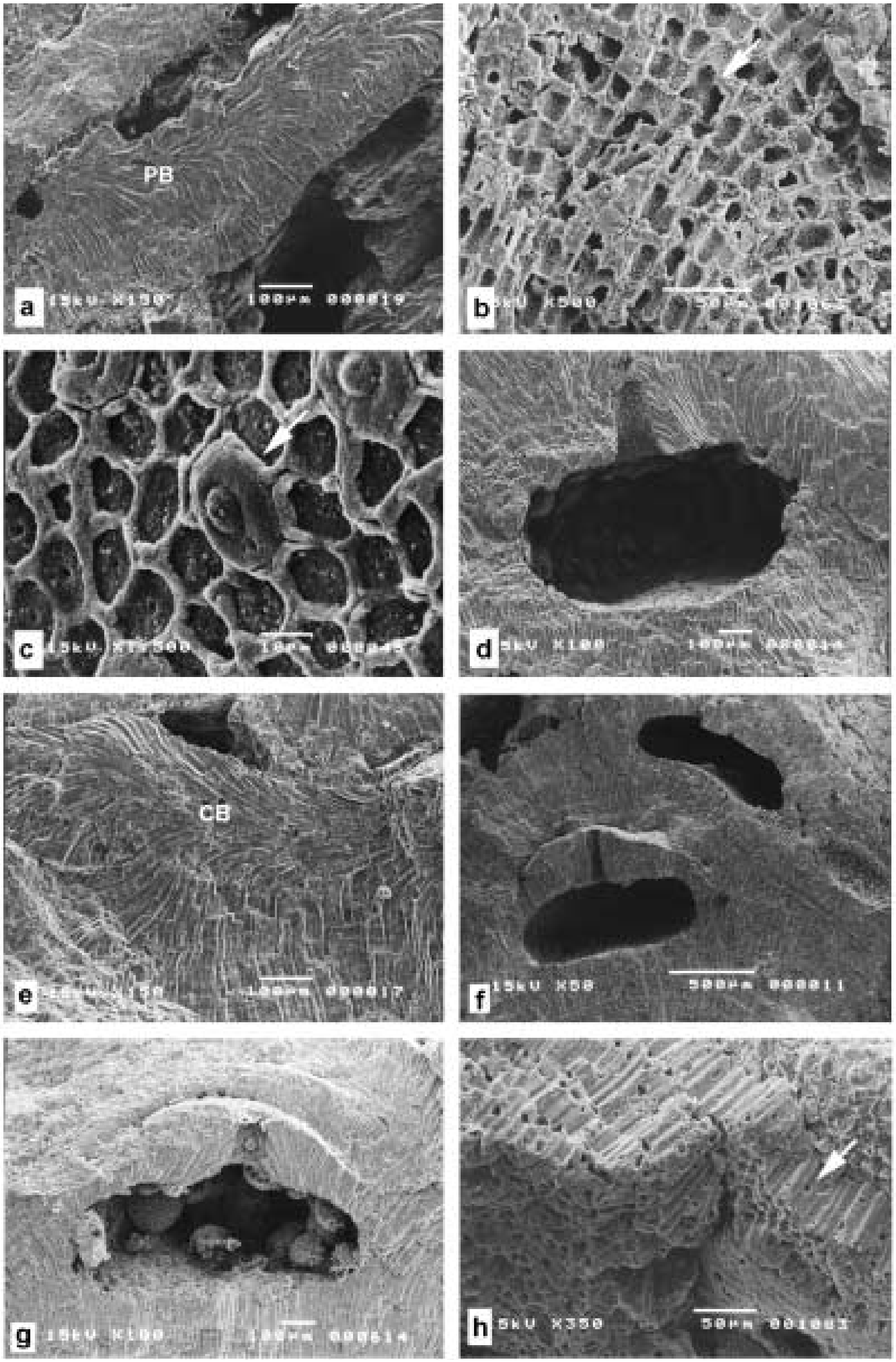

FIGURE 4–*Spongites fruticulosus* Kützing (a-d): plumose (PB) ventral region (a), cell fusions (b, arrow), trichocytes (arrow) and epithallial concavities, uniporate sporangial conceptacle (d). *Neogoniolithon brassica-florida* (Harvey) Setchell & Mason (e-f): coaxial (CB) ventral region (e), uniporate sporangial conceptacle (f). *Lithophyllum incrustans* Philippi: sporangial conceptacle (g). *Titanoderma pustulatum* (Lamouroux) Foslie; detail of palisade cells (h) showing secondary pit connections (arrow).

DISCUSSION

The presence of *Lithothamnion* on the framework of Prainha was not confirmed. It is likely that previous authors (Berthois, 1953a, b; Zbyszewski & Ferreira, 1961) used the term "Lithothamnium" in a general sense.

From the four species identified in the present study, only *Titanoderma pustulatum* is recorded for the recent algal flora of the Azores (Neto, 1994). However, given the identification difficulties of this group, the possibility that the remaining framework species are also present today should not be disregarded.

The main taxonomic problems of the present work concerned the distinction between *Neogoniolithon* and *Spongites*. According to Penrose (1992), the presence or absence of coaxially arranged cells in the ventral region of the thallus should not be regarded as a valuable feature to separate the two genera. Their differentiation should be made according to the distribution and origin of the spermatangia in the conceptacle chamber, and the origin of the gonimoblast filaments. However, these anatomical structures have very low preservation potential in the fossil record (Braga, 2003). In the absence of these characters, we have used the classical palaeontological criteria (see Braga *et al.*, 1993; Braga, 2003). Despite some differences in cell measurements, the Azorean material fits well with the literature descriptions.

The generic composition and specific depth zonation of coralline frameworks are typical for each place, and can be used to make palaeoecological inferences.

Adey (1986) described a general pattern for temperate and subtropical regions, in which the genus *Lithophyllum* dominates the shallow waters (above 10 m), tropical mastophoroid genera like *Neogoniolithon* and *Hydrolithon* occupy medium depth waters (10-50 m), and cold-water melobesioid genera like *Lithothamnion* and *Phymatolithon* are found in mid to deep water (below 50 m).

In tropical areas, mastophoroids are the main components in shallow water algal assemblages (Braga & Aguirre, 2001). The mastophoroid genera *Spongites* and *Neogoniolithon* predominate in the Neogene algal nodules that grew when the western Mediterranean was under tropical/subtropical climatic conditions. *Neogoniolithon brassica-florida*, can even be the main element locally, especially in the warmer southern and eastern regions of the Mediterrean (Adey, 1986). *Lithophyllum* species are subordinate but always present, while melobesioids tend to predominate in the deeper reef slopes.

The predominance of Mastophoroideae in the Prainha algal framework, and the absence of Melobesioideae, fits this tropical zonation pattern.

The irregular growth of the Prainha algal framework leave inter-skeletal spaces which are filled by contemporaneous particulate sediment and alochthonous material. This formation can be regarded as a filled frame reef, a type of skeleton-supported reef *sensu* Riding (2002).

Structures similar to the Prainha algal framework are not known to occur presently in the Azores. Their occurrence, however, is documented for other places, namely in the Mediterranean and West Atlantic (Thorton *et al.*, 1978; Bosence, 1983; Adey, 1986). According to these authors, coralline-algal frameworks develop on rocky substrate at shallow depths, forming flat calcareous patches that have an important role in the stabilization (cementation) of shore conglomerates. These formations develop primarily in seas with narrow tide amplitude (Adey, 1986).

This type of construction suggests an environment with moderate turbulence. Coralline formations that grow in low energy environment are characterized by having a reduced number of species and foliaceous structures, whereas the ones of higher energy environments are characterized by crusts of several species intimately overlapped or densely branched (Bosence, 1983). Moreover, the genera *Neogoniolithon* and *Lithophyllum* (moderately abundant on the Prainha framework) are typical of framewoks with moderate to high hydrodynamics (Steneck & Adey, 1976; Braga & Aguirre, 2001).

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