ORIGINAL ARTICLE

Paleoenvironment and taphonomy of lower Miocene bivalve and macroid assemblages: the Lagos Biocalcarenite (Lagos-Portimão Formation, southern Portugal)

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Abstract

Between Lagos and Albufeira, the Algarve coast of southern Portugal is marked by outcrops of the lower Miocene Lagos-Portimão Formation (LPF) consisting of yellow sandstone and coarse skeletal-rhodolithic limestone. This contribution focuses on the rhodoliths, their paleoecology, taphonomy, and biological composition, in the Lagos Biocalcarenite, the lower member of the LPF. Special attention is paid to the unusual occurrence of numerous rhodoliths nucleated around articulated bivalve shells, as well as to the nature of their biological interactions and taphonomic features. The calcareous algae of the rhodoliths (*Phymatolithon calcareum* and *Spongites* sp.) are commonly interlayered with thin bands of bryozoans and serpulids. Thick beds of non-nucleated spheroidal rhodoliths first appear at approximately 5–6 m above the base of the LPF as a result of a storm event that shifted rhodoliths in a shoreward direction. The bioeroded surface at the top of the Cretaceous Porto de Mós Formation, at the base of the overlying LPF succession, is a wave-cut platform representing the Miocene transgressive surface.

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Introduction

Along the western Algarve shoreline of southern Portugal, over a 45-km distance between Porto de Mós (in the west) to Albufeira (in the east), the lower-middle Miocene Lagos-Portimão Formation (LPF) of yellow bioclastic grain-rudstone and coarse skeletal-rhodolithic limestone is well displayed in coastal exposures. The stratigraphy of the coastal strata has been studied by Boucart and Zbyszewski (1940), Antunes et al. (1981), Cachão and Silva (1992, 2000), Antunes and Pais (1993), Cachão et al. (1998), Pais et al. (2012), and Terrinha et al. (2013). Sedimentary cycles in the Miocene succession have been described by Brachert et al. (2003), Forst (2003), and Pais et al. (2012). This study focuses on the basal section of the LPF with its abundant rhodoliths and the bioeroded basal rock surface at its contact with Lower Cretaceous marl and limestone of the Porto de Mós Formation, well-exposed at Canavial Beach near Lagos (Fig. 1).

The Lagos-Portimão rhodoliths, consisting of nongeniculate coralline red algae, have received little attention and are noteworthy for their unusual nucleation around articulated bivalve shells. The well-preserved material permits the first taxonomic considerations of the rhodolith-forming coralline red algae in the Miocene of Algarve. Further attention is given to the physical sedimentology, the nature of the biological interactions, and the consequent taphonomic features of the basal LPF rhodoliths. Emphasis is also given to the basal LPF stratal surface, which was a low-angle rocky paleoshore represented by an otherwise nearly featureless paraconformity. The existence of wave-cut platforms representing transgressive surfaces affected by bioerosion and marking the base of the Miocene successions in Portugal has been previously documented (Silva et al. 1999; Santos et al. 2008, 2010, 2016; Cachão et al. 2009), but the bioeroded surface developed on the Cretaceous Porto de Mós Formation at Canavial Beach is an excellent example of a wave-cut transgressive surface marking a major stratigraphic boundary (cf. Ghibaudo et al. 1996).

Geographic and stratigraphic setting

Outcropping along the southern coast of the Algarve, from Sagres in the west to Albufeira in the east (Fig. 1), the LPF unconformably overlies a variety of Mesozoic carbonate formations, ranging from Upper Jurassic in Sagres to Lower Cretaceous in Lagos (Pais et al. 2000, 2012; Terrinha et al. 2013). The basal part of the LPF, which is the focus of this study, is dominated by bioclastic
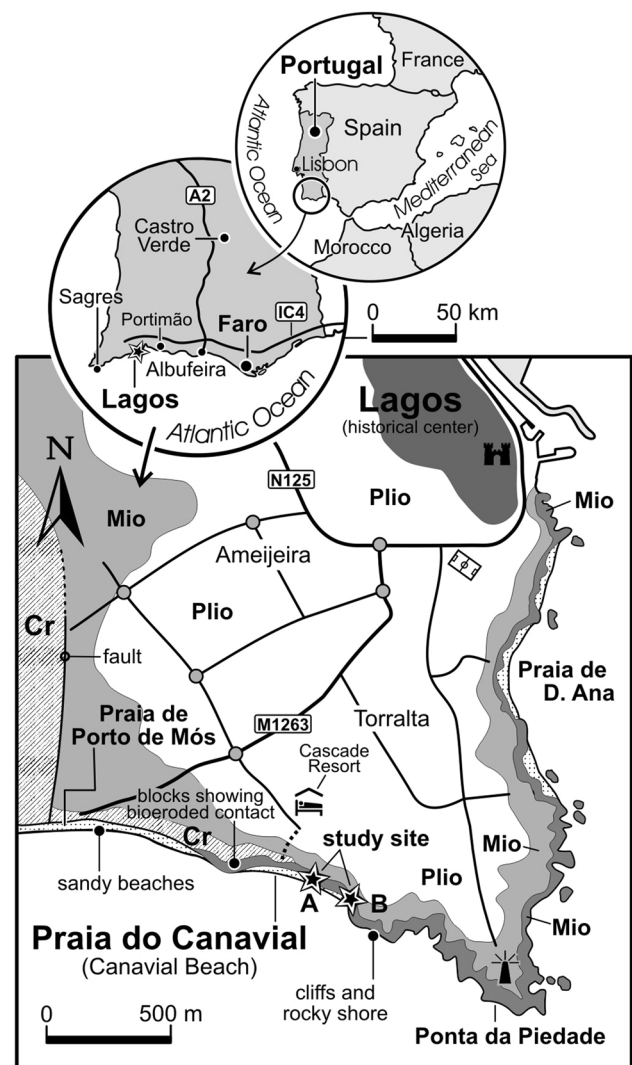

Fig. 1 Geographic location of the study area in Canavial Beach and simplified geological map of the Lagos area (Algarve, southern Portugal). Cretaceous Porto de Mós Formation (Cr), Miocene Lagos-Portimão Formation (Mio), Pliocene formations (Plio)

grain-rudstone. Measuring around 100 m in total thickness, the Miocene succession comprises the Lagos Biocalcarenite (Cachão 1995), corresponding to the lower member of the LPF of Antunes and Pais (1993) and Cachão et al. (1998). At Canavial Beach, the Lagos Biocalcarenite overlies the Porto de Mós Formation (the "Marly limestone of Porto de Mós", sensu Rey 1982), ascribed to the Aptian, Lower Cretaceous (Rey et al. 2006; Terrinha et al. 2013).

Antunes et al. (1981) and Antunes and Pais (1993) assigned the LPF to the Burdigalian, perhaps including the Langhian. Cachão and Silva (1992, 2000) and Cachão (1995) regarded it as Langhian to middle Serravalian (dating also adopted in Cachão et al. 2009 and Terrinha et al. 2013). Subsequently, Pais et al. (2000), suggested middle

Burdigalian to upper Serravalian. According to Pais et al. (2012), based on biostratigraphic data and $^{87}Sr/^{86}Sr$ isotopic age determinations, the sediments making up the strata of the LPF were deposited between the early Burdigalian, 19.5, $+0.2/-0.3$ Ma, e.g. at Arrifão, near Albufeira, and the late Serravalian, 12.2, $+1.2/-1.3$ Ma and 11.5, $+0.8/-0.5$ Ma at Praia da Rocha, 12 km east of Canavial. These same authors dated the bryozoan-rich limestone positioned 3.5–4.5 m above the base of the LPF in the Canavial section (see Log A in Fig. 3, herein) as 17.5 ± 0.7 Ma (upper Burdigalian).

The Lagos Biocalcarenite Member in the Lagos region forms a sharp paraconformity with the underlying, sparsely fossiliferous, Lower Cretaceous marl and limestone of the Porto de Mós Formation (Fig. 2) (Antunes and Pais 1993; Cachão 1995; Forst 2003; Pais et al. 2012; Terrinha et al. 2013). Locally, the basal section of the Lagos Biocalcarenite includes reworked marly limestone pebbles and boulders from the Lower Cretaceous Porto de Mós Formation. According to studies by Forst (2003), Brachert et al. (2003) and Pais et al. (2000, 2012) the sediments that today make up the LPF accumulated along a narrow shelf, influenced by frequent eustatic cycles resulting in synchronous facies variations over the platform.

Methods

Detailed logs were produced for the stratigraphic sections at Canavial. In addition to rhodoliths, other macroids and coated grains (sensu Hottinger 1983 and Baarli et al. 2012), shelly macrofossils and trace fossils (Santos et al. 2014) were recorded. Whole rhodolith specimens from specific stratigraphic intervals (see Fig. 3) were measured across three principal axes (long, intermediate and short). Data from these measurements were marked on a triangular plot among spherical, ellipsoidal, and discoidal shapes according to the format applied to rhodoliths by Bosence (1976, 1983a) as modified from Sneed and Folk (1958).

Vegetative and reproductive structures in the rhodoliths were identified from thin-sections and described following Braga et al. (1993), Irvine and Chamberlain (1994), and Rasser and Piller (1999). Terminology applied to growth forms follows that of Bosence (1983b) and Woelkerling et al. (1993). Cell and conceptacle dimensions were measured according to procedures described by Rasser and Piller (1999) using ImageJ software.

Fig. 2 Outcrop at Canavial Beach spanning the Cretaceous/Miocene boundary showing a paraconformity between Lower Cretaceous limestone and the bottom of the Lower Miocene Lagos Biocalcarenite. The dashed line traces the exposed boundary
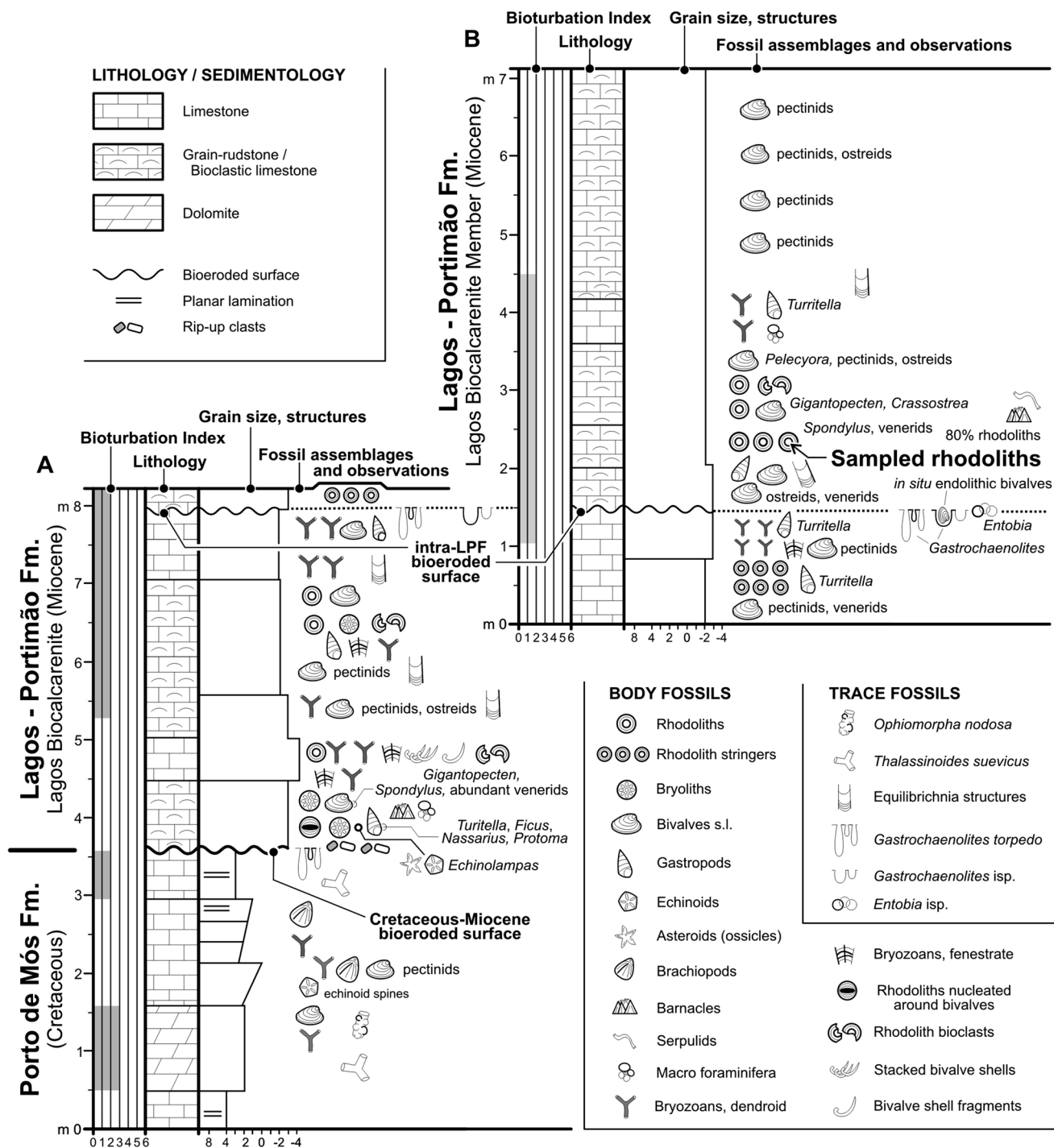
Fig. 3 Logs for stratigraphic sections at Canavial Beach: Log A, central sector of the beach exposing the contact separating the Cretaceous Porto de Mós Formation from the Miocene Lagos Biocalcarenite. Log B, southeastern end of the beach with better access to strata higher in the Miocene succession. Bioturbation Index after Taylor and Goldring (1993)

Results

Lagos-Portimão Formation stratigraphy in the Lagos region

Strata spanning the upper 3.5 m of the Cretaceous Porto de Mós Formation through the lower 10 m of the Miocene LPF at Canavial Beach are represented by graphic logs showing changes in lithology, sedimentology, and fossil content (Fig. 3). The location for Log A

(37°05′02.9″N;08°40′44.0″W) was chosen to meet the thickest available exposure of the Porto de Mós Formation beds near the central sector on the beach at Canavial. Log B (37°05′ 00.2″N;08°40′36.8″W) provided the thickest accessible section of LPF strata at the southeastern end of the beach. The Porto de Mós Formation at Canavial ranges from very fine-grained to fine-grained limestone and dolomite with a sparse fossiliferous content dominated by dendroid bryozoans. This is in marked contrast to the overlying, richly fossiliferous, coarse-grained grain-rudstone of the LPF.

Where visible, throughout the western sector of the southern coast of Algarve, the Mesozoic-Miocene contact is marked by an erosional transgressive surface corresponding to an extended wave-cut platform noted locally for bioerosion structures such as *Entobia* isp., *Maeandropolydora sulcans* Voigt 1965, *Gastrochaenolites* isp. and *G. torpedo* Kelly and Bromley 1984 produced by early Miocene endolithic organisms. That is the case for the Jurassic–Miocene contact in Sagres, 24 km west of Lagos (Silva et al. 1999; Santos et al. 2008), and the Cretaceous–Miocene contact at Arrifão, located near Albufeira, 35 km east of Lagos (Santos et al. 2008). Herein, this same circumstance is also reported and documented for the Cretaceous–Miocene contact at Canavial. However, due to poor exposure and preservation of the bioeroded surface, only *Gastrochaenolites* borings were detected (Fig. 4).

Scattered thin rip-up clasts of Cretaceous limestone of up to 7 cm in length are incorporated in the basal 0.1 m of Miocene grain-rudstone, together with scattered fragments of Miocene echinoid tests belonging to *Echinolampas*, as well as other bioclasts. However, no basal conglomerate is present. The basal grain-rudstone incorporates abundant bryoliths, loose rolling macroids formed by concentric growth of

bryozoans, and diverse gastropods belonging to the genera *Turritella*, *Protoma*, *Ficus*, *?Prozonarina*, *Nassarius*, and bivalves *Gigantopecten*, *Spondylus*, and abundant Veneridae indet.

The 0.5-m interval that commences approximately 0.2 m above the base of the LPF includes the first simple rhodoliths in the Miocene succession, but it is particularly noteworthy for abundant macroids and lumpy encrustations nucleated around molluscan bioclasts that commonly include articulated shells of venerid bivalves. A dozen such lumpy macroids may be seen in the 0.25-m² area shown in Fig. 5. Disarticulated valves of *Gigantopecten* and *Spondylus* are also present. The unique taphonomic history deciphered from the
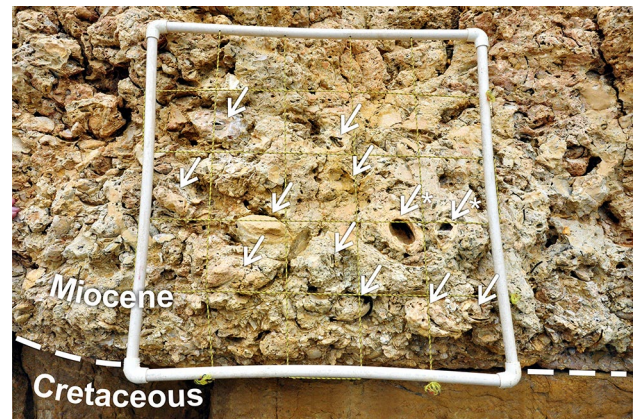

Fig. 5 Sample grid (0.25 m²) covering an interval from approximately 0 to 0.5 m above the base of the Miocene Lagos Biocalcarenite at Canavial Beach (Fig. 3a) with abundant articulated venerid bivalve shells fully encrusted by coralline red algae (white arrows). The macroids marked with an asterisk are depicted in detail in Fig. 7. Each square in the grid measures 10×10 cm
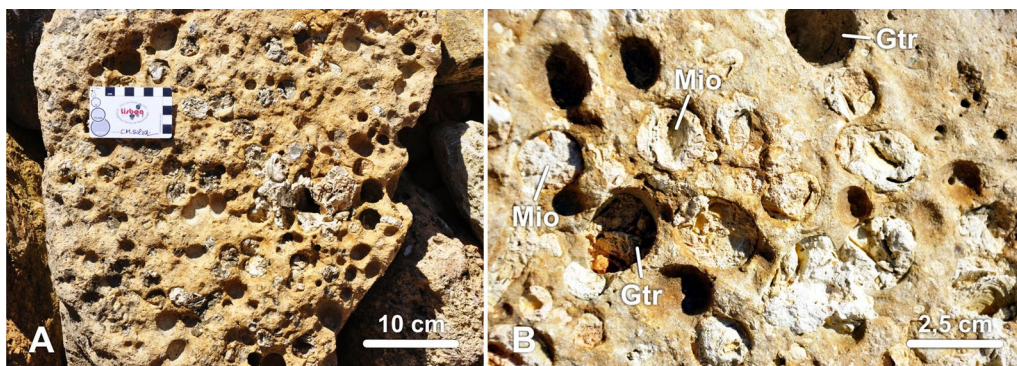

Fig. 4 The top of the Cretaceous Porto de Mós Formation at Canavial Beach (Algarve, Portugal) showing traces of Miocene bioerosion. **a** View of one of the many blocks showing the bioeroded top surface of the Porto de Mós Formation on the northwestern end of Canavial Beach. These blocks are the result of present-day cliff erosion and collapse (see Fig. 1 for location of the blocks). **b** Detail of the Miocene bioeroded surface cut in Lower Cretaceous Porto de Mós Formation limestone exposed in one of the above-mentioned blocks. Note the shallow *Gastrochaenolites torpedo* borings (Gtr), only the distal ends preserved, most of them filled with the light-colored Miocene bioclastic sediment (Mio) of the Lagos Biocalcarenite. This surface corresponds to the Cretaceous–Miocene contact surface marked in Log A of Fig. 3

fossils in this interval is the basis for one of two key topics of rhodolith paleoecology treated herein. The overlying 4 m of grain-rudstone and limestone that completes the section (Fig. 3, Log A) include mainly pectinid bivalves (commonly occurring as stacked, disarticulated valves), oysters, scattered rhodoliths, and dendroid bryozoans.

As a result of a gentle eastward dip of the Miocene strata, overlapping strata from the section at the southeastern end of the beach (Fig. 3, Log B) are readily correlated with the preceding section (Fig. 3, Log A) by means of a distinctive break forming an intra-LPF paraconformity, traceable over the 150-m distance that separates the two sections. This break (see Log B, Fig. 3) is marked by yet another bioeroded surface showing traces of *Entobia* isp. and *Gastrochanolites* isp., some of the latter showing in situ body fossils of the boring bivalves responsible.

A dense accumulation of rhodoliths occurs within an interval between 0.75 and 1.25 m above the break (Log B, Fig. 3). Through correlation by physical stratigraphy, this interval is equivalent to a level starting about 5–6 m above the base of the LPF. The transition from a mainly bryozoan limestone to a molluscan grain-rudstone and a rhodolith rudstone is abrupt (Fig. 6a), marked by the above-mentioned sharp, locally bioeroded surface (Fig. 6b). This rhodolith rudstone represents the first appearance of abundant rhodoliths in the LPF succession in southern Portugal. Stringers of rhodoliths and scattered rhodoliths, in addition to pectinid bivalves, scattered oysters and dendroid bryozoans, commonly occur in overlying strata.

Taphonomic relationships

Within the stratigraphic interval between approximately 0.2 m and 1 m above the base of the LPF, it is possible to identify the venerid and pectinid bivalves discussed herein only at family level due to poor preservation and reduced exposure (Fig. 3). Possessing a mostly calcitic shell, pectinids are preserved as the original shell, whereas venerids, which mostly have aragonitic exoskeletons, are present as internal casts and external moulds. The latter commonly appear as casts of the external surface of the shell left on the inner surface of the rhodolithic crust around the dissolved bivalve. The void where the venerid bivalve shell formerly existed may be as much as 5 cm in diameter and the maximum algal crust surrounding such a void is 1.5 cm in thickness (Fig. 7). Pectinid valves commonly are found encrusted, but unlike venerids from the same horizon none are articulated. The scenario under which the Canavial

Fig. 7 Examples of macroids (marked 1 and 2) 0.2 m above the base of the Miocene Lagos Biocalcarenite at Canavial Beach (see Fig. 5). The example on the left (number 1) shows a void with the external mould of an articulated venerid bivalve that retains the shell's growth lines beneath a thick rind of encrusting coralline red algae. The example on the right (number 2) is less clear but shows partial filling by sediment at the center of the encrustation (see Fig. 8 for taphonomic interpretation)
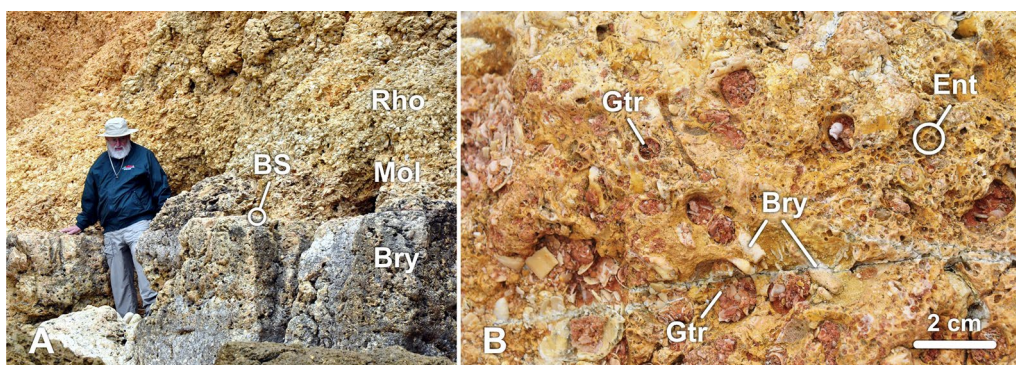

Fig. 6 The Lagos Biocalcarenite at the southeastern end of Canavial Beach, approximately 4–7 m above the base (see log in Fig. 4b). **a** Erosional transition from a bryozoan limestone (Bry) to a molluscan grain-rudstone (Mol) and, above, to a rhodolithic rudstone (Rho) marked by a sharp, intra-LPF bioeroded surface (BS). **b** Detail of the intra-LPF Miocene bioeroded surface carved on the top of the bryozoan limestone bed (remains of dendroid bryozoans, marked Bry) in that same location, showing abundant traces of *Entobia* isp. (Ent) and *Gastrochaenolites* isp. (Gtr) borings filled with reddish bioclastic sediment of the overlying grain-rudstone
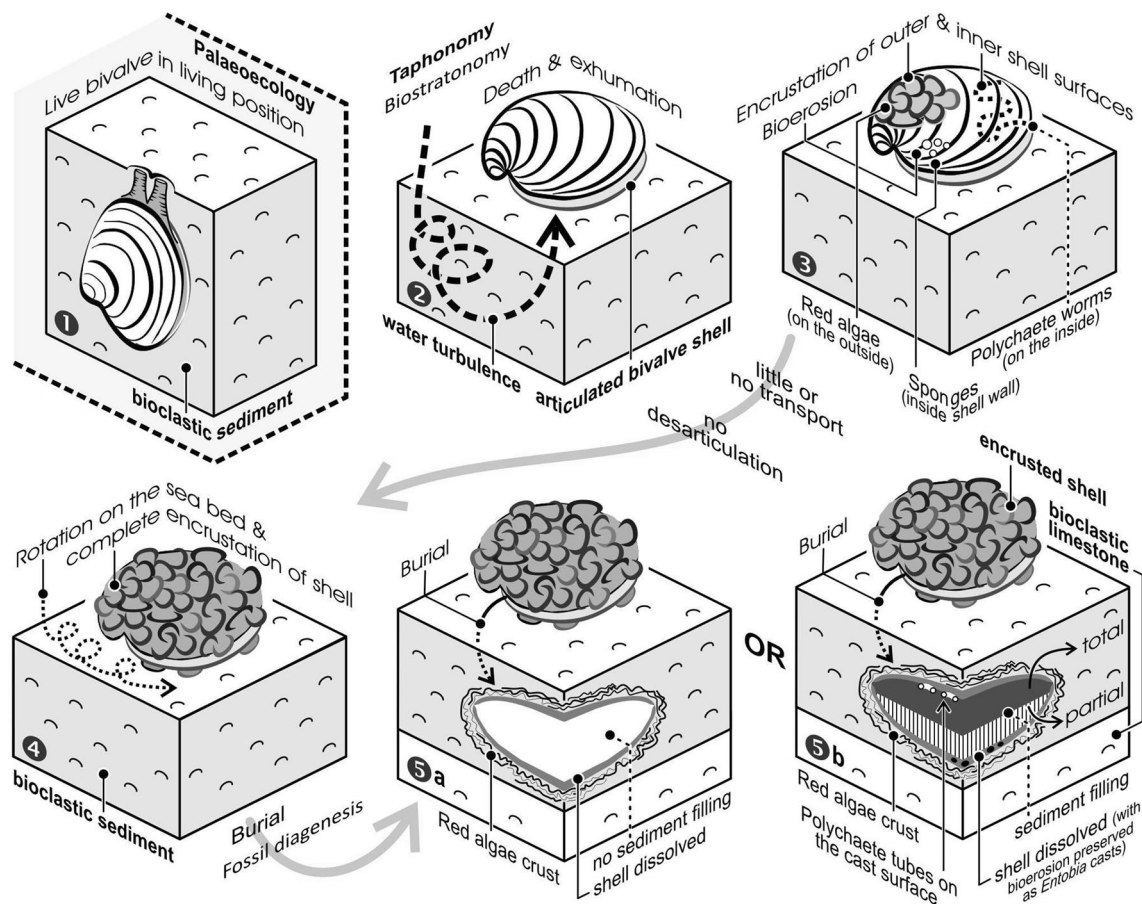
Fig. 8 Interpretative diagram illustrating the taphonomic evolution of Miocene strongly hinged venerid bivalve shells that become disinterred from their original endobenthic habitat and eventually reburied, articulated, after complete encrustation at the surface by coralline red algae

venerids lived and subsequently passed through a post-mortem history marked by the activity of various epibionts is illustrated in Fig. 8 that highlights different taphonomic stages, as discussed further below.

Rhodolith paleoecology

About 5–6 m above the base of the LPF (approximately 0.7–1.25 m above the intra-LPF bioeroded surface marked in Log B of Fig. 3), a 0.5-m-thick bed with abundant rhodoliths makes an abrupt appearance above bioclastic limestone containing pectinid, venerid, and ostreid bivalves, but devoid of rhodoliths. In general, rhodoliths within this 0.5-m-bed range between 4 and 5 cm in diameter and are formed of coralline red algae with a laminar concentric morphotype and, more commonly, branching with protuberances. Gastropod fragments occur scattered between these rhodoliths, but the overall density of rhodoliths accounts for as much as 80% of the bed by volume; there is no internal layering. Except for a barnacle, no other encrusting organisms were observed on the exterior surfaces of the rhodoliths. Based

on a sample of 81 rhodoliths, shape analysis (Fig. 9) shows that 40% fall within the top triangular tier denoting a highly spheroid shape, whereas another 40% fall into the middle section of the tier directly below. The linear trend in plotted points shifts slightly to the lower right, suggesting a very minor tendency toward ellipsoidal shapes in a small portion of the sample. All rhodoliths from this sample were broken on site in order to determine the type of nucleation. No evidence for rock clasts or macroscopic bioclasts (e.g., molluscan) was discerned at the center of the rhodoliths, nor were seen in thin-sections.

Systematic paleontology

In view of the good preservation of some of the specimens collected at Canavial Beach, it has been possible, for the first time, to identify the coralline red algae in the LPF rhodoliths from thin-sections. Rhodolith-forming coralline algal growth forms present in the investigated specimens vary from encrusting to warty and lumpy textures. The
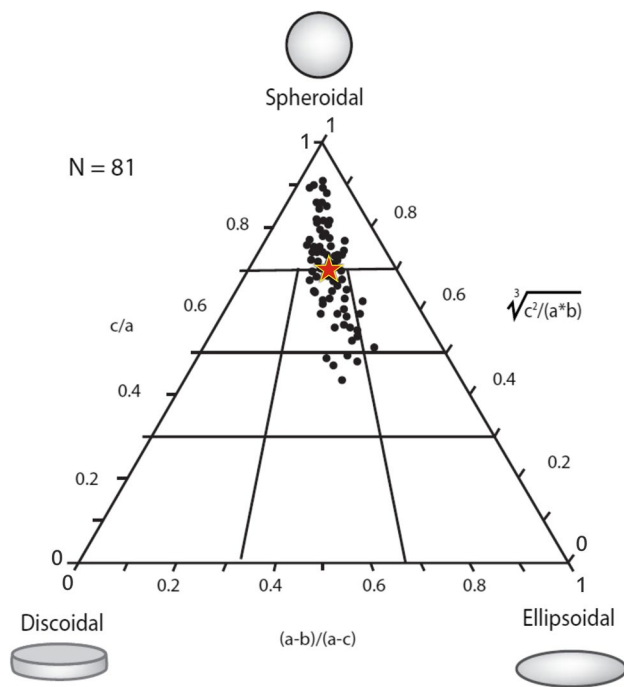
Fig. 9 Triangular plot showing the relative trend in shapes of rhodoliths from the molluscan rhodolith rudstone bed positioned between 0.75 and 1.25 m above the intra-Miocene Lagos Biocalcarenite, bioeroded surface at the southeastern end of Canavial Beach (see Log B in Fig. 3, sampled bed marked). The red star shows the composite shape of a rhodolith based on the average dimensions in three axes for the 81 rhodoliths measured

examined macroids are multi-specific, and formed by thin laminar crusts of coralline algae. Poorly preserved bryozoans and serpulids are also interspersed within the coralline thalli. The sediment within the rhodoliths differs from the surrounding sediment (Fig. 10). In contrast with the overall poor preservation of the rhodoliths found in the lower beds of the LPF, namely the ones enclosing articulated bivalve shells, the good preservation of specimens from the bed 5–6 m above the base of the LPF (approximately 0.7–1.25 m above the intra-LPF bioeroded surface marked in Log B of Fig. 3) has allowed the first taxonomic treatment of the rhodolith-forming coralline red algae in the Miocene LPF of the Algarve. Specimens belonging to the genera *Phymatolithon* and *Spongites* were identified. The subfamily attribution of *Spongites* is still under revision (Rösler et al. 2016), therefore a subfamily assignment for this genus is not given here.

Order Corallinales Silva and Johansen (1986).

Family Hapalidaceae Gray (1864).

Subfamily Melobesioideae Bizzozero (1885).

Genus *Phymatolithon* Foslie (1898).

Diagnosis: Crustose to bushy thalli composed completely of branches and protuberances. The thallus is dorsiventral and monomerous; the core filaments are non-coaxial; epithallial cells are rounded or flattened but not flared, and subepithallial initials are as short or shorter than underlying cells (Irvine and Chamberlain 1994; Rasser and Piller 1999; Iryu et al. 2012).

Phymatolithon calcareum (Pallas) Adey and McKibbin (1970) ex Woelkerling and Irvine (1986) (Fig. 10a, c).

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: Varying from encrusting to lumpy.

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 98 μm to 7.18 mm in thickness; the core itself is 30–60 μm and the peripheral filaments 50–125 μm. Epithallial cells are rounded and flattened, but not flared.

Reproductive features: Several tetra/bisporangial multiporate conceptacles, irregularly distributed in the thallus, with only a few pore canals visible. The conceptacle shape varies from more or less circular to large rectangles with rounded corners. Height 105–250 μm, diameter 400–565 μm. Thickness of roof 30–95 μm, conceptacle pore diameter 60–65 μm. Above some conceptacles there is a concavity void with a more or less triangular shape that is formed after spore release by the overgrowth of the perithallial filaments delimiting the conceptacles.

Remarks: Phymatolithon calcareum was identified based on the type and size of conceptacles and the presence of flat, rounded, but not flared epithallial cells.

Family Corallinaceae Lamouroux (1812).

Genus Spongites Kützing (1841).

Diagnosis: The thallus organization is dimerous or monomerous non-coaxial. The dimerous thallus lacks a basal layer of palisade cells. The filaments around the conceptacle pore canals are subparallel to the roof surface (Penrose
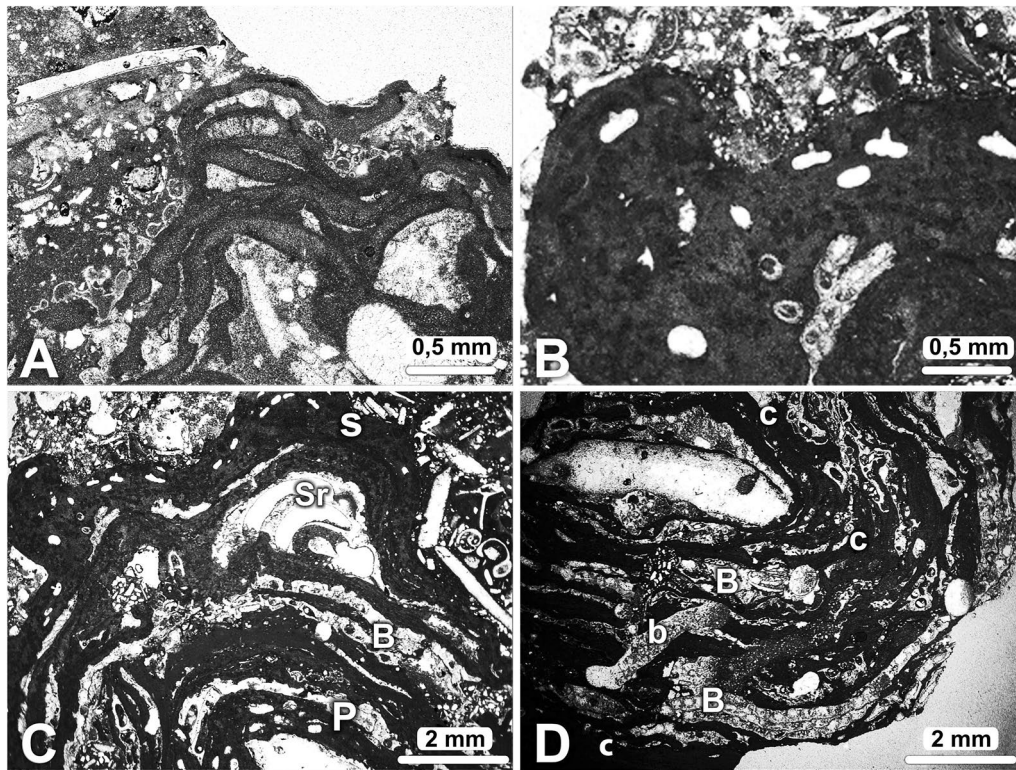
Fig. 10 Taxonomic aspects related to rhodoliths. **a** Thalli of *Phymatolithon calcareum*. **b** Thalli of *Spongites* sp. with lumpy protuberances. **c** From the core to the outer surface: *P. calcareum* (P), bryozoans (B), serpulids (Sr), and *Spongites* sp. (S). **d** Encrusting bryozoans (B) interspersed in the coralline thallus (c) and borings (b)

and Woelkerling 1992; Braga et al. 1993; Rasser and Piller 1999).

Spongites sp. (Fig. 10b, c).

Growth form: Varying from encrusting to lumpy.

Vegetative features: Thallus organization is monomerous non-coaxial. The thallus thickness ranges from 320 to 435 μm. The core filaments curve upwards to become perpendicular to the dorsal surface in the peripheral region. Cells of adjacent filaments are fused.

Reproductive features: Only uniporate conceptacles are present; they are bean to flask-shaped. Height 80–100 μm, diameter 195–235 μm. Thickness of roof 60–75 μm, conceptacle diameter 55–60 μm. Filaments around the conceptacle pore canals are subparallel to the roof surface. In some conceptacles, it is possible to observe a columella.

Remarks: Rösler et al. (2016) recently assigned the genus *Spongites* to the Neogoniolithoideae subfamily. Neogoniolithoideae comprises those corallines with non-geniculate, monomerous, or thin dimerous thalli, primigenous filaments without palisade cells, and trichocytes present (Rösler et al. 2016). The genus *Spongites* was identified based on the filaments surrounding the conceptacle pore canals being subparallel to the conceptacle roof. The species could not be identified as there were no visible trichocytes.

Discussion

Particular attention is given to the level of hydrodynamic energy absorbed by the low-relief rocky shore and the resulting erosion represented by the contact surface between the Porto de Mós Formation limestone and the basal Lagos Biocalcarenite (LPF), at Canavial, and the taphonomy of articulated venerid bivalve shells and rhodoliths.

Depth and water dynamics

Miocene bioerosion at the LPF basal surface is represented by the prolific trace fossils *Gastrochaenolites* isp. and *G. torpedo* (Fig. 4), easily observed in blocks of Porto de Mós limestone at the northwestern end of Canavial Beach, at the transition into Porto de Mós Beach (see location of the fallen blocks in Fig. 1, coordinates 37°05′02.55″

N; 08°40′50.71″ W). The absence of other bioerosion structures and the lack of in situ remains of Miocene epilithobionts on the top surface of the Porto de Mós Fm. is attributed to strong hydrodynamic erosion in a shallow near-shore rocky coastal marine environment, as was in the case of the Oura intra-Miocene bioeroded surface at Albufeira. The bioeroded surface itself is interpreted as a wave-cut platform having been formed in a transgressive context as suggested by the abundant presence of *G. torpedo* structures (see also Cachão et al. 2009 and Santos et al. 2016). This ichnoassemblage produced by shallow-marine endolithic, suspension-feeding bivalves is assigned to the *Entobia* subichnofacies (Bromley 1994) as a subdivision of the *Trypanites* ichnofacies (Frey and Seilacher 1980), marking a transient state from a foreshore setting to shallow-water subtidal conditions (see also Santos et al. 2010).

In addition, rip-up clasts and marl pebbles derived from the Lower Cretaceous Porto de Mós Formation were redeposited in directly overlying Miocene strata. Scant insight on water depth comes from gastropods present in the basal half meter of the Lagos Biocalcarenite, including the Turritellidae and Cypraeidae. Turritellid gastropods are common Cenozoic marine invertebrates and comparisons with living animals indicate that they commonly live in water depths less than 10 m, although more broadly they inhabit water depths less than 150 m (Allmon 1988). Much the same in terms of habitat depth may be said for the living cowries (Moretzsohn 2014), although many species live in shallow waters among corals in tropical settings.

The laminar to branching structures of the rhodoliths found in these beds are characteristic of moderate to high-energy environments (Quaranta et al. 2012). Although the rhodoliths show a reduced number of coralline red algal species, their multi-biological construction and the dense branching suggest they were formed in moderate-energy environments (Bosence 1983a). Genera *Phymatolithon* and *Spongites* identified in LPF rhodoliths higher in the succession are typical of shallow-water environments (Braga and Aguirre 2001; Checconi et al. 2010).

Bryoliths are more abundant in the basal half meter of the Lagos Biocalcarenite, and as such suggest that wave agitation at or above normal wave base was persistent. Bryoliths and turritellid gastropods do reappear at higher levels in the Lagos Biocalcarenite, but nowhere as abundantly as in the basal half meter. Moreover, the complete absence of coral remains in these beds combined with the proliferation of coralline red algae further suggests a high-productivity marine setting probably triggered by coastal upwelling similar to that occurring today along the eastern Atlantic, at lower latitudes, off West African coasts for example, with a similar E–W orientation, there influenced by the Guinea current (Bakun 1978; Chukwuone et al. 2009; Lamptey 2015).

Bivalve taphonomy

Approximately 0.2–0.3 m above the base of the Lagos Biocalcarenite, the scenario shifts from abundant bryoliths to abundant rhodoliths nucleated around reworked pectinid and, surprisingly, around fully articulated venerid bivalve shells (Fig. 7). Notably, there are no published references to abundant fully encrusted closed articulated bivalve shells comparable to the Canavial examples in either the biological or paleontological literature. Gutowski (1984: pl. 2, fig. 4) and Pisera and Studencki (1989: pl. 3, fig. 5) both illustrated a Badenian Miocene rhodolith from the Korytnica Basin, Poland, that had nucleated around an articulated bivalve preserved as an internal cast and external mould of the shell. However, no information is given on the paleoecological or taphonomic context of this occurrence.

Adult pectinids show a diversity of epibenthic life habits that range from sessile, cemented to the substrate, to "swimming", with byssally attached, nestling and free-lying intermediate forms between these extremes (Alejandrino et al. 2011). These bivalves have disodont toothless hinges. Their shells are prone to disarticulation once the ligament deteriorates. Epifaunal life habits also favor post-mortem disarticulation of pectinid shells. In contrast to the epibenthic pectinids, the venerids are mostly endobenthic and subject to transport and disarticulation only after exhumation. Venerids are heterodont bivalves hinged with strong teeth and paired sockets; their shells are more resistant to disarticulation after death. Articulated venerid bivalves sometimes occur preserved in their original life position, but this clearly is not the case here because of the many lumpy macroids that encase the Canavial "ghost" venerids.

The life behavior of such bivalves is infaunal, with siphons for feeding and oxygenation reaching to the sediment–water interface (Fig. 8, stage 1). For the shell to become fully encrusted by epifaunal organisms (Fig. 7), the venerid bivalve had to have perished and its articulated shell become exhumed from the substrate, or vice versa (Fig. 8, stage 2). At some point after exhumation, the animal clearly had expired, and its soft parts decayed away because the inner surface of the articulated shell became accessible for colonization by such organisms as serpulids and bryozoans, while at the same time the shell's outer surface was available for initial colonization by clionaid sponges and encrusting coralline red algae (Fig. 8, stage 3).

Full encrustation by coralline red algae around all outer surfaces of the venerid shell depended on continual rotation of the shelly nucleus of the rhodolith. This rotation, caused by water agitation or biogenic action, should be steady enough to ensure the even growth of the algal rind found in the examined specimens (Fig. 8, stage 4). Burial of the shell-encasing rhodolith was the next step (Fig. 8, stage 5a). Under one scenario, the closed articulated bivalve shell

would be totally overgrown and little or no sediment entered the shell void from the outside and the aragonitic shell eventually dissolved. External bivalve moulds preserved within the rhodoliths are more commonly represented in the studied bed from the lower Miocene section at Canavial.

Sturdy mechanical articulation of venerid valves kept them almost fully shut. During the earlier phase of exposure at the substrate surface (Fig. 8, stage 3), encrustation by coralline red algae was incipient. The fact that at least part of the shell surface remained bare made it possible for endolithic organisms such as clionaid sponges to colonize the outer surface prior to the arrival of coralline red algae. Evidence of sponge colonization is preserved as internal casts of *Entobia* borings in the space between the inner and outer casts on the inside of the rhodolith only, as a result of dissolution of the shell (Fig. 8, stage 5b). The infestation by clionaid sponges, as recorded in similar occurrences by Bromley (1994), testifies to a low or null sedimentation rate in the local marine setting and to the fact that at least a significant part of the external shell surface was kept free from encrusting skeletobionts for some time.

In cases where the algal crust was incomplete with a gap still existing between the valves after burial, the shell was partially or completely filled with sediment, ultimately generating an internal cast (Fig. 8, stage 5b). In this scenario, the fossilized remains of crypto-colonists are preserved on the surface of the internal mould and the bioerosion of those valves would become visible as *Entobia* internal casts in the void between the internal and the external moulds of the shell where former aragonitic valves once existed.

Based on available evidence, it is difficult to decide whether the venerids died prior to exhumation or at some point afterwards. Death may have occurred as a result of exhumation, but if the bivalves were alive at the surface, why were they unable to burrow back into the substrate? The Canavial venerids may have had a low capability to orient themselves and re-burrow, as in the case of the freshwater bivalve *Corbicula largillierti* (Philippi 1844) as discussed in Kotizan and Simões (2006). In another example of exhumation and death of bivalves, Zamorano et al. (1986) reported that once the Antarctic infaunal marine bivalve *Laternula elliptica* (King 1832) becomes exposed by iceberg action, the animal's return into the sediment is hindered by difficulties that include substrate compactness and burrowing bivalve density in the sediment. After exhumation, *L. elliptica* is an easy target for durophagous animals, mainly crabs, and non-durophagous predators such as starfish, soon followed by scavenger worms and gastropods. Similar circumstances may explain the high number of empty articulated shells on the sediment surface, as well as abundant bioclasts. This type of predation affects only those bivalves injured as a result of the exhumation process. Zamorano et al. (1986) reported that most *L. elliptica* bivalves exhumed (circa 60%)

successfully managed to burrow back into the sediment. In regard to the Canavial scenario, it should be noted that isolated marginal ossicles of Astropectinidae starfish are common in the studied bed. *Astropecten* starfish are voracious epibenthic predators, feeding mainly on bivalves and gastropods (Baeta et al. 2016).

Another factor difficult to appraise based on available evidence is the length of time elapsed between the death of the Canavial venerid bivalves and extensive encrustation by coralline red algae. Although there is no clearly determined relationship between the growth form and age of coralline algae (Rivera et al. 2004), several studies (Adey and McKibbin 1970; Adey and Macintyre 1973; Bosence 1983b; Reid and MacIntyre 1988; Littler et al. 1991) have shown that independently of water temperature and depth, non-geniculate coralline algae always grow slowly, ≤ 1 mm per year.

As described in the Results section, colonization of the bivalve shells by boring Clionaidae sponges with access both to internal and external shell surfaces occurred prior to extensive encrustation by coralline red algae. Infestation by clionaid sponges also testifies to a low to null sedimentation rate (Bromley 1994) in the Miocene Canavial shallow-marine environment and to the fact that at least a significant part of the external surface of the shell was free from encrusting skeletobionts for some unknown interval of time. Based on studies in contemporary settings, that interval could have lasted from about 10 months up to 2 years, the average time needed for endolithic organisms to colonize carbonate substrate and produce a significant bioerosion sculpture (Tunnicliffe 1982; Bromley et al. 1990; Bromley and Asgaard 1993; Bromley 1994). Other bivalve bioclasts preserved in the same bed but at a different locations at Canavial Beach, between Log A and Log B, show infestation by clionaid sponges in the form of extensive *Entobia* borings. The resulting *Entobia* ichnofacies suggests long colonization windows in stable substrates in shallow-water near-shore environments under a low sedimentation rate, particularly in relation to hard substrates such as the ones found in shelly or rocky shore settings (de Gibert et al. 1998, 2007; Santos et al. 2010; Ávila et al. 2015). On the other hand, according to Nebelsick et al. (1997), the full encrustation of exhumed endobenthic *Ova canalifera* (de Lamarck 1816) [= *Schizaster canaliferus*] echinoid tests by an array of epibionts, including colonial zoantharians, colonial ascidians, serpulids, red algae, and barnacles, in the present-day Adriatic Sea could take as much as 20 months.

To some degree, the encrusted Canavial venerid bivalve shells remain a paradox. On the one hand, the fact they are articulated shows they were not subject to destructive mechanical wear on account of extensive, post-mortem transportation. On the other hand, the fact that articulated shells are entirely overgrown by coralline red algae in the form of a sizable rhodolith demonstrates that the

macroids experienced some degree of ongoing rotation over a prolonged period of time. The encrustation pattern lacks asymmetry (no distinct preference for encrustation on one side versus the other), showing that the macroid was regularly being overturned. One should not discard the possibility of these bivalve-nucleated macroids being moved by biogenic action. Nebelsick et al. (1997) reported that in present-day marine environments in the Adriatic Sea, fresh, cleaned bivalve and gastropod shells were manipulated, overturned, and dispersed by crabs, starfish, and holothurians. Marrack (1999) showed that in the Gulf of California, biological action is an important mechanism for rhodolith movement. In addition to echinoids, gastropods, and sea cucumbers, she also reported the bioturbation activity of fish. Brandano and Piller (2010) also stressed the role of grazing echinoids in overturning rhodoliths. The same may have occurred with the Canavial macroids.

In summary, the dynamics of wave turbulence in what was a very shallow, near-shore setting typical of the *Entobia* ichnofacies with low or null clastic sedimentation was necessary for both the initial disinterment of venerid bivalves but also for their eventual, complete encrustation as articulated shells by coralline red algae. In the Canavial area, during Miocene times, exhumed articulated bivalve shells became substrates of intermediate longevity, exposed at least 1–2 years, stable enough to support a differentiated, although not very diverse, endolithic and encrusting community dominated by clionaid sponges and red coralline algae.

Teichert (2014) described modern rhodoliths from Svalbard, which are hollow due to bioerosion by the boring bivalve *Hiatella arctica* (Linnaeus 1767). As a result, the originally compact rhodoliths become ecospheres open to the outside and so intensely colonized by benthic organisms. In one example (Teichert 2014: fig. 1D), an Iceland scallop *Chlamys islandica* (Müller 1776) is present nestling within one of these hollow rhodoliths. In this case, the hollow algal nodules serve as micro-caves that shelter a variety of organisms, gastropods, crustaceans, and polychaetes, as well as the scallop and other bivalves.

In the Miocene beds of Canavial, there are abundant remains of pectinid shells, some of them acting as the core of rhodoliths, but none are articulated. In the present-day Svalbard case, the scallop does not fit through the rhodolith opening, being literally trapped inside the nodule. This circumstance suggests an occupation of the hollow rhodolith in an early life stage of the bivalve, maybe even during its larval phase. However, the rhodolith does not actually overgrow the pectinid shell, adhering to it. Furthermore, the Canavial Miocene hollow rhodoliths formed post-mortem, after the burial of the algal nodules, as a result of dissolution of the bivalve shell, which acted as the nucleus of nodule.

Accumulation and remobilization of the rhodolith deposits

Rhodoliths may be divided into those with a rock core and those lacking a rock core (e.g., Bosellini and Ginsburg 1971; Aguirre et al. 2017), but with a nucleus of a tiny rhodolith fragment or other bioclast. Rock cores in fossil rhodoliths may markedly differ in size, largely as a function of proximity to a rocky shoreline with cobbles and pebbles (Johnson et al. 2016a, b). For example, basalt cores at the center of Miocene rhodoliths from the volcanic paleoshore at Pedra de Água on Ilhéu de Cima off Porto Santo (Madeira Archipelago, Portugal) are unusually large: up to 3.5 cm in diameter in a 5-cm rhodolith (Santos et al. 2012). In this case, the rhodoliths are preserved in a thin bed directly adjacent to the paleoshoreline. Rhodoliths with an equally large exterior diameter but lacking an internal rock core may be transported shoreward across a volcanic shelf ending in a supratidal setting (Johnson et al. 2016a, b). In that case, the assumption is made that the rhodoliths accreted in deeper waters beyond the source of cobbles and pebbles. In fact, no basal conglomerate exists in the Lagos Biocalcarenite and the few rip-up Cretaceous limestone clasts present are not significantly rounded. Regardless, the fact remains that in the basal layers of the studied section rhodoliths accreted around bioclastic cores provided by articulated venerid shells, as well as by scattered valves and bioclasts of other bivalves, namely pectinids. There is no evidence that Miocene rhodoliths nucleated around limestone clasts eroded from the underlying Lower Cretaceous Porto de Mós Formation at Canavial.

The depositional setting changed, however, at a point recorded in the stratigraphic succession starting about 5–6 m above the base of the Lagos Biocalcarenite (about 0.7–1.25 m above the intra-LPF bioeroded surface marked in Log B of Fig. 3). It is at this level both stratigraphically and in terms of facies that rhodoliths lacking cores of any kind first accumulated in substantial volume. Overall, the rhodolith samples from this bed, based on the interpretation of the shape analysis given in Fig. 9, are consistent with a scenario that suggests high mobility and transport under wave or bottom current action (Johnson et al. 2016a, b). The multi-species composition of these rhodoliths, with *Phymatolithon calcareum* and *Spongites* sp. inter-layered with encrusting bryozoans and serpulids, indicates that accretion took place piecemeal during a discontinuous history over a relatively lengthy stretch of time.

Based on the taphonomic model developed by Johnson et al. (2016b), rhodoliths are especially vulnerable to remobilization by storms and currents leading to accumulations of thick deposits in a range of subtidal to supratidal settings in banks, bars, and berms. Those rhodoliths at the bottom of the half-meter-thick deposit would have been deprived

of sunlight and been unable to survive. Taking into account the absence of internal layering within the deposit, it may be argued that it formed during a storm event that selectively transported the most spherical rhodoliths in a more landward direction.

The extraordinary rhodoliths that accreted around articulated venerid bivalve shells lower in the succession are absent higher in the section, although non-nucleated rhodoliths of the kind that first appeared approximately 5–6 m above the base of the formation made numerous reappearances in substantial deposits elsewhere (e.g., Brachert et al. 2003), probably under similar conditions.

Conclusions

Four major results are reached regarding the Lagos Biocalcarenite, the lower member of the lower Miocene Lagos-Portimão Formation in southern Portugal, and the contact surface separating this and the underlying Lower Cretaceous limestone of the Porto de Mós Formation at the Canavial Beach:

1. Wave action directed against an early Miocene rocky shore cut into Lower Cretaceous limestone is recorded by a bioeroded marine wave-cut platform, representing a transgressive surface that today marks the Lower Cretaceous Porto de Mós Formation/Miocene Lagos-Portimão Formation boundary in the Lagos region (Southern Portugal).
2. Within the first 0.2 to 0.7 m of the basal Lagos Biocalcarenite, thick crusts of non-geniculate coralline red algae commonly occur upon articulated venerid bivalve shells. The environment must have been sufficiently energetic to first disinter the bivalves from their infaunal habitat, and thereafter to maintain prolonged and consistent overturning, probably aided by the action of bioturbating organisms, enabling even accretion of coralline red algae through protracted time. No other example of common articulated bivalve shells as the center of biological accretion by coralline red algae is currently known from the paleontological or biological literature.
3. Thick beds of red algal macroids without discernible rock or bioclastic nuclei first appear at approximately 5–6 m above the base of the Lagos Biocalcarenite, likely generated by a storm event that shifted highly spheroidal rhodoliths in a shoreward direction. Comparable rhodolith deposits reappear in parts of the succeeding Miocene section interspersed with shelly deposits dominated by pectinid bivalves and diverse shelly fragments.
4. For the first time, it has been possible to identify coralline red algae in some of the Miocene Lagos-Portimão Formation rhodoliths: *Phymatolithon calcareum* and

Spongites sp. In these rhodoliths, coralline red algae are interlayered with thin bands of bryozoans and serpulids that accreted in a discontinuous fashion over a protracted time prior to burial.

References

Adey WH, McKibbin D (1970) Studies on the maerl species *Phymatolithon calcareum* (Pallas) nov. comb. and *Lithothamnion coralloides* Crouan in the Ria de Vigo. Bot Mar 13:100–106

Adey WH, MacIntyre IG (1973) Crustose coralline algae: a re-evaluation in the geological sciences. Geol Soc Am Bull 84(3):883–904

Aguirre J, Braga JC, Bassi D (2017) Rhodoliths and rhodolith beds in the rock record In: Riosmena-Rodríguez R, Nelson W, Aguirre J (eds), Rhodolith/Maërl Beds: A Global Perspective, Coastal Research Library, Springer Verlag 15: 105–138

Alejandrino A, Puslednik L, Serb JM (2011) Convergent and parallel evolution in life habit of the scallops (Bivalvia: Pectinidae). BMC Evol Biol 11:164

Allmon WD (1988) Ecology of Recent Turritelline gastropods (Prosobranchia, Turritellidae): current knowledge and paleontological implications. Palaios 3:284–295

Antunes MT, Bizon G, Nascimento A, Pais J (1981) Nouvelles données sur la datation des dépôts miocènes de l'Algarve (Portugal) et l'evolution géologique regionale. Ciências da Terra (UNL) 6:153–168

Antunes MT, Pais J (1993) The Neogene of Portugal. Ciências da Terra (UNL) 8:55–64

Areschoug JE (1852) Ordo XII. Corallinaceae. In: Agardh JG (ed) Species, Genera, et Ordines Algarum, Vol. 2, Part 2, C.W.K. Gleerup, Lund, pp 506–576

Ávila PS, Ramalho R, Habermanng JM, Quartau R, Kroh A, Berning B, Johnson M, Kirby MX, Zanon V, Titschacko J, Goss A, Rebelo AC, Melo C, Madeira P, Cordeiro R, Meireles R, Bagaço L, Hipólito A, Uchman A, Silva CM da, Cachão M, Madeira J (2015) Palaeoecology, taphonomy, and preservation of a lower Pliocene Shell bed (coquina) from a volcanic oceanic island (Santa Maria Island, Azores). Palaeogeogr Palaeoclimatol Palaeoecol 430:57–73

Baarli BG, Santos A, Silva CM da, Ledesma-Vázquez J, Mayoral E, Cachão M, Johnson ME (2012) Diverse macroids and rhodoliths from the Upper Pleistocene of Baja California Sur, Mexico. J Coastal Res 28:296–305

Baeta M, Galimany E, Ramón M (2016) Growth and reproductive biology of the sea star A*stropecten aranciacus* (Echinodermata, Asteroidea) on the continental shelf of the Catalan Sea (northwestern Mediterranean). Helgol Mar Res 70:1

Bakun A (1978) Guinea current upwelling. Nature 271:147–150

Batters EAL (1892) Additional notes on the marine algae of the Clyde sea area. Journal of Botany, British and Foreign 30:170–177

Bizzozero G (1885) Flora Venetta Crittogamica. Parte 2. Seminario, Padova

Bosellini A, Ginsburg RN (1971) Form and internal structure of recent algal nodules (rhodolites) from Bermuda. J Geol 79:669–682

Bosence DWJ (1976) Ecological studies on two unattached coralline algae from western Ireland. Palaeontology 19:71–88

Bosence DWJ (1983a) Coralline algal reef frameworks. Journal of the Geological Society London 140:365–376

Bosence DWJ (1983b) The occurrence and ecology of Recent rhodoliths—a review. In: Peryt TM (ed) Coated Grains. Springer, Berlin, pp 217–224

Boucart J, Zbyszewski G (1940) La faune de Cacela en Algarve (Portugal). Comunicações dos Serviços Geológicos de Portugal 31:3–60

Brachert TC, Forst MH, Pais JJ, Legoinha P, Reijmer JJC (2003) Lowstand carbonates, highstand sandstones? Sed Geol 155:1–12

Braga JC, Bosence DWJ, Steneck RS (1993) New anatomical characters in fossil coralline algae and their taxonomic implications. Palaeontology 36:535–547

Braga JC, Aguirre J (2001) Coralline algal assemblages in upper Neogene reef and temperate carbonates in Southern Spain. Palaeogeogr Palaeoclimatol Palaeoecol 175:27–41

Brandano M, Piller WE (2010) Coralline algae, oysters and echinoids: a liaison in rhodolith formation from the Burdigalian of the Latium-Abruzzi Platform (Italy). Int Assoc Sedimentol Spec Publ 42:149–163

Bromley RG, Hanken N-M, Asgaard U (1990) Shallow marine bioerosion: preliminary results of an experimental study. Bull Geol Soc Den 38:85–99

Bromley RG, Asgaard U (1993) Endolithic community replacement on a Pliocene rocky coast. Ichnos 2:93–116

Bromley RG (1994) The palaeoecology of bioerosion. In: Donovan SK (ed) The Palaeobiology of Tracefossils. Wiley, Chichester

Cachão M, Silva CM da (1992) Neogene paleogeographic evolution of Algarve Basin (Southern Portugal): a two-step model. Prelim Data Gaia 4:39–42

Cachão M (1995) Utilização de nanofósseis calcários em biostratigrafia, paleoceanografia e paleoecologia. Aplicações ao Neogénico do Algarve (Portugal) e do Mediterrâneo Ocidental (ODP 653) e à problemática de *Coccolithus pelagicus*. PhD thesis, University of Lisbon

Cachão M, Boski T, Moura D, Dias R, Silva CM da, Santos A, Pimentel N, Cabral J (1998) Proposta de articulação das unidades sedimentares neogénicas e quaternárias do Algarve. Comunicações do Instituto Geológico e Mineiro 84(1):A169–A172

Cachão M, Silva CM da (2000) The three main depositional cycles of the Neogene of Portugal. Ciências da Terra (UNL) 14:303–312

Cachão M, Silva CM da, Santos AG, Domènech R, Martinell J, Mayoral E (2009) The bioeroded megasurface of Oura (Algarve, S Portugal): implications for the Neogene stratigraphy and tectonic evolution of SW Iberia. Facies 55:213–225

Checconi A, Bassi D, Carannante G, Monaco P (2010) Re-deposited rhodoliths in the Middle Miocene hemipelagic deposits of Vitulano (Southern Apennines, Italy): coralline assemblage characterization and related trace fossils. Sed Geol 225:50–56

Chukwuone NA, Ukwe CN, Onugu A, Ibe CA (2009) Valuing the Guinea current large marine ecosystem: estimates of direct output impact of relevant marine activities. Ocean Coast Manag 52(3–4):189–196

de Gibert JM, Martinell J, Domènech R (1998) *Entobia* ichnofacies in fossil rockyshores, Lower Pliocene, Northwestern Mediterranean. Palaios 13:476–487

de Gibert JM, Domènech R, Martinell J (2007) Bioerosion in shell beds from the Pliocene Roussillon Basin, France: implications for the (macro)bioerosion ichnofacies model. Acta Palaeontologia Polonica 52(4):783–798

de Lamarck JBM (1816) Histoire naturelle des animaux sans vertèbres. Tome troisième, Deterville/Verdière

Forst MH (2003) Zur Karbonatsedimentologie, Biofazies und sequenzstratigraphischen Architektur eines fossilen Hochenergie-Schelfs aus dem Neogen der Algarve (Miozän, Südportugal). PhD thesis, Johannes Gutenberg-Universität in Mainz

Foslie M (1898) Systematical survey of the Lithothamnia. Det Kongelige Norske Videnskabers Skrifer 1898(2):1–7

Foslie M (1905) Remarks on northern Lithothamnia. Det Kongelige Norske Videnskabers Skrifer 3:1–138

Frey RW, Seilacher A (1980) Uniformity in marine invertebrate ichnology. Lethaia 13:183–207

Ghibaudo G, Grandesso P, Massari F, Uchman A (1996) Use of trace fossils in delineating sequence stratigraphic surfaces (Tertiary Venetian Basin, northeastern Italy). Palaeogeogr Palaeoclimatol Palaeoecol 120:261–279

Gray JE (1864) Handbook of British Water-Weeds or Algae. R. Hardwicke, London

Gutowski J (1984) Sedimentary environment and synecology of macrobenthic assemblages of the marly sands and red-algal limestones in the Korytnica Basin (Middle Miocene; Holy Cross Mountains, Central Poland). Acta Geologia Polonica 34(3–4):323–339

Harvey WH (1849) Nereis Australis. II. Reeve, London, pp 65–124

Hottinger L (1983) Neritic macroid genesis, an ecological approach. In: Peryt TM (ed) Coated Grains. Springer-Verlag, Berlin, pp 38–55

Iryu Y, Bassi D, Woelkerling WJ (2012) Typification and reassessment of seventeen species of coralline red algae (Corallinales and Sporolithales, Rhodophyta) described by W. Ishijima during 1954-1978. J Syst Paleontol 10:171–209

Irvine LM, Chamberlain M (1994) Seaweeds of the British Isles. Vol. 1 Rhodophyta, Part 2B Corallinales, Hildenbrandiales. London, HMSO

Johnson ME, Baarli BG, Silva CM da, Cachão M, Ramalho RS, Santos A, Mayoral EJ (2016a) Recent rhodolith deposits stranded on the windward shores of Maio (Cape Verde Islands): historical resource for the local economy. J Coast Res 32:735–743

Johnson ME, Ledesma-Vázquez J, Ramalho R, Silva CM da, Rebelo AC, Santos A, Baarli BG, Mayoral E, Cachão M (2016b) Taphonomic range and sedimentary dynamics of modern and fossil rhodolith beds: Macaronesian Realm (North Atlantic Ocean). In: Riosmena-Rodríguez R, Nelson W, Aguirre J (eds) Rhodolith/Maërl beds: a global perspective, coastal research library, vol 15. Springer, Berlin, pp 221–261

Kelly P, Bromley RG (1984) Ichnological nomenclature of clavate borings. Palaeontology 27(4):793–807

King PP (1832) Description of the Cirrhipeda, Conchifera and Mollusca, in a collection formed by the officers of H.M.S. Adventure and Beagle employed between the years 1826 and 1830 in surveying the southern coasts of South America, including the Straits of Magalhaens [sic] and the coast of Tierra del Fuego. Zool J 5:332–349

Kotizan CB, Simões MG (2006) Taphonomy of recent freshwater molluscan death assemblages, Touro Passo Stream. Southern Brazil. Revista Brasileira de Paleontologia 9(2):243–260

Kützing FT (1841) Über die 'Polipiers calcifères des Lamouroux'. F. Thiele, Nordhausen

Lamptey E (2015) Eco-functional benthic biodiversity assemblage patterns in the Guinea Current Large Marine Ecosystem. PhD thesis, University of Ghana

Lamouroux JVF (1812) Sur la classification des Polypiers coralligénes non entiérement pierreux. Nouveau Bulletin des Sciences par la Société Philomathique de Paris 3:181–188

Linnaeus C (1767) Systema naturae per regna tria naturae: secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Ed. 12. 1., Regnum Animale. 1 and 2. Holmiae, Laurentii Salvii. Holmiae [Stockholm], Laurentii Salvii, pp. 1–532 [1766] (**pp. 533–1327 [1767]**)

Littler MM, Littler DS, Hanisak MD (1991) Deep-water rhodolith, productivity, and growth history at sites of formation and subsequent degradation. J Exp Mar Biol Ecol 150:163–182

Marrack EC (1999) The Relationship Between Water Motion and Living Rhodolith Beds in the Southwestern Gulf of California, Mexico. Palaios 14:159–171

Moretzsohn F (2014) Cypraeidae: how Well-Inventoried is the Best-Known Seashell Family? American Malacological Bull 32(2):278–289

Müller OF (1776) Zoologiae Danicae Prodromus seu Animalium Daniae et Norvegiae indigenarum characteres, nomina, et synonyma imprimis popularium. Hafniae, Typiis Hallageriis

Nebelsick J, Schmid B, Stachowitsch M (1997) The encrustation of fossil and recent sea-urchin tests: ecological and taphonomic significance. Lethaia 30:271–284

Pais J, Legoinha P, Elderfield H, Sousa L, Estevens M (2000) The Neogene of Algarve (Portugal). Ciências da Terra (UNL) 14:277–288

Pais J, Cunha P, Pereira D, Legoinha P, Dias R, Moura D, Brum A, Kullberg JC, González-Delgado JA (2012) The Paleogene and Neogene of Western Iberia (Portugal). A Cenozoic Record in the European Atlantic Domain. Springer Briefs in Earth Sciences. Springer, Berlin

Pallas PS (1766) Elenchus Zoophytorum. P. van Cleef, Hague

Penrose D, Woelkerling WJ (1992) A reappraisal of *Hydrolithon* and its relationship to *Spongites* (Corallinaceae, Rhodophyta). Phycologia 31:81–88

Philippi RA (1844) Descriptiones testaceorum quorundam novorum, maxime chinensium. Zeitschrift für Malakozoologie 1:161–167

Pisera A, Studencki W (1989) Middle Miocene rhodoliths from the Korytnica Basin (Southern Poland): environmental significance and palaeontology. Acta Palaeontol Pol 34(4):179–209

Quaranta F, Tomassetti L, Vannucci G, Brandano M (2012) Coralline algae as environmental indicators: a case study from the Attard member (Chattian, Malta). Geodiversitas 34:151–166

Rasser MP, Piller WE (1999) Application of neontological taxonomic concepts to Late Eocene coralline algae (Rhodophyta) of the Austrian Molasse Zone. J Micropalaeontol 18:67–80

Reid RP, MacIntyre IG (1988) Foraminiferal-algal nodules from the Eastern Caribbean: growth history and implications on the value of nodules as palaeoenvironmental indicators. Palaios 3:424–435

Rey J (1982) Le Crétacé dans la région de Faro (Algarve, Portugal). Comunicações dos Serviços Geológicos de Portugal 68(2):225–236

Rey J, Dinis J, Callapez P, Cunha P (2006) Da rotura continental à margem passiva. Composição e evolução do Cretácico de Portugal, Cadernos de Geologia de Portugal. Instituto Geológico e Mineiro, Lisboa

Rivera MG, Riosmena-Rodríguez R, Foster MS (2004) Age and growth of *Lithothamnion muelleri* (Corallinales, Rhodophyta) in the southwestern Gulf of California, Mexico. Ciencias Marinas 30(1B):235–249

Rösler A, Perfectti F, Peña V, Braga JC (2016) Phylogenetic relationships of Corallinaceae (Corallinales, Rhodophyta): taxonomic implications for reef-building corallines. J Phycol 52(3):412–431

Santos A, Mayoral E, Silva CM da, Cachão M, Domènech R, Martinell J (2008) Trace fossil assemblages on Miocene rocky shores of southern Iberia. In: Wisshak M, Tapanila L (eds) Current developments in bioerosion. Springer, Berlin, pp 431–450

Santos A, Mayoral E, Silva CM da, Cachão M, Kullberg JC (2010) *Trypanites* Ichnofacies: Palaeoenvironmental and tectonic implications. A case study from the Miocene disconformity at Foz da Fonte (Lower Tagus Basin, Portugal). Palaeogeogr Palaeoclimatol Palaeoecol 292(1–2):35–43

Santos A, Mayoral E, Johnson ME, Baarli BG, Silva CM da, Cachão M, Ledesma-Vázquez J (2012) Basalt mounds and adjacent depressions attract contrasting biofacies on a volcanically active Middle Miocene coastline (Porto Santo, Madeira Archipelago, Portugal). Facies 58:573–585

Santos A, Mayoral E, Baarli G, Cachão M, Silva CM da, Johnson M (2014) Estructuras de domicilio-equilibrio producidas por Gastrochaenidae (Bivalvia) en el Mioceno medio del sector de Lagos-Albufeira (Algarve, Portugal). In: Royo-Torres R, Verdú FJ, Alcalá L (eds) XXX Jornadas de Paleontología. Sociedad Española de Paleontología, Teruel, Fundamental 24:219–222

Santos A, Mayoral E, Silva CM da, Cachão M (2016) Two remarkable examples of Portuguese Neogene bioeroded rocky shores: new data and synthesis. Comunicações Geológicas 103(Especial I):121–130

Silva P, Johansen HW (1986) A reappraisal of the order Corallinales (Rhodophyceae). Eur J Phycol 21(3):245–254

Silva CM da, Cachão M, Martinell J, Domènech R (1999) Bioerosional evidence of rocky palaeoshores in the Neogene of Portugal. Bull Geol Soc Den 45:156–160

Sneed ED, Folk RL (1958) Pebbles in the lower Colorado River, Texas, a study in particle morphogenesis. J Geol 66:114–150

Taylor AM, Goldring R (1993) Description and analysis of bioturbation and ichnofabric. J Geol Soc 150:141–148

Taylor PD, Wilson MA (2003) Palaeoecology and evolution of marine hard substrate communities. Earth Sci Rev 62:1–103

Teichert S (2014) Hollow rhodoliths increase Svalbard's shelf biodiversity. Sci Rep 4:6972

Terrinha P, Rocha R, Rey J, Cachão M, Moura D, Roque C, Martins L, Valadares V, Cabral J, Azevedo MR, Barbero L, Clavijo E, Dias RP, Matias H, Madeira J, da Silva CM, Munhá J, Rebelo L, Ribeiro C, Vicente J, Noiva J, Youbi N, Bensalah MK (2013) A Bacia do Algarve: Estratigrafia, Paleogeografia e Tectónica. In: Dias R, Araújo A, Terrinha P, Kullberg JC (eds) Geologia de Portugal, Lisboa, II. Escolar Editora, Lisboa, pp 29–166

Tunnicliffe V (1982) The role of boring sponges in coral fracture. Colloques Internationaux du C.N.R.S. 291:309–315

Voigt E (1965) Über parasitische Polychaeten in Kreide-Austern sowie einige andere in Muschelschalen bohrende Würmer. Paläontologische Zeitschrift 39(3):193–211

Woelkerling WJ, Irvine LM (1986) The typification and status of *Phymatolithon* (Corallinaceae, Rhodophyta). Br Phycol J 21:55–80

Woelkerling WJ, Irvine LM, Harvey AS (1993) Growth-forms in non-geniculate coralline red algae (Corallinales, Rhodophyta). Aust Syst Bot 6:277–293

Zamorano JH, Duarte WE, Moreno CA (1986) Predation upon Laternula elliptica (Bivalvia, Anatinidae): a Field Manipulation in South Bay, Antarctica. Polar Biol 6:139–143