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SYMBIOTIC ASSOCIATION OF A PYRGOMATID BARNACLE WITH A CORAL FROM A VOLCANIC MIDDLE MIOCENE SHORELINE (PORTO SANTO, MADEIRA ARCHIPELAGO, PORTUGAL)

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Abstract: The bioclaustration of the pyrgomatid barnacle *Ceratoconcha* aff. *costata* within the carbonate skeleton of a colonial hermatypical coral (*Tarbellastrea reussiana*) is described from a middle Miocene basaltic rocky palaeoshore on a small north-eastern Atlantic islet of Porto Santo (Madeira Archipelago, Portugal). The resulting structure is named as a new trace fossil *Imbutichnus* igen. nov., characterized by a small, funnel-like cavity, a circular to oval cross-section, with a nearly cylindrical shape in the upper part and a conical shape towards the base. *Imbutichnus costatum* isp. nov. is defined as a bioclaustration structure produced by the overgrowth of a pyrgomatid barnacle by a coral. From an ethologic point of view, *Imbutichnus* is attributed to the Impedichnia category. In terms of palaeoecology, it is interpreted as the result of a parasitic relationship. This is also the oldest record of pyrgomatid barnacles in the eastern Atlantic and clearly demonstrates that the Miocene palaeogeographic range of *Ceratoconcha* was much wider than previously assumed.

Key words: bioclaustration, symbiosis, new ichnogenus, new ichnospecies, coral-inhabiting barnacles, corals.

THE carbonate skeleton of corals – living or dead – commonly provides an excellent hard substrate for biocolonization in various different marine environments (e.g. Patton 1976; Zann 1987; Edinger and Risk 1994; Scoffin and Bradshaw 2000). The interactions between the infesting organisms and the coralliferous hard substrate are diverse and complex, depending on a series of biological and environmental factors as follows: (1) whether the host corals were living or dead at the time of the interaction, (2) whether the corals outlived the colonizers, (3) what organisms were responsible for the colonization and (4) what life habits characterize the colonizer organisms. With regard to the latter, there are several possibilities. Questions of interest include whether the colonizing organisms were symbionts with a more commensal or mutualist relationship with the corals and the degree to which they occupied niches as boring, nestling or encrusting organisms. In addition, unlike the majority of such biological interactions, these coral/colonizer relationships leave a permanent trace, a mark produced in the skeletal hard parts. This is paramount in palaeobiological studies.

In this article, the occurrence of an association between a pyrgomatid barnacle and a coral from a volcanic middle Miocene shoreline in Porto Santo, Madeira Archipelago, is reported, analysed and discussed from a palaeoecological point of view. In addition, the traces produced by the barnacle within the carbonate skeleton of the living host coral are described as a new bioclaustration structure.

CORALS AND SYMBIONTS, A LONG AND DEEP RELATIONSHIP

Studies on symbiont assemblages in live hosts, specifically corals, in modern ecosystems are common. Studies that focus on the fossil record are also becoming more abundant. The literature dealing with fossil coral symbionts deals mainly with mollusks (e.g. Savazzi 1982; Kleemann 1982; Pisera 1987; Morton 1990; Edinger and Risk 1994), sipunculans and polychaetes (e.g. Elias 1980, 1986; Zibrowius *et al.* 1975; Rice 1976; Liu and Hsieh 2000; Stolarski *et al.* 2001; Tapanila 2004; Zapalski 2007; Vinn

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and Mõtus 2008; Martinell and Domènech 2009), barnacles (e.g. Withers 1926; Bałuk and Radwański 1967; Ross and Newman 1973; Newman and Ladd 1974; Moissette and Saint Martin 1990; Collins *et al.* 1997; Zullo and Portell 1991; Pasternak *et al.* 2001) and brachiopods (e.g. Richards and Dyson-Cobb 1976; Pitrat and Rogers 1978; Alvarez and Taylor 1987; Tapanila and Holmer 2006).

Such associations commonly produce structures that exhibit highly characteristic and preservable structures and morphologies. The potential for them to be preserved as trace fossils and used to understand ancient organisms and ecosystems, and their evolution was highlighted by Tapanila and Ekdale (2007) and Tapanila (2008).

According to Darrell and Taylor (1993) and Tapanila (2004), the fossil record of a symbiotic lifestyle in host corals extends back to at least the Late Ordovician. Evidence of this relationship may be preserved as a special group of biogenic structures that represent dwelling cavities produced by a symbiont organism (the 'settler symbiont') as it was embedded within the growing skeleton of a living host organism (the 'host symbiont'), as defined by Tapanila (2005) and Tapanila and Ekdale (2007).

Bromley (1970) recognized the cavities resulting from this type of symbiotic interaction as a special class of trace fossils and called them 'embedment structures'. Later, Palmer and Wilson (1988) introduced the term bioclaustration to define the product of the embedment of infesting organisms by growth of the skeleton of its host.

According to Taylor (1990), bioclaustration, together with substratum bioimmuration and epibiont bioimmuration, is one of the three main types of bioimmuration (or biomuration, as originally defined by Vialov 1961, p. 1511), i.e., the overgrowth of one living organism by the skeletal growth of another.

As pointed out by Palmer and Wilson (1988), structures resulting from bioclaustration could easily be mistaken for borings, because the end result – even when the infesting organism has a mineralized skeleton – is often a hole in the skeleton of the host. In the case of bioclaustration, however, the walls of such cavities exhibit no evidence of having been cut by an intruder, but rather show evidence of deformation of the host's skeleton.

CORAL-INHABITING BARNACLES

In modern communities, barnacles of the family Pyrgomatidae are among the most common and well-known obligatory associates of host scleractinian corals, alcyonarians, hydrozoans and sponges (Hiro 1935; Moyse 1971; Ross and Newman 1973; Ogawa and Matsuzaki 1992; Ross and Newman 2000). These organisms live embedded in the skeleton of their hosts and feed on plankton using their thoracic cirri. The association of pyrgomatid barnacles with corals dates from at least the Miocene (Ross and Newman 2000). The pyrgomatid genus *Ceratoconcha* Kramberger-Gorjanović, 1889, is restricted to hermatypic corals and in Recent seas known only from the tropical western Atlantic. It is represented by four living obligatory symbiont species (Ross and Newman 2000).

The abundant and diverse fauna of Recent pyrgomatid coral-dwelling barnacles was described first in the early nineteenth century (see Holthuis 1982; Ross and Newman 2002*a*). Later works on the symbiotic relationship between these organisms and their coral hosts were focused mainly on taxonomy (e.g. Hiro 1935; Holthuis 1982; Newman and Ross 1973; Ross and Newman 1973, 1996, 2002*a*, *b*), biogeography (e.g. Ross and Newman 1973; Achituv and Langsam 2005) and phylogeny (e.g. Anderson 1992; Simon-Blecher *et al.* 2007). Embedment structures resulting from this barnacle/coral interaction have, however, not been considered from an ichnological perspective.

Most of the information on the distribution and abundance of living pyrgomatid barnacle associates on their coral hosts is from the western Atlantic: Brazil and Costa Rica (Young and Christoffersen 1984; Young 1986, 1988, 1989; Oigman-Pszczol and Creed 2006), Belize (Highsmith *et al.* 1983), Trinidad (Bacon 1976), Jamaica and Barbados (Scott 1987), Florida (Wells 1966) and Bermuda (Zullo *et al.* 1972; Bromley 1978). There is virtually no information on Recent or fossil material in the eastern Atlantic.

In this article, a new middle Miocene bioclaustration structure in corals is described from Ilhéu de Cima (Porto Santo, Madeira, Portugal). This occurrence is also the oldest record of the Ceratoconchitinae in the fossil record of the eastern Atlantic (see Moissette and Saint Martin 1995 for occurrences in the Messinian of Morocco).

GEOLOGICAL SETTING

The Portuguese Madeira Archipelago is located 750 km offshore of Morocco in North Africa. Porto Santo is an outlying volcanic island situated 50 km north-east of the main island of Madeira (Fig. 1). Its present-day area is 41 km^2, but Porto Santo is a deeply eroded island that occupies only about a third of its initial presumed area taking into consideration surrounding bathymetry. Ferreira (1997) produced a geological map of Porto Santo, including its several satellite islets. The second largest islet is Ilhéu de Cima with a perimeter of approximately 3 km and a maximum elevation of 114 m. Fossiliferous sedimentary rocks occur in several locations on the north and west sides of the island in association with the transition between two major volcanic units: (1) a trachytic to basaltic submarine basal volcanic complex with an age between 18.8 and 13.5 Ma and (2) a subaerial alkali basaltic to ha-

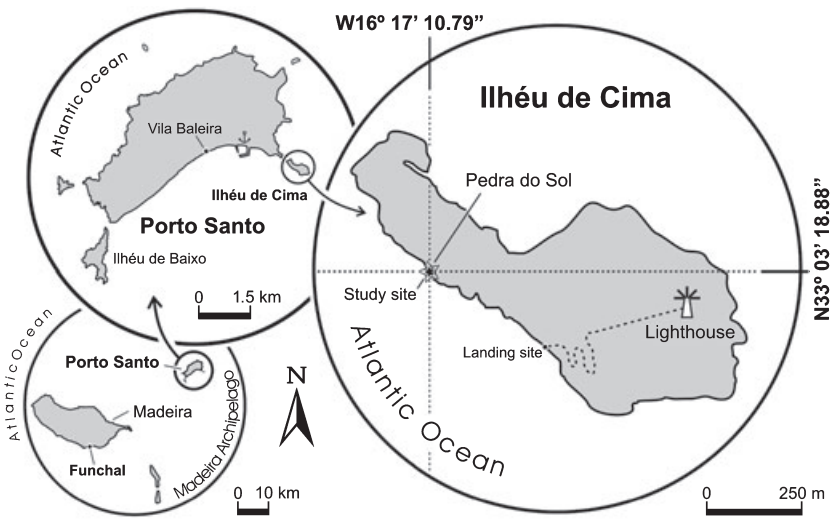


FIG. 1. Geographical location of Ilhéu de Cima, Porto Santo, Madeira Archipelago, Portugal. The star marks the location of the study site at Pedra do Sol.

waiitic complex dated between 14 and 10.2 Ma (Ferreira 1985). Based on calcareous nannofossil assemblages on the east side of Porto Santo at Lombinhos, Cachão *et al.* (1998) dated these sedimentary units as middle Miocene, lower Serravalian (Calcareous Nanofossil biozone CN4 of Okada and Bukry 1980). A comparable age of about 15 to 14 Ma is postulated for the sedimentary rocks intercalated with volcanic rocks on Ilhéu de Cima.

According to Schmidt and Schmincke (2002), the north end of Ilhéu de Cima opposite Porto Santo preserves foreset-bedded, steeply dipping, pillow breccias overlain by, but connected with, horizontal flows interpreted to have been derived from subaerial eruptions that entered the sea as a lava delta. Considered together with the diverse range of fossil-rich carbonates intercalated with volcanic deposits on the north and west sides of the island, it appears that Ilhéu de Cima was a separate island at least during part of its Miocene history. An example of a rare occurrence of a basaltic palaeoshore influenced by active volcanism was given by Santos *et al.* (2011). The study site described in this article is approximately 350 m NW of the only landing place on the islet (Fig. 1), immediately below the lava flow locally known as the 'sun stone' (Pedra do Sol) at an elevation of 2–3 m above mean sea level. It corresponds to a fossilized rocky shore in a volcanic setting stratigraphically positioned below the example described by Santos *et al.* (2011), but also attributed to a middle Miocene (Langhian–Serravalian) age.

MATERIAL ANALYSED

Fossil corals were observed on the vertical face of a middle Miocene rocky shore and an adjacent platform. A limited number of samples were collected, in compliance with guidelines for sites and locations protected within the Parque Natural da Madeira, which includes Ilhéu de Cima.

The family Pyrgomatidae is currently divided into three subfamilies: Megatrematinae, Ceratoconchitinae and Pyrgomatinae (Ross and Newman 2000), but this is the subject of on going revision (Mokady and Brickner 2001). We assign the fossil barnacles to *Ceratoconcha* aff. *costata* Kramberger-Gorjanović, 1889. The barnacles occur on the surface of the coral, embedded in the colonial skeleton, and as bioclaustrations within the coral. The coral-inhabiting barnacle has a cup-shaped calcareous base plate (0.9–5.2 mm diameter, average 3.4 mm) and occurs in clusters (Fig. 2). All specimens were found in association with the colonial coral *Tarbellastrea reussiana* (Milne-Edwards and Haime 1850).

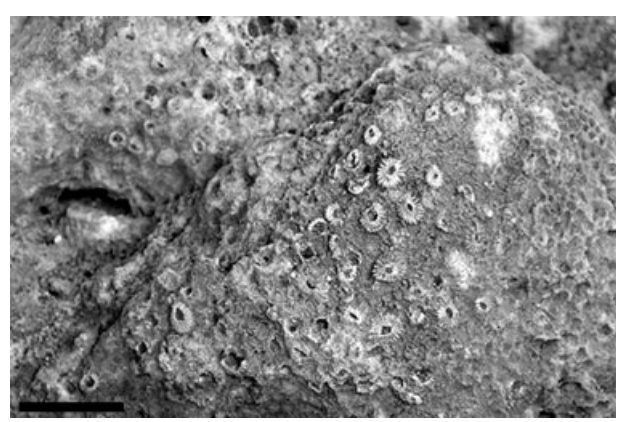
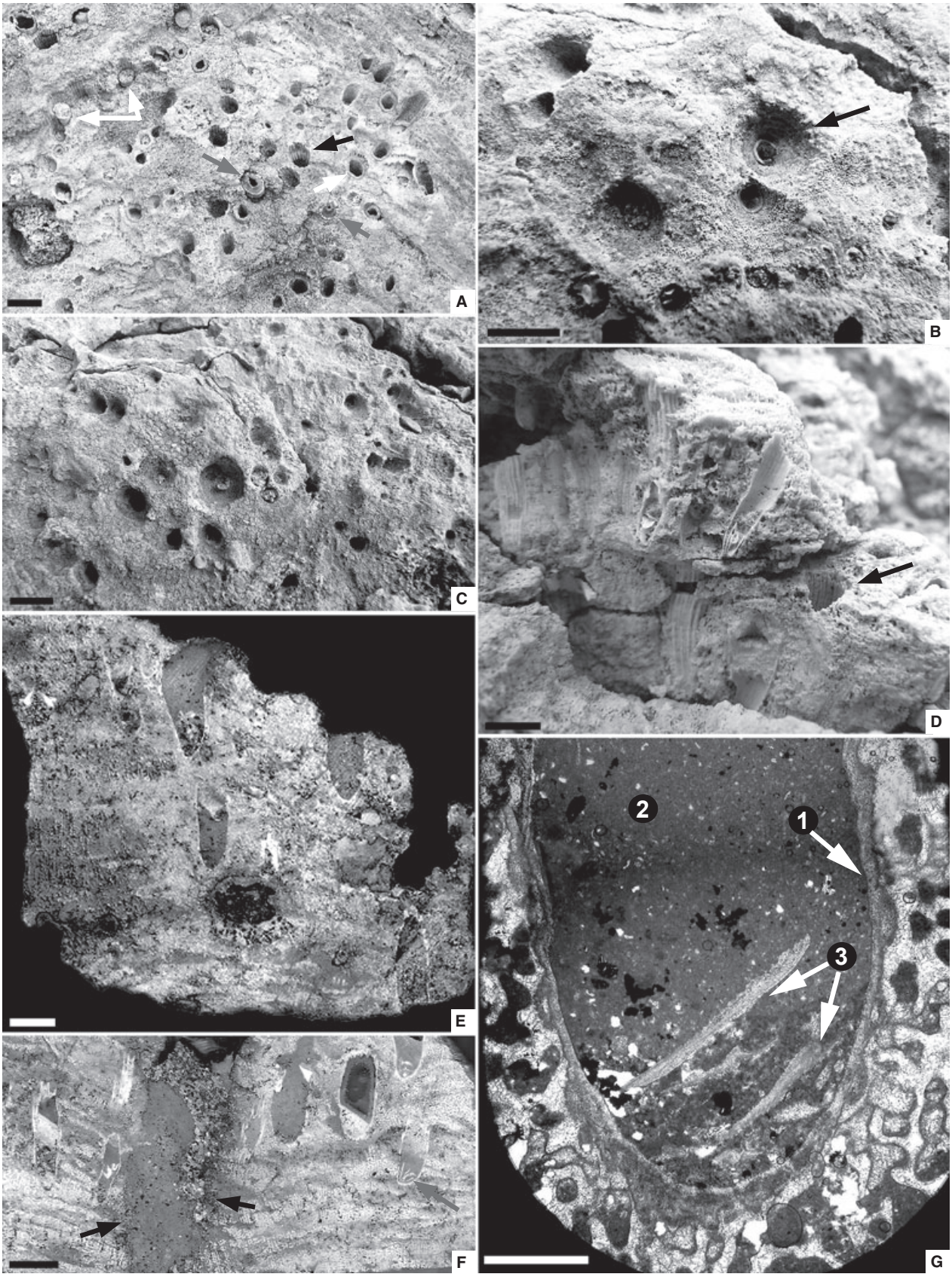


FIG. 2. Clusters of *Ceratoconcha* aff. *costata* Kramberger-Gorjanović, 1889, inhabiting the colonial coral *Tarbellastrea reussiana* (Milne-Edwards and Haime 1850). Scale bar represents 1 cm.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SYSTEMATIC PALAEOICHNOLOGY

Repository. All material studied and illustrated is from the Pedra do Sol outcrop (Ilhéu de Cima, Porto Santo, Portugal) and is of middle Miocene age. Specimens, including the types of the newly erected ichnospecies are, housed in the E. Mayoral Neogene Bioerosion Collection at the University of Huelva, Spain (abbreviation: EM-UH). The specimens of the new ichnospecies are catalogued under the reference numbers EM-UH/09/PS100 to EM-UH/09/PS103.

Ichnogenus IMBUTICHNUS igen. nov.

Derivation of name. After the Latin word *imbūtum*, funnel, and Greek *ichnos*, trace.

Diagnosis. Funnel-like cavity, circular to oval in cross-section. In longitudinal section, the cavity is nearly cylindrical shape in its upper part and much more conical towards the base. The inner surface of the cavity has a longitudinal ornamentation.

Imbutichnus costatum isp. nov.
Figure 3A–G

Derivation of name. After the Latin word *costa*, rib; *costatum*, ribbed.

Type locality. Pedra do Sol outcrop, Ilhéu de Cima, Porto Santo, Portugal (Fig. 1).

Type horizon. Lowermost fossiliferous sedimentary bed associated with a rocky shore intercalated within a volcanogenic sequence (Langhian–Serravalian, middle Miocene; biochronological estimated age of 14–15 Ma (Cachão *et al.* 1998)).

Holotype. EM-UH/09-PS100 (Fig. 3A).

Paratypes. EM-UH/09/PS101 to EM-UH/09/PS103 (Fig. 3A).

Diagnosis. Imbutichnus showing a deep funnel-like depression in the surface of the host, 3–4 mm deep, and circular to oval–subpolygonal in outline. The inner surface of the bioclaustration is ornamented by a marked set of narrow grooves.

Description. The structures are funnel to subcylindrical-shaped cavities perpendicular to the growth surface of the host corallum with parallel longitudinal costae along their length.

On the surface of the corallum, these structures appear as funnel-shaped depressions (narrowing down) with openings that are commonly circular to elliptical in outline, and between 0.5 and 6.6 mm (3.5 mm average) in diameter (Fig. 3A–C). In longitudinal section, the cavities are slightly arcuate, showing a series (15–30) of longitudinal costae separated narrow grooves (Fig. 3D, see arrow). In the top of the funnel-shaped structure, these costae are normally lacking (Fig. 3C). The visible depth of each cavity is on average 7.9 mm and the maximum 19.4 mm (Fig. 3D). The growth lines of the corallum are deflected downwards where in contact with the cavity. (Fig. 4).

Remarks. These trace fossils are considered as bioclaustration structures produced by overgrowth of a pyrgomatid barnacle. This is demonstrated because the structures closely resemble the trace makers, which also sometimes occur as body fossils inside the coral skeleton. Pieces corresponding to the terga and/or the scuta of the barnacles are frequently found collapsed into the bottom of the fossils, indicating that they were passively infilled (Fig. 3F, G).

The specimens of *Imbutichnus* igen. nov. studied in this work were produced by the pyrgomatid barnacle *Ceratoconcha* aff. *costata* Kramberger-Gorjanović, 1889 (Fig. 2).

Imbutichnus igen. nov. should be included in the ethological category Impedichnia, as it records the behaviour of an endosymbiont that inhibits the skeletal growth of its host and, simultaneously, produces a cavity which it uses as a dwelling structure (Tapanila 2005).

In the substrate studied, the density of these structures tends to be very high, up to 103 specimens in an area of 100 cm^2. This fact is attributed to the gregarious behav-

FIG. 3. A, a cluster of *Imbutichnus costatum* isp. nov. on the surface of *Tarbellastrea reussiana*. Holotype EM-UH/09-PS100 (Black arrow). Paratypes (White arrows) from left to right EM-UH/09-PS101 to PS103 showing the internal passive fill (left side) and remains of the calcified wall of *Ceratoconcha* aff. *costata* (right side). Grey arrows indicate partially dissolved carapaces of *Ceratoconcha*. B, plan view of the typical funnel-like structure of *Imbutichnus costatum* isp. nov., showing fairly well-preserved narrow grooves (black arrow) and the calcified wall tube of the producer with a passive infill. C, general appearance of poorly preserved *Imbutichnus costatum* isp. nov. when the surface of the coral is eroded slightly. D, sections of several specimens of *Ceratoconcha* aff. *costata* adjacent to an example of *Imbutichnus costatum* isp. nov.(see arrow). E, polished longitudinal section showing successive generations of *Imbutichnus costatum* isp. nov. preserving the walls of the producer and the passive infill. F, polished longitudinal section of a set of *Imbutichnus costatum* isp. nov. oriented parallel to a larger *Gastrochaenolites* isp. (black arrows). All show passive infill. Grey arrow points to the collapsed terga and scuta of a specimen of *Ceratoconcha* aff. *costata.* G, microphotograph of a longitudinal section of *Imbutichnus costatum* isp. nov. showing: 1, wall of the producer, 2, passive infill and 3, plates corresponding to the terga and/or scuta. Scale bars represent 5 mm (A–F) and 1 mm (G), respectively.

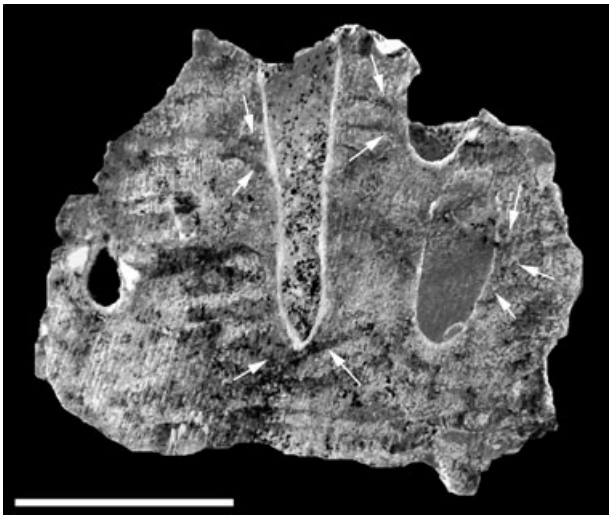

FIG. 4. Longitudinal section of *Imbutichnus costatum* isp. nov. Specimens preserving the wall of the producer inside the structure (white lines) show passive infill and deformation of the growth lines of the coral in response to the inhabiting barnacle (white arrows). Scale bar represents 1 cm.

iour observed today in the larvae of *Ceratoconcha* spp. during settlement (Ross and Newman 1973). The regular spacing observed in the distribution of these structures on the surface of the host probably results from territoriality among endosymbiont neighbours vying for nutrients (Tapanila 2005).

To date, most bioclaustration structures the ichnotaxonomy of which is resolved are limited almost exclusively to the Palaeozoic (Tapanila 2005) and differ from those studied here. *Chaetosalpinx rex* (Tapanila 2002) from the Late Ordovician of Anticosti Island (Québec, Canada) has some similarity to *Imbutichnus costatum* isp. nov. such as the outline of the aperture which is lenticular in cross-section with a fairly constant width: length ratio of 0.6) and being funnel like in longitudinal section. *C. rex*, however, lacks ornamentation on the inside, and the length of the cavities is much greater than that in material from Porto Santo; the maximum length may reach 35 mm for Anticosti material.

Imbutichnus costatum isp. nov. resembles the structures from the Pleistocene of Jamaica termed 'Indeterminate Ichnogenus A' by Perry (2000, fig. 3F). However, the latter are much wider and shorter (only 4 mm long) compared with those from Porto Santo. Perry (2000) compared 'Indeterminate Ichnogenus A' with the traces produced by the barnacle *Ceratoconcha domingensis* (Moullins, 1866) in Recent coral reefs that were described by Bromley (1978).

Embedment cavities resembling *Imbutichnus costatum* isp. nov. are noted by Lamond and Tapanila (2003) in stromatolites and oncolites from the Eocene of Wyoming (USA) and the Plio–Pleistocene Lake Turkana (Kenya), although these were not assigned to any ichnotaxon. These Cenozoic embedment structures are funnel-shaped depressions and have a calcite inner wall (although discontinuous), but lack longitudinal costae and grooves. Their size, and the average length of the cavities, is much greater than any of the specimens from Porto Santo (7 mm in diameter and between 1–200 mm long for Wyoming material, and 6.9–12.3 mm in diameter and 100 mm long for the Kenyan specimens). The density of these North American and African structures is also much lower: 15–33 cavities per 100 cm^2 in Wyoming and 18 cavities per 100 cm^2 in Kenya.

Stratigraphic and geographic range. Middle Miocene. To date, these structures are known only from middle Miocene (Langhian–Serravalian) of the Ilhéu de Cima (Porto Santo, Madeira).

THE NATURE OF *CERATOCONCHA/TARBELLASTREA* SYMBIOSIS

As discussed by Tapanila (2008), and suggested by Starr (1975), mutualism and parasitism can be viewed as the end point members of a continuum of symbiotic association; mutualism being beneficial and parasitism detrimental, with commensalism as the neutral midpoint. In this regard, it is a challenge to fix the nature of the *Ceratoconcha/Tarbelastrea* relationship within this continuum.

The symbiotic relationship between pyrgomatid barnacles and their hosts, both living and fossil, has received some attention over the last decades, with the focus mostly on the trophic aspects. Some (e.g. Hiro 1938; Moissette and Saint Martin 1990; Tapanila 2004) would view the relationship as commensalism. Tapanila (2008) states that the identification of mutuals and parasites should reject the null hypothesis of commensalism. However, others (Abel 1928; Zapalski 2007) disagreed and, based mainly on the fact that the infesting organism modifies the growth phenotype of the host, consider this biotic relationship as a clear example of parasitism.

Tapanila (2008) considers true parasitism to be only when the parasite gains nutrients directly from the host. In this scenario, at least some coral-dwelling pyrgomatid barnacles are true parasites. Ross and Newman (1969) reported that one species of pyrgomatid (*Hoekia monticulariae* Gray, 1831) shows only vestigial cirral limbs and feeds by nibbling away at the coenosarc of the host coral. According to the 'structural classification of symbioses' by Darrell and Taylor (1993), the physical relationship seen in the *Ceratoconcha/Tarbellastrea* association falls under the category of intergrowth symbioses, which represents an endosymbiotic relationship. From the perspective of relative size, this particular symbiosis could be considered an anisosymbiotic relationship because a clear distinction

can be made between the larger host (coral) and smaller symbiont (barnacle).

In an attempt to determine the type of symbiosis represented in this case, we should bear in mind that the settler symbiont is found only in this coral; its settling there was clearly beneficial. Possible benefits might include habitat for the pyrgomatid barnacle as well as protection from predators and prime filter feeding location, on top of a coral colony. These benefits are in accordance with observations made by Patton (1976) who emphasizes that living corals offer the opportunity to not only gather food but also habitat: shelter and hard substratum. In contrast, there are visible negative effects on the host. This association results in changes in skeleton anatomy and growth – such as inhibition of skeletal growth and modification of coral wall geometry – that do not occur in corals of the same species lacking symbiont barnacles.

There are further indications that the period of initial attachment and disruption of the coral tissues by the settler symbiont may have had an adverse effect on the host coral. According to Moyse (1971) and Ross and Yamaguchi (2001), the cyprid larvae of modern pyrgomatids perforate and briefly reside within the living epithelium of the host polyp. Afterwards, the base plates of these barnacles become anchored in the host coral skeleton and the barnacle shell is then covered by a thin layer of the host coenosarc except for a small area where the cirral feeding net can protrude through the operculum (Moyse 1971). We assume that the same happened with the pyrgomatid barnacles from Ilhéu de Cima.

Subsequently, they follow the coral skeleton's vertical growth by elongating the sides of their cup-shaped calcareous base plate (Ross and Newman 1973) progressively moulding their embedment cavity. This arrangement helps prevent pyrgomatids inhabiting relatively fast-growing corals from becoming entombed (Ross and Newman 2002*b*). The presence of the barnacle interferes with the coral's normal growth pattern, as well as causing it to lay down additional skeleton as a stress reaction. All the specimens of *Tarbellastrea* examined that host *Ceratoconcha* showed signs of deformation in the axial growth of the corallum and a tendency to modify skeletal organization, either at the same time as or, more often, shortly after the attachment of the settler organism. Upon demise of the barnacle, the coral may simply cease overgrowing it, or may seal over the cup-shaped cavity, producing a gall-like structure on its surface. This interaction is therefore positive for the settler and negative for the host, which suffered damage and was forced to expend energy modifying its normal anatomical growth pattern. As a result of these barnacle-induced morphological changes, the coral, to some degree, loses fitness.

There are several Recent pyrgomatid species, such as *Hoekia monticulariae* (Gray, 1831) and *Pyrgoma anglicum* (Sowerby, 1823), that have a parasitic relation with the host coral (Ross and Newman 1969; Moyse 1971). Although the symbionts described herein do not obtain their energy from living host tissues (these animals are filter feeders that obtain food from the water column using their thoracic cirri), there is a long-term negative relationship which, according to Combes (2001), is another important aspect characteristic of parasitism. According to Zapalski (2007), perforation of the host's soft tissue and skeleton, long-term infestation and modification of the host's phenotype are clear signs of parasitism.

In summary, given the continuum of symbioses envisaged by Tapanila (2008), the middle Miocene *Ceratoconcha* aff. *costata/Tarbellastrea reussiana* association reported herein would be towards the deleterious end of that continuum, entering the field of parasitism. The overall result of the barnacle/coral relationship is beneficial for the barnacle and negative for the coral.

CONCLUSIONS

The main conclusions of this study on bioclaustration structures from a middle Miocene coral substrate community in Ilhéu de Cima (Porto Santo, Portugal) are the following:

1. This is the oldest record of pyrgomatid barnacles – *Ceratoconcha* aff. *costata* – in the eastern Atlantic Miocene.
2. The occurrence of these barnacles in obligatory association with the coral *Tarbellastrea reussiana* is interpreted as a symbiotic association.
3. The null hypothesis of commensalism was rejected for this association, and some degree of parasitic relationship between the endosymbiont pyrgomatid barnacle and the host coral existed.
4. The resulting bioclaustration structure – *Imbutichnus costatum* – constitutes a new ichnogenus and ichnospecies and is assigned to the ethological category Impedichnia.
5. From a biogeographical point of view, this oldest record of *Ceratoconcha* barnacles in the eastern Atlantic clearly demonstrates that geographic range in the Miocene was much wider than previously thought.

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