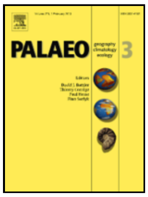
Palaeogeography, Palaeoclimatology, Palaeoecology xxx (xxxx) xxx-xxx

Contents lists available at ScienceDirect

Palaeogeography, Palaeoclimatology, Palaeoecology

journal homepage: http://ees.elsevier.com



Diverse bioerosion structures in lower Pliocene deposits from a volcanic oceanic island: Baía de Nossa Senhora section, Santa Maria Island, Azores (central North Atlantic)

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ARTICLE INFO

Keywords
Bioerosion
Trace fossils
Ichnology
Hard substrate
Geosites

ABSTRACT

Pliocene body fossils from Santa Maria Island, Azores, have been studied for decades, but only more recently have ichnofossils received their due attention. Calcareous Pliocene deposits from the Baía de Nossa Senhora section contain numerous, diverse, well-preserved natural casts of invertebrate borings. The study of this type of fossils adds to knowledge on the dispersal of benthic faunas across oceans to volcanic oceanic islands. The borings belong to seven ichnogenera and twenty-two ichnotaxa at the ichnospecies level with more than half pertaining to *Entobia*, which is produced by clionaid sponges. Other borings found were produced by bivalves (*Gastrochaenolites*), polychaete worms (*Caulostrepsis* and *Maeandropolydora*), sipunculid worms (*Trypanites*), phoronid worms (*Talpina*) and ctenostome bryozoans (*Iramena*). The occurrence, ichnogeny, distribution and preservational state of the borings suggest that the bearing bioclasts have been exposed for several years on the sea floor. The borings derive from different bathymetric zones on the shelf, and their formation took place during several bioerosional phases. The association of borings belongs to the *Entobia* ichnofacies, which is typical of carbonate rocky shores, and shows close similarity to those described from the Paratethys, Mediterranean and partly the eastern Atlantic regions. This fits the idea that most of the Neogene shallow-water marine fauna in the Azores is biogeographically related to the eastern Atlantic shores.

1. Introduction

The fossil record of volcanic oceanic islands is key to understanding the processes and patterns of marine biogeography and evolution in archipelagic/insular environments (Ávila et al., 2019). The Macaronesia geographic region, which comprises the archipelagos of the Azores, Madeira, Selvagens, Canaries and Cabo Verde, has been the subject of intensive studies during the last two decades, with the description of new fossiliferous outcrops, new species and comprehensive checklists of both vertebrate and invertebrate marine groups (Gerber et al., 1989; Zazo et al., 2002, 2007; Johnson et al., 2011, 2012, 2014; Baarli et al., 2013; Ávila et al., 2018; Mayoral et al., 2018; Meco et al., 2020). In the Azores, Santa Maria Island represents an outstanding palaeontological heritage as two out of its twenty referenced fossiliferous geosites are of international relevance (Ávila et al., 2016a; Raposo et al., 2018). Body fossils from the Pliocene (e.g., Janssen et al., 2008; Kroh et al., 2008; Winkelmann et al., 2010;

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https://doi.org/10.1016/j.palaeo.2021.110284
Received 17 September 2020; Received in revised form 3 February 2021; Accepted 3 February 2021

Madeira et al., 2011; Meireles et al., 2012; Ávila et al., 2012, 2015a, 2020; Hyžný et al., 2021) and Quaternary (e.g., Callapez and Soares, 2000; Ávila et al., 2010, 2015b) on the island received considerably more attention than ichnofossils, which have been studied in detail only since a few years ago (Santos et al., 2015; Uchman et al., 2016, 2017a, 2018, 2020). However, ichnofossils can convey much information on ecosystems, depositional processes and environments from the geological past, and as in this paper, they may contribute to the advancement of palaeobiogeographic considerations.

As most organisms producing bioerosion traces are confined to nearshore calcareous substrates, their occurrence on oceanic volcanic islands is unexpected. It appears that they can be present even in habitats geographically far distant from their usual areas of occurrence and even in volcanic lithologies (Madeira et al., 2010; Santos et al., 2010, 2015; Ramalho et al., 2013). This is the case for Santa Maria Island, where Pliocene and Quaternary marine calcareous deposits are preserved in the geological record and exposed above sea level due to uplift (Ramalho et al., 2017). These sedimentary layers contain abundant bioclasts and occasional calcareous and non-calcareous (basalt and pyroclastic) clasts presenting macroborings; this is especially common in the Pliocene deposits preserved in volcanic sequences. Among those, borings of clionaid sponges and small bivalves are commonly present. Borings produced by sponges (*Entobia* being the most common), spionid (*Caulostrepsis*, *Maeandropolydora*) and phoronid polychaetes (*Talpina*), although not abundant, were found by Wisshak et al. (2011) in recent substrates from the island of Faial in the Azores. Besides the paper by Santos et al. (2015), which describes echinoid borings in the Ichnofossils' Cave section (another geosite, located in the southern shores of Santa Maria Island), sponge and other boring types from Pliocene deposits from Santa Maria have also been reported in papers by Ávila et al. (2015b, 2015c), Rebelo et al. (2016), Johnson et al. (2017) and Uchman et al. (2017a, 2020).

The Baía de Nossa Senhora section is a Pliocene geosite included in the PalaeoPark Santa Maria, a palaeontological heritage classification attributed by the Regional Government of the Azores, supported by the International Palaeontological Association (Ávila and Rodrigues, 2013; Ávila et al., 2016a; Raposo et al., 2018). In this section, *Entobia* is exceptionally well preserved in natural casts and is accompanied by other macroborings. Their description and interpretation are the subject of this paper. The similarity between the assemblage of Santa Maria's Pliocene borings and those from the Paratethys, Mediterranean, and eastern Atlantic coasts is also discussed. Furthermore, this paper contributes to biogeographic problems related with the dispersal of benthic fauna across wide oceanic barriers to isolated, volcanic oceanic islands (Ávila et al., 2009, 2015b, 2019; Meireles et al., 2012; Baarli et al., 2017; Baptista et al., 2019; Freitas et al., 2019).

2. Geological setting

2.1. Azores Archipelago and Santa Maria Island

The Azorean islands are located in the central Atlantic Ocean (Fig. 1A). This volcanic archipelago is a group of nine reefless oceanic islands located in a complex tectonic setting, the "Azores Geosyndrome" area (Vogt and Jung, 2017), a regional feature that includes the Azores Archipelago, the Azores Plateau and the triple junction between the North American, Eurasian and Nubian (Africa) lithospheric plates (Fig. 1B).

Santa Maria Island is the south-easternmost island of the Archipelago, located about 840 km from Madeira Island, and 1380 km from mainland Portugal, the closest continental region. It is also the oldest insular volcanic edifice in the archipelago with a complex geological history involving several volcanic stages and significant vertical movements (Ramalho et al., 2017). The first island of Santa Maria emerged at about 6 Ma as a result of surtseyan activity followed by strombolian activity, whose products correspond to the Cabrestantes and Porto Formations, respectively (Serralheiro et al., 1987; Serralheiro, 2003; Ramalho et al., 2017; Fig. 1C). The area of this initial island grew considerably, as volcanic activity increased and, between 5.8 and 5.3 Ma, a broad shield volcano (the Anjos Volcanic Complex) was formed (Serralheiro, 2003; Sibrant et al., 2015; Ramalho et al., 2017). From 5.3 up to ca. 4.1 Ma, as a result of subsidence, erosion, mass wasting and decreased volcanic activity, the initial island was destroyed, originating a large seamount with the probable occurrence of a few islets protruding above sea level. Extensive marine sedimentation occurred during this period, and the remnants of the life-forms that thrived on this shoal are nowadays accessible on several exposed Pliocene fossiliferous outcrops from the Touril Volcano-sedimentary Complex (e.g., Pedra-que-pica, Figueiral, Ponta do Castelo, Malbusca, Ichnofossils' Cave, Cré and Ponta do Cedro) and, to a lesser extent, from the base of the Pico Alto Volcanic Complex (Kirby et al., 2007; Meireles et al., 2013; Rebelo et al., 2014, 2016; Ávila et al., 2015c, 2016b, 2018, 2020; Santos et al., 2015; Ramalho et al., 2017; Johnson et al., 2017; Uchman et al., 2016, 2017a, 2018, 2020).

The volcanic edifice re-emerged as a consequence of renewed volcanism during a first rejuvenated stage that lasted from 4.1 to 3.5 Ma (the Pico Alto Volcanic Complex). This new volcanic edifice was built off-centred to the east of the initial island, with extensive progradation of lava deltas to the west and to the east of the Pico Alto volcanic ridge (Ramalho et al., 2017; Uchman et al., 2020). The latest volcanic activity on Santa Maria Island occurred sporadically during a second rejuvenated stage, from 3.2 to 2.8 Ma, as a result of low-volume, monogenetic volcanism (resulting in the Feteiras Formation), although evidence of very recent (late Pleistocene) volcanism has been found underwater, on the north shelf of the island (Ramalho et al., 2020). Crucially, a subsidence trend that lasted from ca. 6 Ma up to ca. 3.5 Ma, at a rate of about 100 m/Myr (Ramalho et al., 2017), reversed at about 3.5 Ma to uplift at ca. 59 m/Myr (from 3.5 to 2.1 Ma), and to a slower uplift trend of ca. 42 m/Myr from 2.1 Ma to the present (Ricchi et al., 2018). This peculiar combination of geological events thus converged to form some of the best exposed volcano-sedimentary island sequences worldwide, for which the island is famous. Also, the complex interplay between Pleistocene glacio-eustatic changes, the island's uplift trend, the morphology of the shelf, the lithology of the stratigraphic units and the intensity/effective time of marine erosion resulted in a series of subaerial and submerged marine terraces that are distributed, respectively, between 7 and 230 m in elevation, and between −40 and −140 m in depth (Ricchi et al., 2018, 2020).

2.2. Baía de Nossa Senhora section

The outcrop at Baía de Nossa Senhora – adjacent to Ponta da Malbusca, the southernmost tip of the island – is located at the base of exposed submarine eruptive sequences on Santa Maria, formed during the early Pliocene (Ramalho et al., 2017). The almost vertical sea cliff exposes a section in the volcano-sedimentary Touril and Pico Alto Volcanic Complexes (Fig. 2A). The sequence – which has been described in detail by Rebelo et al. (2016), Johnson et al. (2017) and Ramalho et al. (2017) – comprises from the base to the top: (1) closely-packed basaltic pillow lavas from 0 to ~16 m in elevation; (2) unconformably lying above the pillow lavas, from ~16 m to ~20 m in elevation, a sequence of fossiliferous marine sediments and subordinated levels of hydromagmatic tuffs – the focus of this study – which is only preserved on the eastern side of the bay, where it was covered by a lava delta; (3) from ~20 m to ~40 m in elevation, a westward-dipping sequence of pillow-lavas and hyaloclastites corresponds to the foreset unit of a lava delta (whose topset has been removed by erosion), which

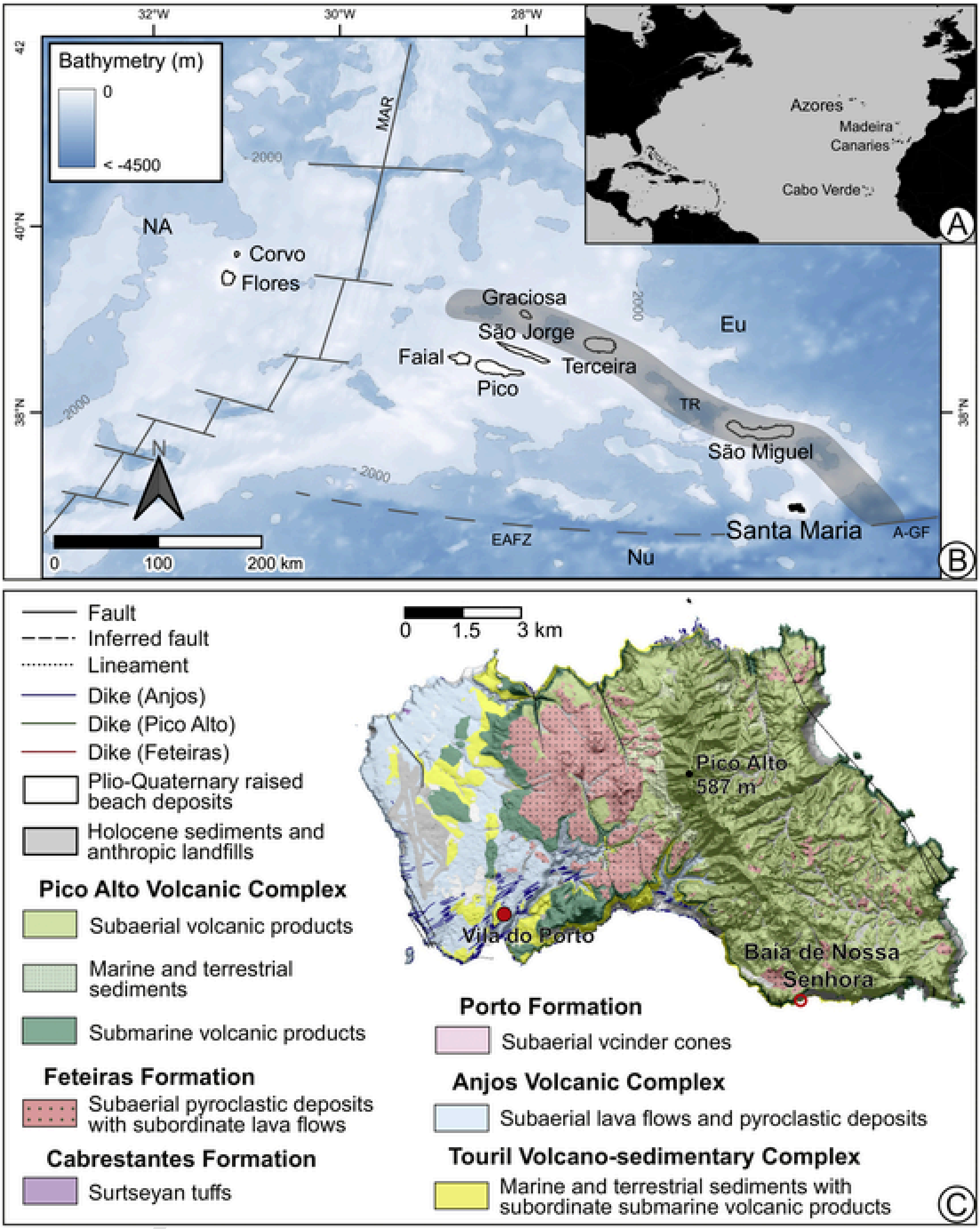


Fig. 1. Location of the Azores, Santa Maria Island and the studied section. **A.** Location of the Azores within the Central Atlantic Ocean. **B.** Shaded relief map illustrating the "Azores Geosyndrome" area (Vogt and Jung, 2017), a regional feature that includes the Azores Archipelago, the Azores Plateau (white shaded area above the 2000 m isobath) and the triple junction between the Nubian (Nu), North American (NA) and Eurasian (Eu) lithospheric plates. MAR: Mid-Atlantic Rift. EAFZ: Eastern Azores Fracture Zone. A-GF: Azores-Gibraltar Fault. TR: Terceira Rift (grey shaded area). The bathymetry is derived from GEBCO 2019 (http://www.gebco.ne). **C.** Geological map of Santa Maria Island (based on Serralheiro et al., 1987 and Ramalho et al., 2017). Red circle marks the Baía de Nossa Senhora section. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

is only present on the eastern side of the bay; (4) a complex succession of marine fossiliferous sediments mostly comprising calcarenites, sandstones and tuffites (see Rebelo et al., 2016; Johnson et al., 2017) onlapps against the frontal surface of the lava delta and, to the west, lies on the basal pillow-lavas; (5) conformably over these sediments (and unconformably above the eroded lava delta), an extensive sequence of thick tabular basaltic submarine sheet flows and pillow lavas, with occasional interbedded sediments, up to approximately 145 m in elevation; (6) conformably over the submarine succession, is a 15–25 m package of subaerial lava flows; and (7) a basaltic spatter cone (Pico Maloás; Fig. 2B). Units 1–4 are considered to be part of the Touril Volcano-sedimentary Complex, whilst units 5–7 are considered as part of the Pico Alto Volcanic Complex (Serralheiro et al., 1987; Serralheiro, 2003; Rebelo et al., 2016; Ramalho et al., 2017) (Fig. 2B).

In terms of age constraints, K—Ar and Ar—Ar geochronology by Sibrant et al. (2015) and Ramalho et al. (2017) suggests that the

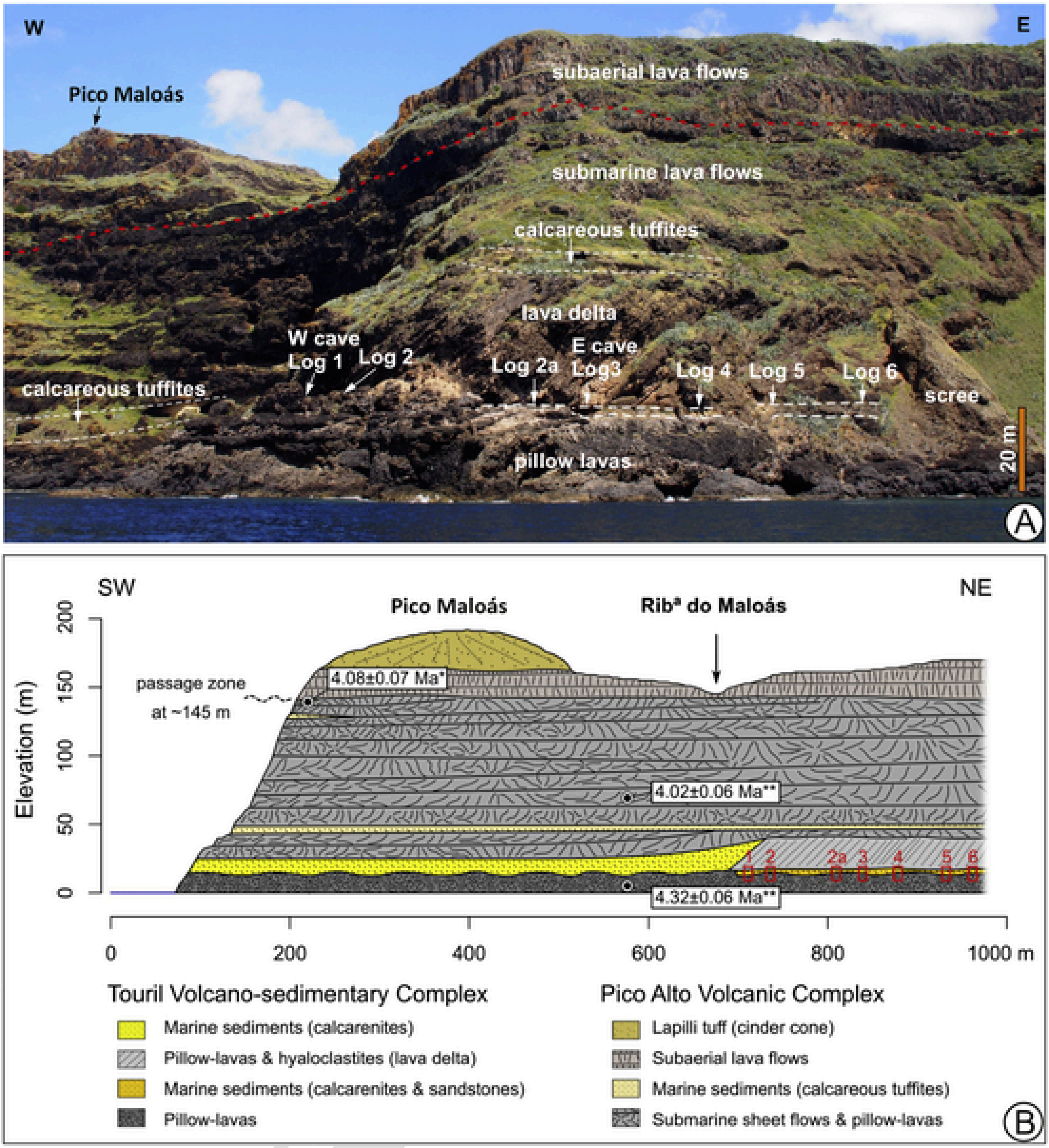


Fig. 2. View and cross section of the study area. **A.** View of the sea cliff where the studied sediments crop out, with indication of the old extraction sites (W cave, E cave), lava delta, and location of the logs represented in Fig. 3. **B.** General geological section of the sea cliff indicating the main features in the outcrop and published ages (* – Ramalho et al., 2017; ** – Sibrant et al., 2015).

whole sequence was deposited/extruded between approximately 4.32 and 4.0 Ma. Effectively, unit 1 and the lower part of unit 5 have been dated, respectively, at 4.32 ± 0.06 Ma and 4.02 ± 0.06 Ma by Sibrant et al. (2015), whereas the top of unit 5 was dated at 4.08 ± 0.07 Ma by Ramalho et al. (2017) – the latter two ages overlapping within their uncertainty interval envelops. Accordingly, these ages suggest a very rapid deposition of the whole volcano-sedimentary sequence during a transgressive period between 4.32 and 4.0 Ma (Ramalho et al., 2017).

The studied sediments form a lens at least 140 m-long, up to 3 m-thick intercalated within the volcanic sequence, varying from fine to very coarse arenitic rocks which are formed essentially by biogenic grains (bioclasts) with variable amounts of lithoclasts and mineroclasts of volcanic and volcaniclastic origin. The sedimentary rocks cover an unevenly abraded surface cut into basaltic pillow lavas, and locally on tuffite and peperite that fill local depressions up to 2 m deep. In the lower part, a bioclastic ashy calcarenite is present. It is up to 3 m thick in the depressions and very thin where elevated (Figs. 3, 4A–D). Its palaeontological content includes dominant rhodoliths, rare echinoderms [*Clypeaster altus* (Leske, 1778)], numerous bivalve (e.g., *Arca noae* Linnaeus, 1758; *Gigantopecten latissimus* (Brocchi, 1814); *Spondylus concentricus* Bronn, 1831; *Ostrea* sp.*, Pecten dunkeri* Mayer, 1864; *Scapharca crassissima* Macsotay and Campos, 2001) and gastropod shells (*Persististrombus coronatus* (Defrance, 1827); *Cerithium crenulosum* Bronn, 1862*; Xenophora* sp.), which show variable degrees of fragmentation and display traces of bioerosion and abrasion. Moreover, benthic foraminifers, microgastropods, bryozoans, coralline algae and echinoid spines are visible in thin section (Fig. 5A–C). Among the rhodoliths, *Phymatolithon calcareum* (Pallas) Adey and McKibbin ex Woelkering and Irvine, 1986, *Phymatolithon* sp. 1,?*Phymatolithon* sp. 2, *Lithophyllum* sp. 1 and *Lithophyllum* sp. 2 are recognised. Some of the rhodoliths are bored with *Entobia* isp. indet. (Fig. 6A–F).

In the eastern part, the bioclastic ashy calcarenite is covered by a tuffitic calcarenite to calcareous tuffite, which is burrowed with *Bi-*

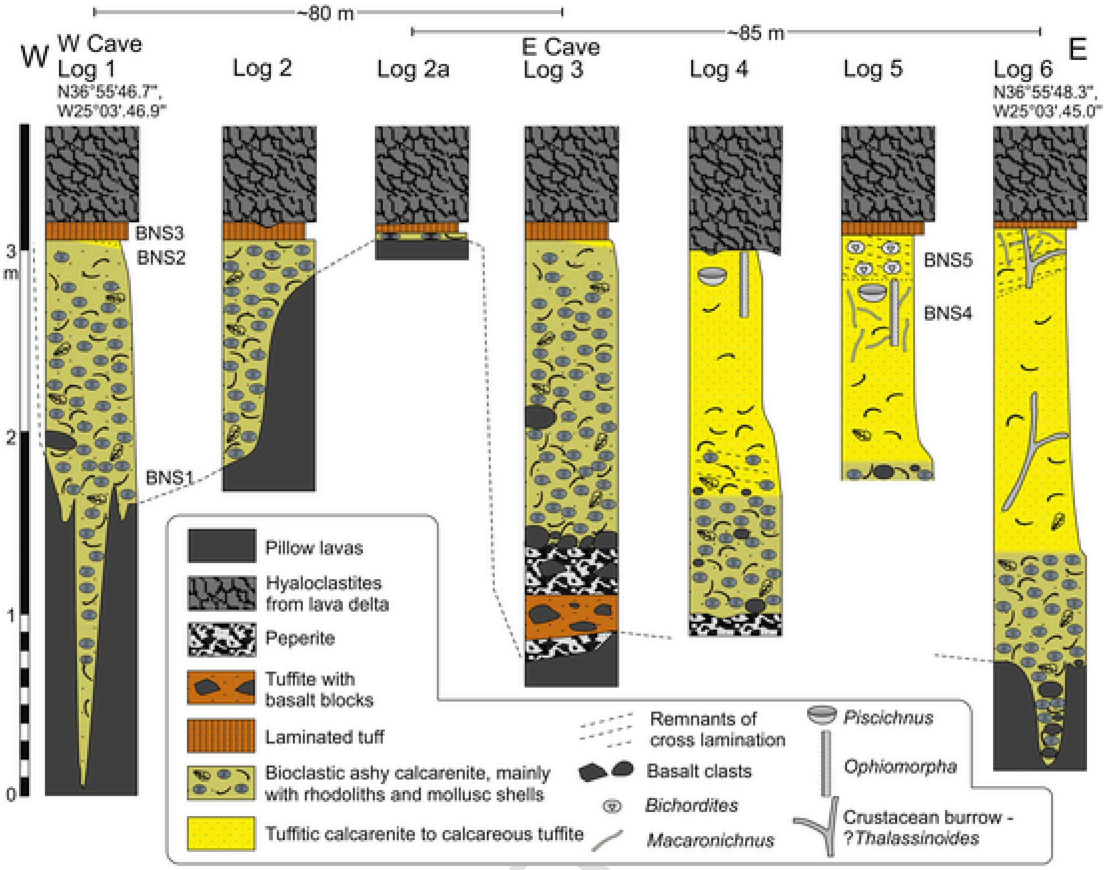


Fig. 3. Stratigraphic logs from the Baía de Nossa Senhora study section. Location of the logs is marked in Fig. 2A. BNS1 to 5 references mark the position of relevant thin sections.

chordites isp. (Fig. 5D), variably oriented *Macaronichnus segregatis* Clifton and Thompson, 1978 (Fig. 5E), *Thalassinoides*-like crustacean burrows (Fig. 5E), *Ophiomorpha* isp. (Fig. 5F), and *Piscichnus waitemata* Gregory, 1991. These burrows trap benthic foraminifers, crushed mollusc shells and fragments of coralline algae (Fig. 5E–H). Both facies are covered by a thin layer of laminated tuff, which is overlain by hyaloclastites from the lava delta sequence (Fig. 3).

Exploitation of the carbonated sedimentary rocks for quick-lime production originated two artificial caves. The cave walls constitute the best exposures of the sedimentary body and the best palaeontological samples were obtained from the smaller, westernmost cave (hereafter western cave, Fig. 4A), particularly from loose blocks leftover from the mining activity. In addition to detailed field observations and descriptions, 113 samples displaying borings were collected and analysed. Measuring and counting data of the different bioerosion structures has been carried out using InkScape 0.92.5 graphical software. Their description and illustrations (Figs. 7–12) constitute the next section. The specimens (i.e. individual clasts) are housed in the Nature Education Centre of the Jagiellonian University (CEP) – Museum of Geology (Kraków, Poland) under the acronym INGUJ249P.

3. Ichnotaxonomical description

The dominant ichnogenus is *Entobia* Bronn, 1838, which is represented by twelve camerate forms at the ichnospecies level. Their morphological features are shown in Fig. 7. A list of specimens presenting the described trace fossils is available in Supplementary Table 1. Morphometric parameters of the *Entobia* ichnospecies are provided in Supplementary Table 2.

Entobia cateniformis Bromley and D'Alessandro, 1984 (Fig. 8A) is a complex network of cylindrical galleries and sub-globose chambers. The galleries are L- or Y-shaped at intersections. Apertures are small and numerous. Short, well-developed apertural canals rarely occur. The growth phases B and C are represented by long galleries and sub-spherical chambers. This boring is stenomorphic due to thin molluscan shells in which it is developed. *E. cateniformis,* like other ichnospecies of *Entobia*, is produced by clionaid sponges and referred specifically to *Cliona vermifera* Hancock (Bromley and D'Alessandro, 1984).

Entobia cf. *cateniformis* Bromley and D'Alessandro, 1984 (Fig. 8B) is a network of cylindrical galleries and elongated chambers which are filled with sand or calcite, or occur as natural moulds. Moreover, a row of small apertures can also be observed. The boring shows the growth phases B—C and C—D. Constrictions are shorter and narrower comparing with the ones of *E. cateniformis.*

Entobia geometrica Bromley and D'Alessandro, 1984 (Fig. 8C) shows polyhedral and subspherical chambers interconnected by numerous intercameral canals. The network of borings is developed parallel to the substrate surface in two tiers. The stenomorphic character is shown by the low number and short intercameral canals and flattened chambers, in some cases. *E. geometrica* is similar to borings of the sponge *Cliona celata* Grant, 1826 (see Bromley and D'Alessandro, 1984; Bromley and Asgaard, 1993a). This cosmopolitan sponge lives mostly from intertidal to shallow subtidal zones (Hartman, 1957), but Rosell and Uriz (2002) provided a bathymetric range from 0.5 to 200 m. Bromley and D'Alessandro (1990) indicated that *E. geometrica* is relatively abundant in infralittoral Plio-Pleistocene and distinctly rarer in bathyal Pliocene in the Mediterranean area. *Cliona celata* occurs nowadays in the Azores (Xavier and Costa, 2010).

Entobia cf. *geometrica* Bromley and D'Alessandro, 1984 (Fig. 8D) shows the growth phase A represented by long, locally bifurcating exploratory threads. The chambers are small and mostly spherical (growth phases B, C and D). The number of the intercameral canals is less, in comparison with the idiomorphic development of the bioero-

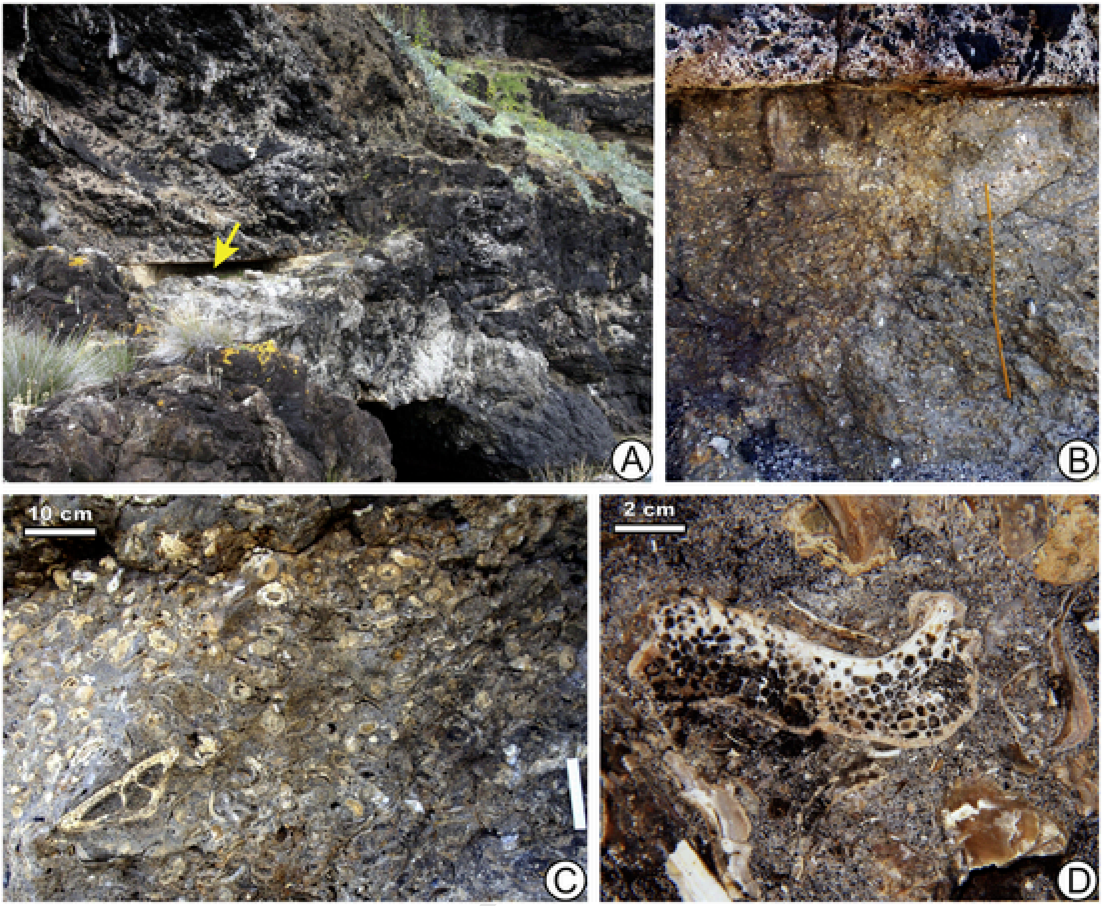


Fig. 4. Details of the outcrop and sedimentary facies of the Baía de Nossa Senhora section. **A.** The western cave (1.2–1.4 m high) is indicated by arrow. **B.** Contact between the top of the sediments and the overlying hyaloclastites from the lava delta sequence at the eastern cave (scale is 1 m long). **C.** Sedimentary deposits composed of calcareous lithic sandstone containing abundant rhodoliths and bioclasts (large *Clypeaster altus* in the lower left part). Scales: ruler graduated in cm in C and D, and 20 cm long in E. **D.** Bioeroded bioclast with *Entobia* isp. indet. in the surface of the outcrop.

sion structure. This boring is preserved on the external surface of the substrate as a natural mould and covers it in patches. The highest growth phase chambers are 1.63–3.48 mm (mean 2.13 mm) long and 0.91–1.82 mm (mean 1.41 mm) wide (Supplementary Table 2). The described boring differs from *Entobia geometrica* in (1) the prevailing irregular shape, (2) higher number of elongated or flattened chambers, and (3) much lower number of short intercameral canals (only two or three are observed). Moreover, only one tier is developed.

Entobia laquea Bromley and D'Alessandro, 1984 (Figs. 8E, F, 11D, 12D) shows great morphological variety of chambers, including subtriangular, irregularly oval or subglobose form. They are dominantly filled with calcite or fine-grained sand. However, eroded, half-cut, empty chambers also occur in some specimens. Intercameral canals, forming constrictions, are short and reduced to a tapering neck. Apophyses are rare, probably due to the state of preservation. The growth phase C is characteristic. According to Bromley and D'Alessandro (1984), *E. laquea* is very similar to borings produced by the sponge *Cliona viridis* (Schmidt, 1862), which lives in symbiosis with green algae, mostly in the shallow sea, but also in deeper shadowed places (Rosell and Uriz, 2002). *C. viridis* occurs nowadays in the Azores (Xavier and Costa, 2010). However, Bromley and Asgaard (1993a) pointed *Pione vastifica* (Hancock, 1849) (formerly *Cliona vastifica*) as the tracemaker of *E. laquea*. *P. vastifica* is a cosmopolitan species occurring mostly from the lower intertidal to shallow subtidal rocky shores (Hartman, 1957), but Rosell and Uriz (2002) indicated a bathymetric range from 1 to 600 m. Nowadays, it is not reported from the Azores (Xavier and Costa, 2010). In the deep-sea coral *Lophelia*, it can be produced by the clionaid sponge *Spiroxya heteroclita* Topsent, 1896 (Beuck and Freiwald, 2005). Bromley and D'Alessandro (1990) indicated that *E. laquea* is relatively abundant in bathyal Pliocene and less abundant in infralittoral Plio-Pleistocene of the Mediterranean environments.

Entobia?*laquea* Bromley and D'Alessandro, 1984 (Fig. 8G) is characterized by the approximately lace-like arrangement and the moderately flattened, subglobose shape of the eroded, mostly empty chambers. The growth phases B and C can be assumed. The constrictions are longer than wide (Supplementary Table 2). Because of the lack of other characteristic features, a closer determination is not possible.

Entobia ovula Bromley and D'Alessandro, 1984 (Fig. 9A) shows short exploratory threads and oval, or globose shaped chambers connected by quite short intercameral canals. The crowded network of chambers is arranged in two tiers. The growth phases C and D are present. Borings of *Pione vastifica* Hancock, 1849 and *Cliona glomerata* Michelin, 1846 resemble *E. ovula* (see Bromley and D'Alessandro, 1984). *P. vastifica* is a cosmopolitan species that occurs mostly from the lower intertidal to shallow subtidal rocky shores (Hartman, 1957) but Rosell and Uriz (2002) mentioned it from the bathymetric range 1–600 m. Bromley and Asgaard (1993a) added *Cliona schmidtii* (Ridley, 1881) and *C. vermifera* Hancock, 1867 (= *Bernatia vermifera*) as recent trace makers of *E. ovula*. *C. schmidtii* has a bathymetric range of 0.5 to 180 m (Rosell and Uriz, 2002), and presently does not occur in the Azores. Bromley and D'Alessandro (1990) indicated that *E. ovula* is relatively abundant in infralittoral Plio-Pleistocene and distinctly rarer in bathyal Pliocene from the Mediterranean area.

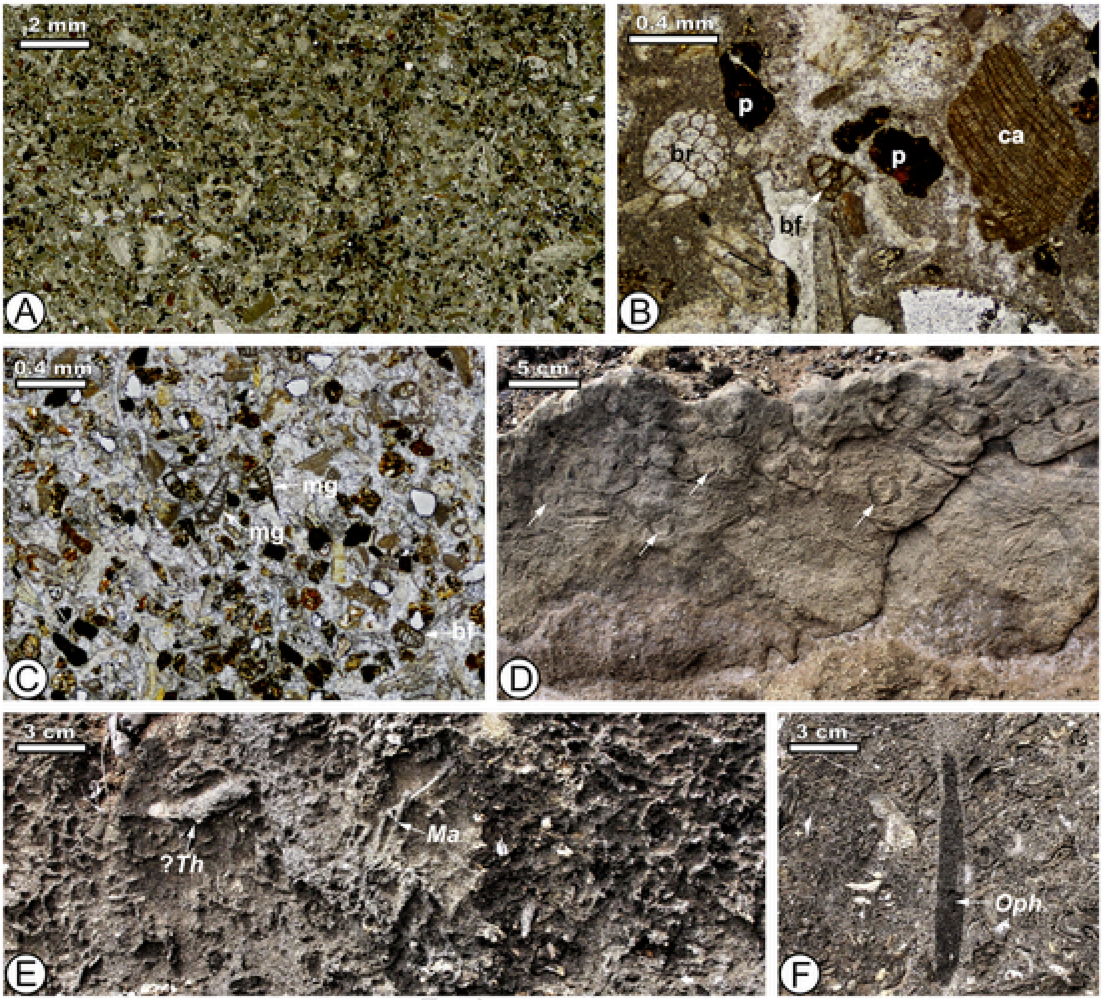


Fig. 5. Microphotographs of thin sections and trace fossils. **A.** Tuffite with bioclasts and calcareous cement, locally transitioning into ashy calcarenite, BNS4. **B.** Ashy calcarenite with micritized bivalve shells, benthic foraminifers (bf), bryozoans (br), coralline algae (ca) and pyroclastic grains (p), BNS1. **C.** Ashy calcarenite containing microgastropods (mg) and benthic foraminifers (bf), BNS5. **D.** *Bichordites* isp. (some indicated by white arrows), vertical cliff face. **E.** *Macaronichnus segregatis* (*Ma* and similar cylindrical burrows) and?*Thalassinoides* isp. (?*Th*), vertical cliff face. **F.** *Ophiomorpha* isp. (*Oph*), vertical cliff face.

Entobia?*paradoxa* (Fischer, 1868) (Fig. 9B, C) is characterized by a network of slightly elongated, amoeboid or polygonal chambers, which are arranged parallel to the substrate surface. Gradual tapering of the chambers before interconnections is clearly visible in the artificial cast of the sample (Fig. 9C). The growth phase C can be observed. The sizes of chambers and the connections between them show large variation. The preservation state of the examined specimen is poor. The diagnostic features, such as the size of apertures, length of apertural canals, or the depth of penetration into the substrate cannot be observed. According to Bromley and Asgaard (1993a), *E. paradoxa* is produced by the sponge *Cliona celata*, which occurs nowadays in the Azores (Xavier and Costa, 2010). Bromley and D'Alessandro (1990) indicated that *E. paradoxa* is relatively abundant in bathyal Pliocene and less abundant in circumlittoral Pleistocene in the Mediterranean environments.

Entobia isp. 1 (Fig. 9D) is preserved as a single network of poorly preserved globose and ovoid chambers, which differ in diameter and shape and are filled with sand in some cases. There are no apertures or intercameral canals. This boring shows a weak similarity to *E. laquea* and to *E. ovula.* A more precise determination is not possible as it lacks any other diagnostic features.

Entobia isp. 2 (Fig. 9E) consists of small bulbous, slightly oval shaped chambers, which are connected with two or three extremely tiny intercameral canals. The small, uniform chambers are constant in size and developed in more or less parallel rows forming dense networks. The crowded morphological elements resemble *E. ovula*, but the chambers do not form a boxwork. The dense arrangement of chambers is partly similar to *E. mammillata* Bromley and D'Alessandro, 1984, but in contrast to this ichnospecies, the chambers do not form clusters and the robust terminal apophyses are missing.

Entobia isp. 3 (Fig. 9F) is represented by rounded, oval chambers connected to one or two intercameral canals and short pieces of exploratory threads covering the surface of bivalve borings or bivalve shell fragments. Two distinct types of chambers can be observed. The smaller ones are slightly elongated, while the larger ones are bulbous. The chambers do not form any network but small groups on the surface of bivalve borings. This trace fossil was formed within the shell of the producer (not preserved) and/or a cemented filling (also not preserved).

Entobia isp. 4 (Fig. 10A, B) is characterized by heavily calcified rounded and amorphous chambers. Most of them show amorphous appearance and lack intercameral canals due to the high degree of calcification. The boring resembles *E. geometrica* because it presents bulbous or elongated chambers in one tier. However, the lack of intercameral canals and apertures makes the exact determination impossible.

Caulostrepsis taeniola Clarke, 1908 (Fig. 11A) is a partially preserved, pouch-like, U-shaped, straight or slightly winding boring pene-

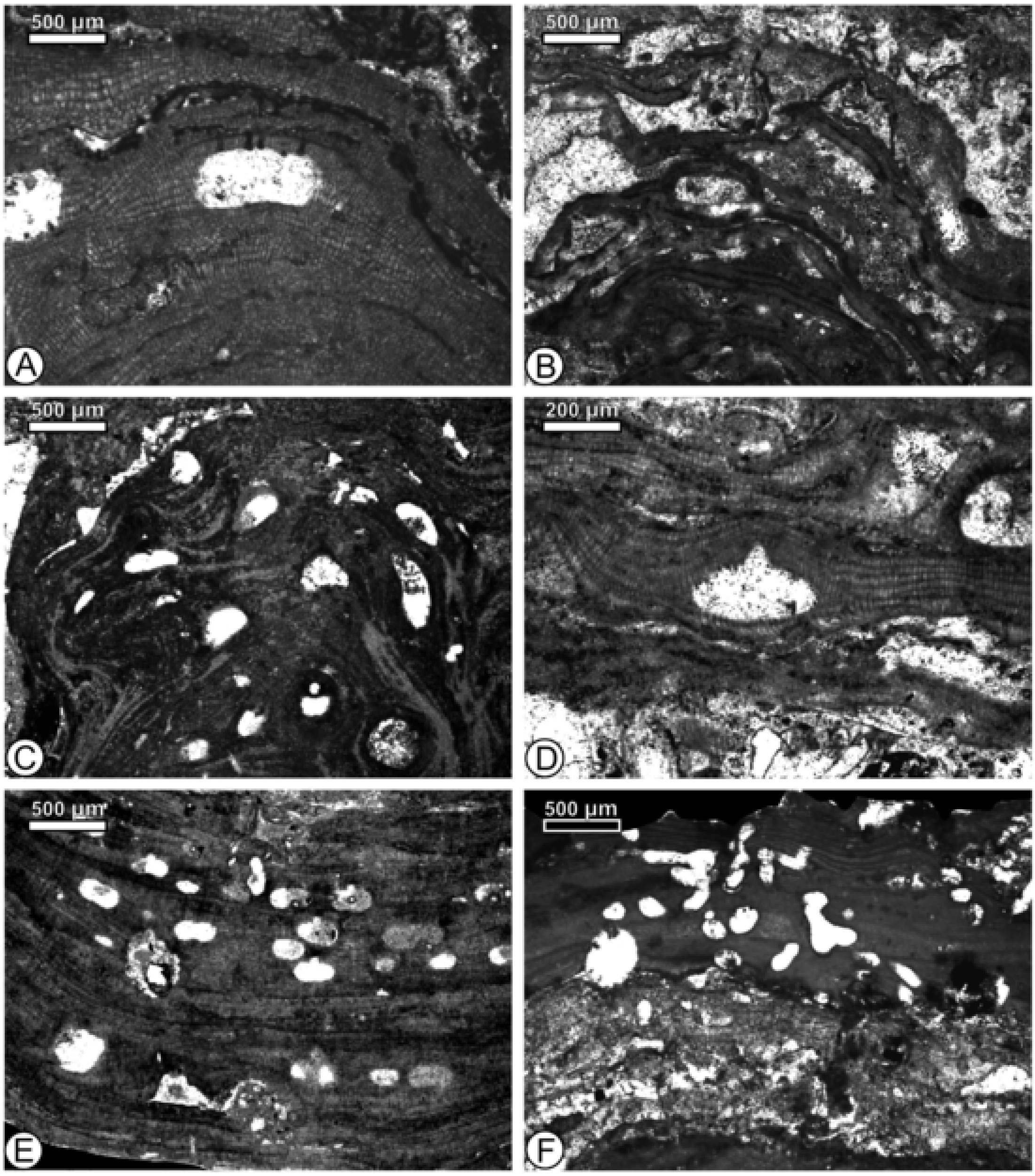


Fig. 6. Representative rhodolith forming species from Baía de Nossa Senhora section. The white spots (calcite filled tunnels) mostly correspond to borings, mainly *Entobia*. **A.** *Phymatolithon calcareum*. **B.** *Phymatolithon* sp. 1. **C.**?*Phymatolithon* sp. 2. Note both uniporate and multiporate conceptacles on the same thallus. **D.** *Lithophyllum* sp. 1. **E.** *Lithophyllum* sp. 2. **F.** Borings *Entobia* in the thalli of the rhodolith forming coralline algae.

trating the host shell parallel or obliquely. Its gallery is cylindrical and slightly widening distally, forming a narrow tongue. The aperture cannot be seen because of the sinuous shape of the boring. The vane (the area between the limbs) is wider than the limbs, which are of equal width. The boring is up to 21 mm long and up to 2.5 mm wide. *Caulostrepsis* Clarke, 1908 (for ichnotaxonomy see Bromley and D'Alessandro, 1983) is a spionid polychaete boring produced mostly by *Polydora* Bosc, 1802 (Boekschoten, 1966), particularly *P. ciliata* (Johnston, 1838), which is common in mid-latitude Atlantic coasts (Radwański, 1969, and references therein), mostly no deeper than 25 m (Boekschoten, 1966); this polychaete is not reported nowadays for the Azores (Cordeiro et al., 2019). The eunicid polychaete *Lysidice ninetta* Audouin and H. Milne-Edwards, 1833, which lives in the Atlantic – including the Azores (Cordeiro et al., 2019) – and the Indo-Pacific, can also produce this boring (Bromley, 1978, 2004). *Polydora* is adapted to different substrates and conditions; it can also live in polar regions (Hanken et al., 2012) and in brackish waters (D'Andrea et al., 1996; Murina, 1997). *Caulostrepsis* ranges since the Devonian to present (Clarke, 1908; Bromley, 2004). It occurs mostly in the infralittoral Plio-Pleistocene and the recent Mediterranean coasts (Bromley and D'Alessandro, 1990), but mostly in the lower intertidal and subtidal zones, rarely deeper and very rarely on the continental slope and the abyssal zone (Ekdale et al., 1984: p. 127).

Maeandropolydora sulcans Voigt, 1965 (Fig. 11B) is represented by irregularly contorting cylindrical galleries, which are 0.8–1.2 mm wide and 3–3.2 mm long. Apertures can be detected. All of them occur in bivalve shell fragments and show diverse states of preservation, including natural casts, natural casts filled with fine grained sediment or grooves in the inner side of the valve. In one case (INGUJP42), the gallery starts from an empty bivalve boring filled with sediment. *Maeandropolydora*

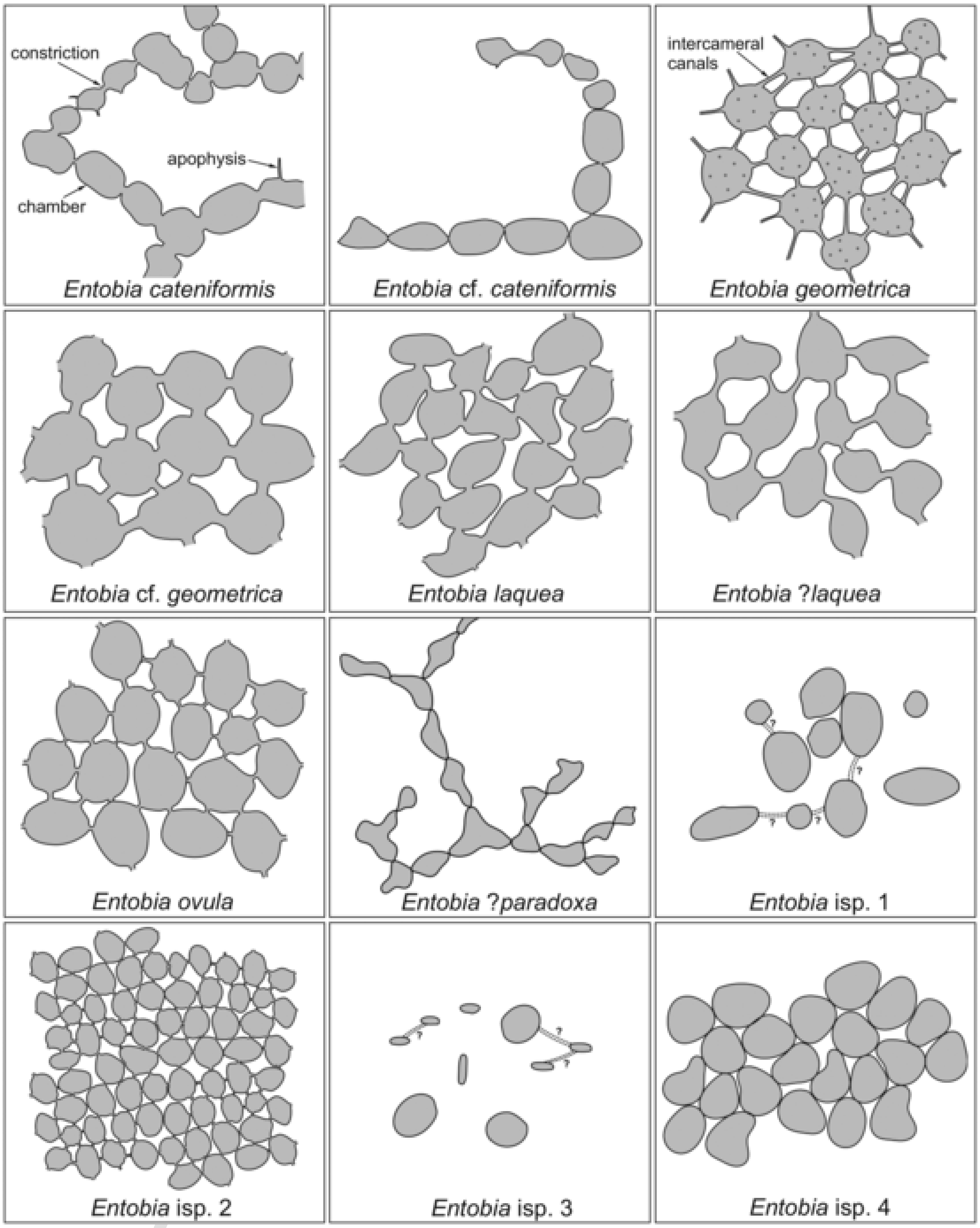


Fig. 7. Basic morphologic features of the *Entobia* ichnospecies described in this paper.

Voigt, 1965 is a boring of suspension-feeding spionid polychaetes (e.g., Bromley and D'Alessandro, 1983).

Maeandropolydora elegans Bromley and D'Alessandro, 1983 (Fig. 11C) is composed of thin cylindrical galleries running as parallel, paired limbs touching but not fused. It is exposed in a 15.2 mm length as a natural cast enveloped by thin calcareous film. The limbs are 1.0–12 mm wide. The other parts are carved into the substrate and filled with coarse-grained sand.

Maeandropolydora isp. (Fig. 11D) shows straight segments of galleries composed of parallel tubes preserved as natural casts or at least hollow tubes thickly lined with calcite. The tubes are 0.7–0.8 mm in diameter and 0.3–04 mm apart. Paired limbs suggest *Maeandropolydora*, but the short available segment and partly preserved apertures prevent a closer determination.

Gastrochaenolites lapidicus Kelly and Bromley, 1984 (Fig. 12A, B) is an elongate, smooth, clavate borings preserved either in half-cut cavities in longitudinal section or as natural casts. In the latter case, the widest part and the rounded base of the main chamber are clearly recognisable. Some of the half-cut borings are filled with sand and contain incomplete valves of the borer. The measured five specimens are 2.98–11.97 mm in diameter and 7.5–27.31 mm long. Characteristic features, which allow distinction of this ichnospecies from other *Gastrochaenolites* ichnospecies include 1) the widest part situated at central position within the chamber, and 2) the basal part of the paraboloid

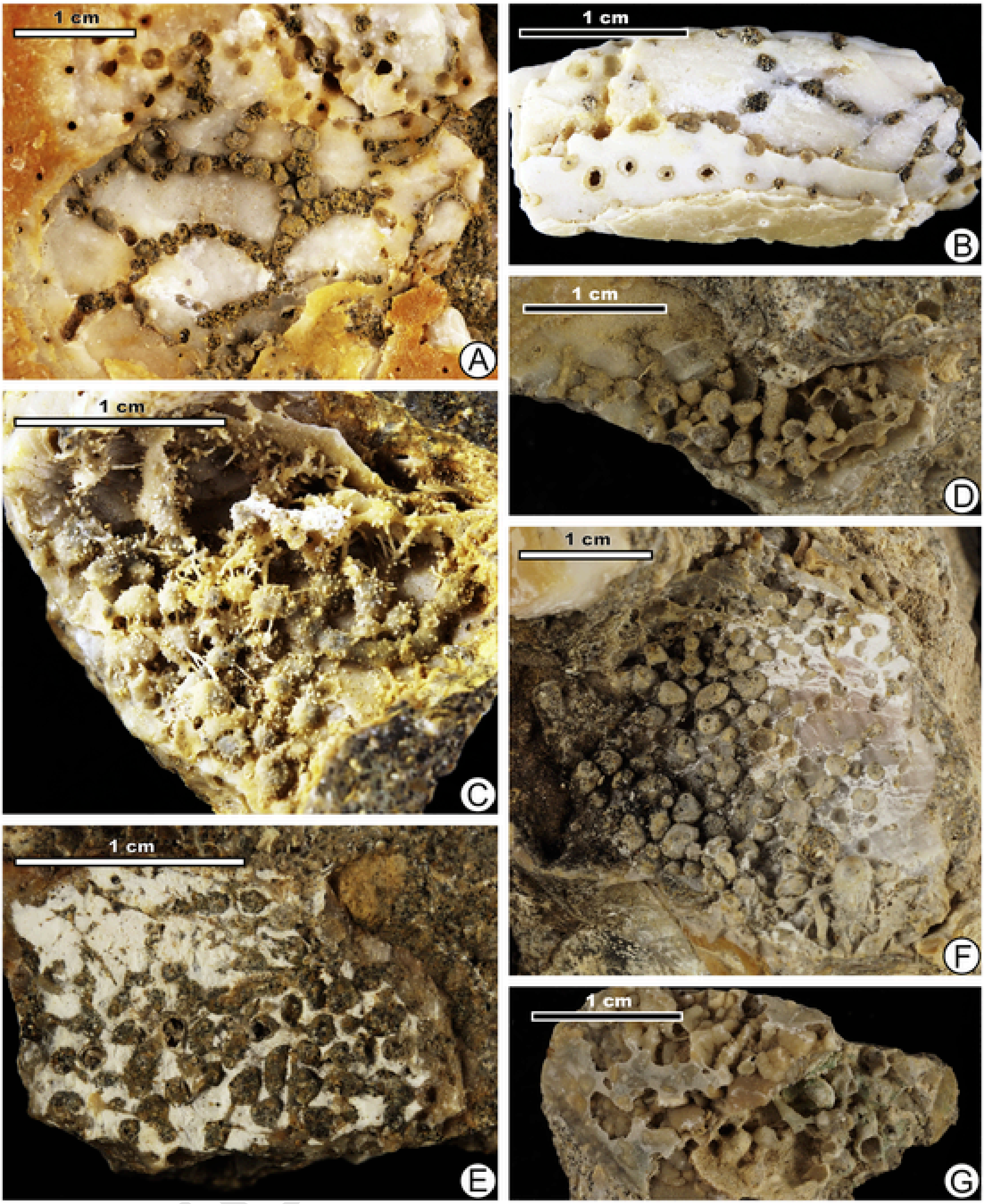


Fig. 8. *Entobia* in bioclasts from the Baía de Nossa Senhora section. **A.** *Entobia cateniformis,* INGUJ249P5 in *Spondylus* sp. **B.** *E.* cf. *cateniformis* in Bivalvia indet., INGUJ249P25. **C.** *E. geometrica* in *Ostrea* cf. *lamellosa,* INGUJ249P8. **D.** *E.* cf. *geometrica*, INGUJ249P100 in *Spondylus* sp. **E.** *E. laquea* in Bivalvia indet., INGUJ249P16. **F.** *E. laquea* in *Ostrea* sp., INGUJ249P10. **G.** *E.?laquea* in Bivalvia indet., INGUJ249P101.

outline. *Gastrochaenolites* Leymerie, 1842 is produced by bivalves and, according to Kelly and Bromley (1984), *G. lapidicus* by representatives of *Lithophaga* Röding, 1798 (Mytilidae) and *Hiatella* Bosc, 1801 (Hiatellidae). Bromley and Asgaard (1993a) showed that *G. lapidicus* can also be produced by *Gastrochaena dubia* (Pennant, 1777) (Gastrochaenidae), presently *Rocellaria dubia* (see Carter et al., 2008), which can also produce *G. dijugus* Kelly and Bromley, 1984. Finally, Uchman et al. (2017b) reported *Parapholas* sp. (Pholadidae) shells in Oligocene *G. lapidicus*.

Gastrochaenolites cf. *torpedo* Kelly and Bromley, 1984 (Fig. 12C) are elongated, torpedo-like smooth borings, 13–14 mm long and 6.54 mm wide on average. The acutely parabolic shaped base can be observed in most specimens. Several specimens are heavily eroded and only the rounded cross-sections refer to the ichnospecies. The apertures are missing. The neck region is preserved in some specimens. Some borings are filled with sand; some contain natural casts of sponge borings; moulds also occur. *Gastrochaenolites torpedo* is diagnosed by an elongate torpedo-like chamber and a neck which is oval or in figure-of-eight in cross section (Kelly and Bromley, 1984). In the material presented, the torpedo-like chamber is well visible, but it is much smaller than in the Mediterranean and the eastern Atlantic coast *G. torpedo* (see Kelly and Bromley, 1984; Santos et al., 2010) produced by *Lithophaga lithophaga* (Linnaeus, 1758), which is a chemical borer living in very shallow (mostly 0–6 m deep), clean waters (Kleemann,

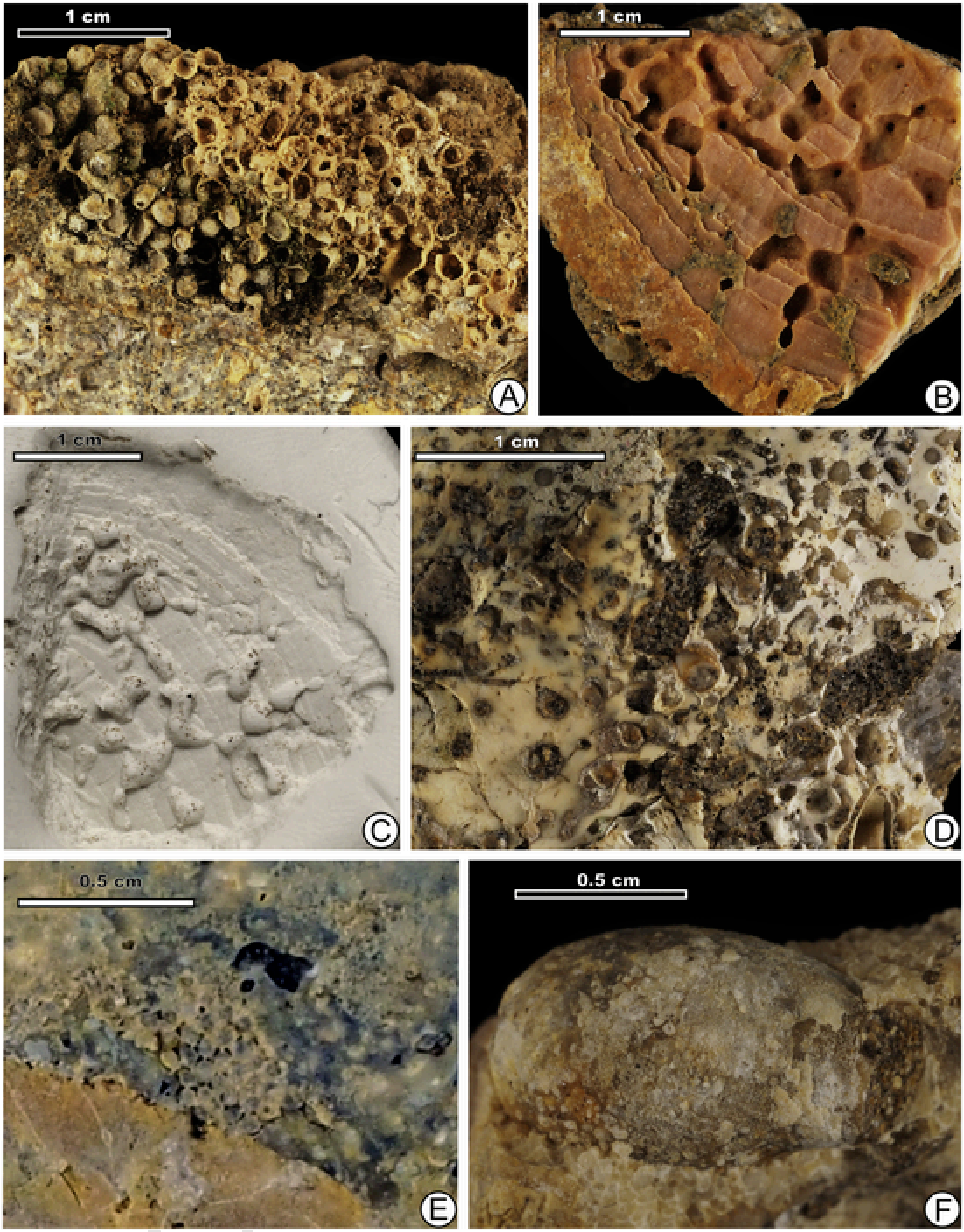


Fig. 9. *Entobia* in bioclasts from the Baía de Nossa Senhora section. **A.** *Entobia ovula* INGUJ249P9 in *Ostrea* sp. **B.** *E.?paradoxa* in *Ostrea* sp., INGUJ249P18. **C.** Plasticine cast of specimen in B. **D.** *Entobia* isp. 1 in Gastropoda indet., INGUJ249P14. **E.** *Entobia* isp. 2, in Bivalvia indet., INGUJ249P32. **F.** *Entobia* isp. 3 in Bivalvia indet., INGUJ249P91.

1973, 1974, 1990; Galinou-Mitsoudi and Sinis, 1995, 1997), commonly on steep or overhanging surfaces (Bromley and Asgaard, 1993a). *G. torpedo* can also be produced by other species of *Lithophaga* (Mytilidae) (Jones and Pemberton, 1988) and relative genera (e.g., *Leiosolenus*, Lithophaginae), and by *Gastrochaena* (Gastrochaenidae) (Kelly and Bromley, 1984; Uchman et al., 2017b). In Pliocene and Quaternary deposits from Santa Maria (Azores), small boring *G.* cf. *torpedo*, as in the material presented, is produced by the lithophagous bivalve *Leiosolenus aristatus* (Dillwyn, 1817) (= *Myoforceps aristatus*) (Mytilidae) (Ávila et al., 2010; Uchman, 2017).

Gastrochaenolites isp. (Fig. 12D) is an empty or sediment-filled bioerosion structure. The apertures and the neck region are lacking. The poorly preserved moulds are 3.02–12.09 mm wide. The length, cross-section, shape and the base of the main chamber cannot be observed. In the absence of the above-mentioned diagnostic features it is not possible to identify the borings at the ichnospecies level.

Talpina ramosa Hagenow, 1840 (Fig. 13A, B) occurs as unbranched or rarely Y-branched winding tunnels preserved as natural cast or as grooves on the surface of shells. Their course is more or less parallel to the shell surface. They may occur on slightly different levels and in

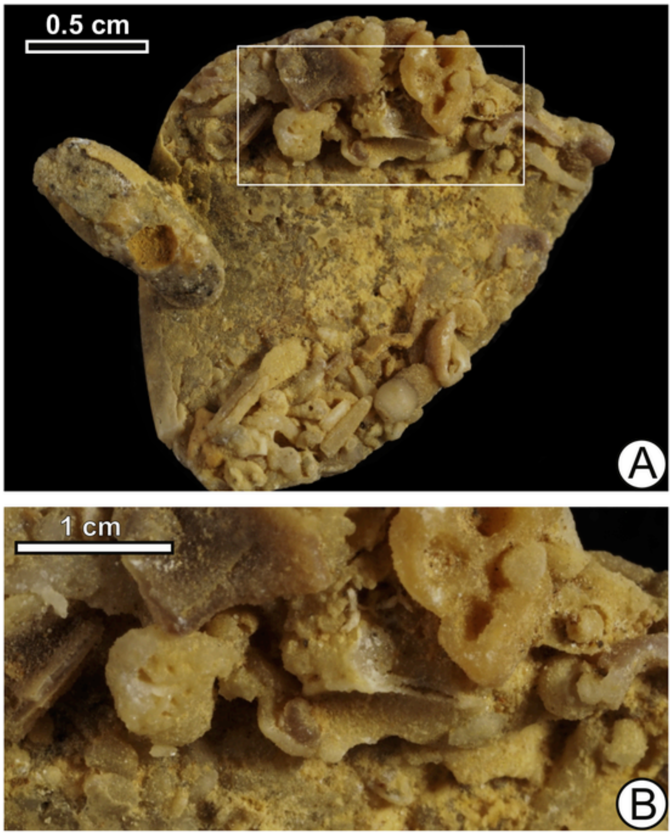


Fig. 10. *Entobia* in bioclasts from the Baía de Nossa Senhora section. **A.** *Entobia* isp. 4 in Bivalvia indet., INGUJ249P108. **B.** Closer view of *Entobia* isp. 4 in Bivalvia indet., INGUJ249P108.

patches. The tunnels are 0.26–0.6 mm (mean 0.42 mm) in diameter. The described borings correspond to the material described by Voigt (1975, 1978) or Zonneveld and Bistran (2013). *Talpina* Hagenow, 1840 is produced by colonial species of phoronid worms (Taylor and Wilson, 2003).

Trypanites solitarius (Hagenow, 1840) (Fig. 13C, D) is a straight, locally slightly winding cylindrical tube, which is 0.33–0.59 mm (mean 0.435 mm) in diameter and 6.8–6.61 mm long. *Trypanites* Mägdefrau, 1932 is a dwelling and feeding structure of filter-feeding “worms”, mainly sipunculoids, polychaetes, and acrothoracican barnacles (Ekdale et al., 1984; Neumann and Wisshak, 2008; Wisshak, 2008).

Iramena danica Boekschoten, 1970 (Fig. 13E, F) is a boring system showing an irregular network of primary tunnels, where longer and short ones are bifurcated. They are 0.057–0.074 mm (mean 0.066 mm) wide. Small, rounded apertures are situated along the tunnels. This boring is a network of stolon tunnels with apertures produced by ctenostome bryozoans similar those produced by the genus *Penetrantia* Silén, 1946 (e.g., Boekschoten, 1970; Barrier and D'Alessandro, 1985) or *Immergentia* Silén, 1946 (Mayoral, 1988; Fischer and Aguilar, 2001). This trace fossil occurs in marine environments from the littoral to neritic zones in calcareous substrates.

4. Discussion

4.1. Producers, palaeoenvironment and preservation

Bioerosion trace fossils from the Pliocene deposits from the Baía de Nossa Senhora section belong to seven ichnogenera and twenty-two ichnotaxa at the ichnospecies level (Table 1). They are preserved mostly in molluscan, predominantly bivalve, shells (Table 2). They were produced as domiciles mostly by clionaid sponges (*Entobia* isp.), less by bivalves (*Gastrochaenolites*), polychaete worms (*Caulostrepsis*, *Maeandropolydora*), phoronids (*Talpina*) and ctenostome bryozoans (*Iramena*), while *Trypanites* may represent sipunculids, polychaetes or other worms (see Table 3). The assemblage of borings belongs to the *Entobia* ichnofacies (Gibert et al., 1998), which requires an exposure of the hard substrate for, at least, some years (Bromley and Asgaard, 1993b). The borings occur on both sides of the mollusc shells and valves, which show different degrees of abrasion and fragmentation. The occurrence of borings on both sides of shells attests to post-mortem bioerosion. The bioclasts have had to have been rotated and then stabilized for some time enabling colonisation. Some of the filled bivalve borings (*Gastrochaenolites*) are commonly truncated by erosion. This suggests post-filling exhumation and abrasion. Some *Gastrochaenolites* are only partly embedded in the shell. This suggests that an already hardened substrate containing clasts and shells was bored, then fragmented, exhumed and abraded. One of two *Maeandropolydora elegans* observed in specimen INGUJ249P57 is filled with coarse-grained sand. The other is filled with finer and lighter sand. The difference in the filling of the two borings suggests that they were formed in different environments and/or different moments. In some specimens, two *Gastrochaenolites* ichnospecies can be seen in a single shell, while other ichnotaxa co-occur in the same bioclasts (Supplementary Table 3). Encrusting Bryozoa colonies were observed inside an empty *G.* cf. *torpedo* cavity. The clionaid borings (*Entobia*) occur inside some bivalve borings. Entobian growth phases occur in great variety, but the growth phase C is dominant (Fig. 14), which means that the sponges were well developed. All these features also point to a long exposure, thus enabling several phases of colonisation by borers and encrusters. Such interpretation agrees with the general interpretation of the section, where bioclasts were concentrated by winnowing in the marginal part of the shoal/island.

Such borings are presently more abundant at intertidal and shallow-subtidal depths, including *Entobia geometrica*, *E. ovula*, and *Gastrochaenolites torpedo* (see remarks on the Ichnotaxonomical description section). *Entobia laquea* requires the photic zone when produced by *Cliona viridis* (Schmidt, 1862), which lives in symbiosis with green algae. But it can also occur in deeper environments, where it is even more abundant than in shallower zones, similarly to *E. paradoxa* (*E.*?*paradoxa* in the studied material) (Bromley and D'Alessandro, 1990). The observed assemblage of borings suggests a mixture from different bathymetric ranges, where bioerosion took place in several phases during periods of substrate stabilisation. Finally, they were accumulated on an uneven abrasion platform above the fair-weather wave base in the bioclastic ashy calcarenite. The occurrence of *Bichordites* (produced by irregular echinoids) higher in the section relatively to *Macaronichnus*, *Ophiomorpha* and *Piscichnus* (Fig. 3, log 6) points to a transition from the *Skolithos* to the *Cruziana* ichnofacies up section. This suggests a deepening trend from foreshore to shoreface in generally transgressive conditions. This interpretation is in accordance with the same trend observed in the nearby Malbusca section (Rebelo et al., 2016; Johnson et al., 2017).

Nearly all the bioerosion traces, chiefly the sponge borings, are preserved as natural casts infilled by calcite, fine-grained sand, coarse-grained sand and bioclasts, although empty chambers also occur. Formation of the natural casts was possible through selective dissolution of the substrate and filling of the borings, when the filling is more resistant to solution than the substrate (cf. Radwański et al., 2011; Gurav and Kulkarni, 2018; Belaústegui et al., 2018; Łaska et al., 2021). This is very common in the case of aragonitic substrates and calcitic (e.g., Palmer and Plewes, 1993) or dolomitic fillings (Pleydell and Jones, 1988). However, subtler differences in the chemistry of calcite between the substrate and the filling can produce the same effect. It is

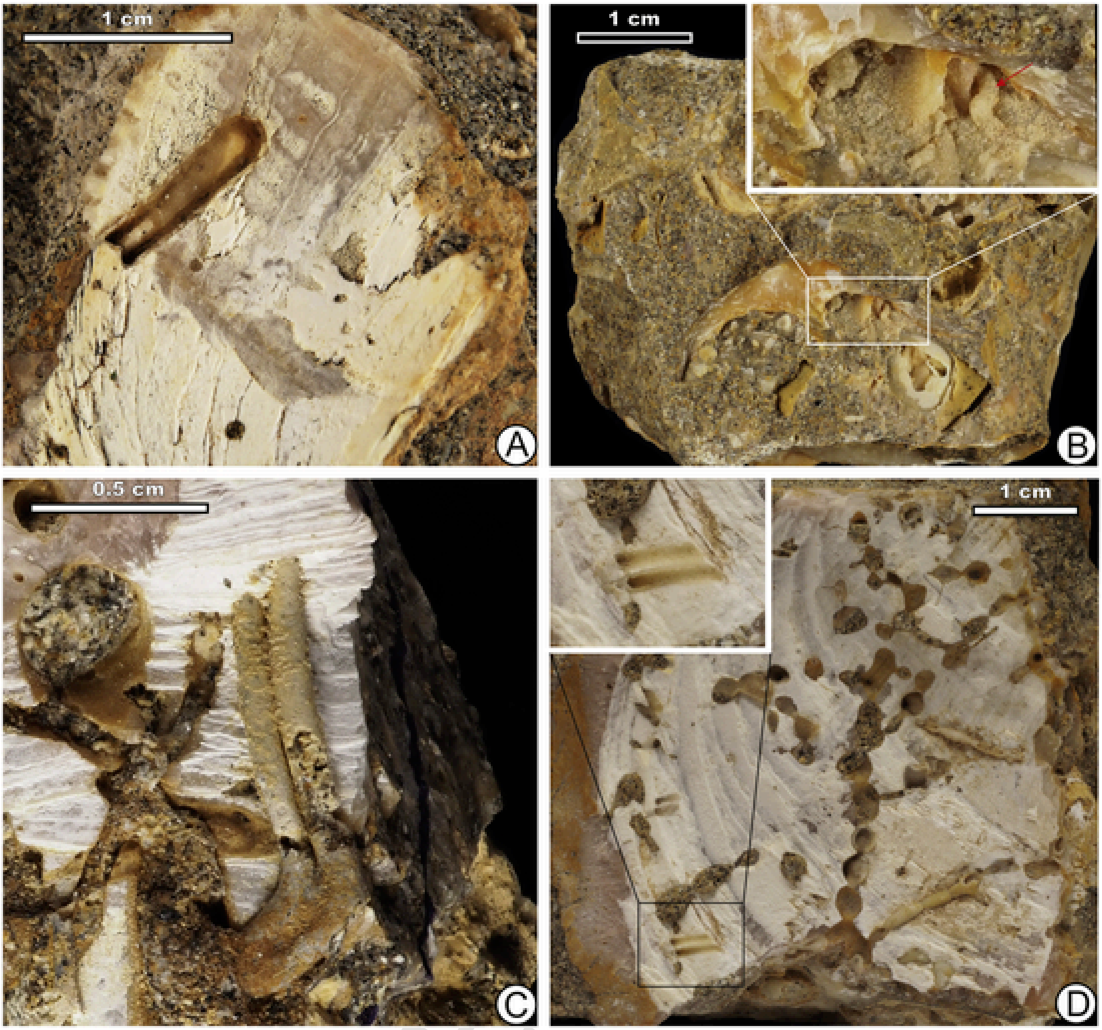


Fig. 11. Polychaete borings from the Baía de Nossa Senhora section. **A.** *Caulostrepsis taeniola* in Bivalvia indet., INGUJ249P26. **B.** *Maeandropolydora sulcans* in Bivalvia indet., INGUJ249P40A. **C.** *Maeandropolydora elegans* in Bivalvia indet., INGUJ249P57. **D.** *Maeandropolydora* isp. and *Entobia laquea* in *Spondylus* sp., INGUJ249P49.

not clear why the natural casts are almost exclusively found in the western cave. This cave is located very close to the cliff face, and it is not excluded that meteoric waters infiltrated rocks in this place for long periods and caused the dissolutions. If so, the formation of natural casts was a local, recent, post-lithification process conditioned by geomorphological changes.

Radwański et al. (2011) suggested that the clionaid sponges *Pione vastifica* and *Cliona celata* and their borings (*Entobia ovula* and *E. geometrica*, respectively) do not occur together, in reference to Miocene and recent examples. However, these borings co-occur in the section studied. The same appears in a late Miocene rocky palaeoshore in the Bozcaada Island in Turkey (Demircan, 2012). This implies that the suggestion by Radwański et al. (2011) is not universal, or that the borings are not in situ and were transported in bioclasts from different settings within the island. In the latter case, the borings and body fossils will represent a time averaged association.

4.2. Comparisons and migrations

Composition of the observed association of borings characterized by the dominance of *Entobia*, *Gastrochaenolites* and polychaete borings (*Caulostrepsis, Maeandropolydora*) is very similar to those recorded in the fossil rocky shores in the Neogene of the Tethys and Paratethys realms, including the Miocene of Poland (e.g., Radwański, 1969), Czech Republic (Mikuláš and Pek, 1995), Turkey (Uchman et al., 2002; Demircan, 2012), Hungary (Dávid, 2010), Spain (Belaústegui et al., 2018; Łaska et al., 2021), Portugal (Santos and Mayoral, 2008) and Egypt (El-Hedeny and El-Sabbagh, 2018); the Pliocene of Italy, Spain and Greece (Bromley and D'Alessandro, 1990; Bromley and Asgaard, 1993a; Mayoral and Reguant, 1995; Gibert et al., 1998); the Pleistocene of Italy (Bromley and D'Alessandro, 1983); the Miocene to Pleistocene of Cabo Verde (Mayoral et al., 2013); and also on the recent Dutch Atlantic coast (Boekschoten, 1966). A compelling argument in support of trans-Atlantic migrations of marine biotas from the Paratethys and Mediterranean seas to the western Atlantic revolves around the relative proximity of different archipelagos acting as stepping-stones for dispersal (Baarli et al., 2017). The cited study is restricted to coral-dwelling pyrogomatid barnacles (subfamily Ceratoconchinae) and embraces a broader time range between the middle Miocene and late Pleistocene. Baarli et al. (2017) hypothesize about the role of former islands now represented by seamounts and other now inactive tectonic islands in the transferal of biotas to Madeira and onward to the Cabo Verde islands, but also consider a counter-flow of biotas from west to east aided by strong marine currents crossing the North Atlantic from Bermuda.

Most of the shallow-water marine organisms that presently occur in the Azorean islands are biogeographically related with eastern Atlantic shores (including Iberia, NW Africa and the Mediterranean Sea) and

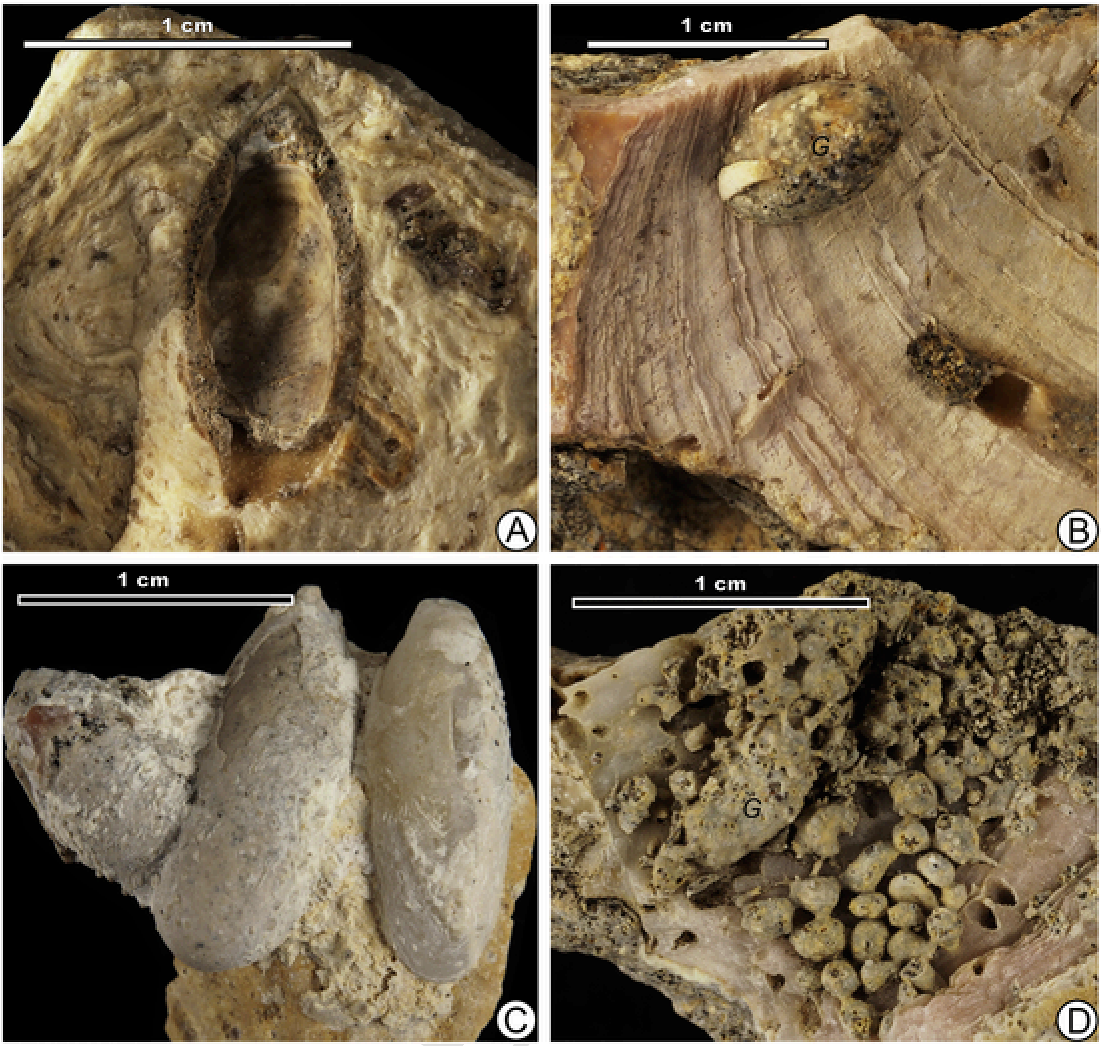


Fig. 12. Bivalve borings from the Baía de Nossa Senhora section. **A.** *Gastrochaenolites lapidicus* in Gastropoda indet. INGUJ249P27. **B.** *Gastrochaenolites lapidicus* in Bivalvia indet. INGUJ249P39. **C.** *Gastrochaenolites* cf. *torpedo* in calcareous material, INGUJ249P28. **D.** *Gastrochaenolites* isp. (G) and *Entobia laquea* in *Ostrea* sp., INGUJ249P88.

with the Webbnesia ecoregion (which includes the archipelagos of Madeira, Selvagens and Canaries) (Freitas et al., 2019). The analysis of the Last Interglacial (MIS 5e) marine gastropods found in the fossiliferous outcrops at Santa Maria Island, Ávila et al. (2009) concluded that "the bulk of the Azorean malacofauna, both in the Pleistocene (71.3%) and in Recent times (75.6%) is biogeographically related with the eastern Atlantic". The few recent biogeographic analyses for the Pliocene Azorean marine biota seem to corroborate this pattern, with the ancestrals of the Azorean fauna reportedly related within the NE Atlantic, the Mediterranean Sea, and the NW shores of Africa (Meireles et al., 2012; Ávila et al., 2016b, 2020). These eastern Atlantic/Mediterranean relationships are ancient, and probably occurred since the earliest colonisation of Santa Maria Island in the late Miocene–early Pliocene, aided by sea surface currents possibly different from the present ones, which, set in place by coeval easterly trade winds, promoted the dispersal of larvae and juveniles/small adults (these attached to rafts) of marine species from European shores towards the western Atlantic. It is known that some were able to reach and successfully colonise American Atlantic shores (Harzhauser et al., 2002; Baarli et al., 2017) and a few reached the Pacific Ocean (Meco et al., 2016) prior to the closure of the Isthmus of Panama. Thus, it is very probable that during the Pliocene, Santa Maria Island was colonized by the larvae of borers from a Mediterranean region or eastern Atlantic/Macaronesian archipelago, similarly to other Pliocene benthic organisms fossilized in the sedimentary deposits of the island (Kroh et al., 2008; Janssen et al., 2008; Winkelmann et al., 2010; Madeira et al., 2011; Ávila et al., 2012, 2015c, 2016b, 2020; Meireles et al., 2012; Rebelo et al., 2014, 2016; Santos et al., 2015; Johnson et al., 2017; Uchman et al., 2016, 2017a, 2018, 2020). Finally, it is not excluded that the presence of similar borings in the middle Eocene to middle Miocene of Jamaica (Blissett and Pickerill, 2004) and Oligocene-Miocene of Grand Cayman (Pleydell and Jones, 1988) might represent a trace of such colonisation of American coasts before that of the Pliocene. The *Entobia* and *Gastrochaenolites* associations in the rocky shores are known from the "Old World" at least since the Cretaceous, with its components at least since the Jurassic (see Gibert et al., 1998 for a review), suggesting that a nursery of the considered rock borers is more probable somewhere in the Tethys than in other parts of the World.

5. Conclusions

Bioerosion structures from the Pliocene deposits of the Baía de Nossa Senhora section, Santa Maria Island (Azores Archipelago) belong to seven ichnogenera and twenty-two ichnotaxa at the ichnospecies level. These were produced dominantly by clionaid sponges (*Entobia*), and in a lesser amount by bivalves (*Gastrochaenolites*), by polychaetes

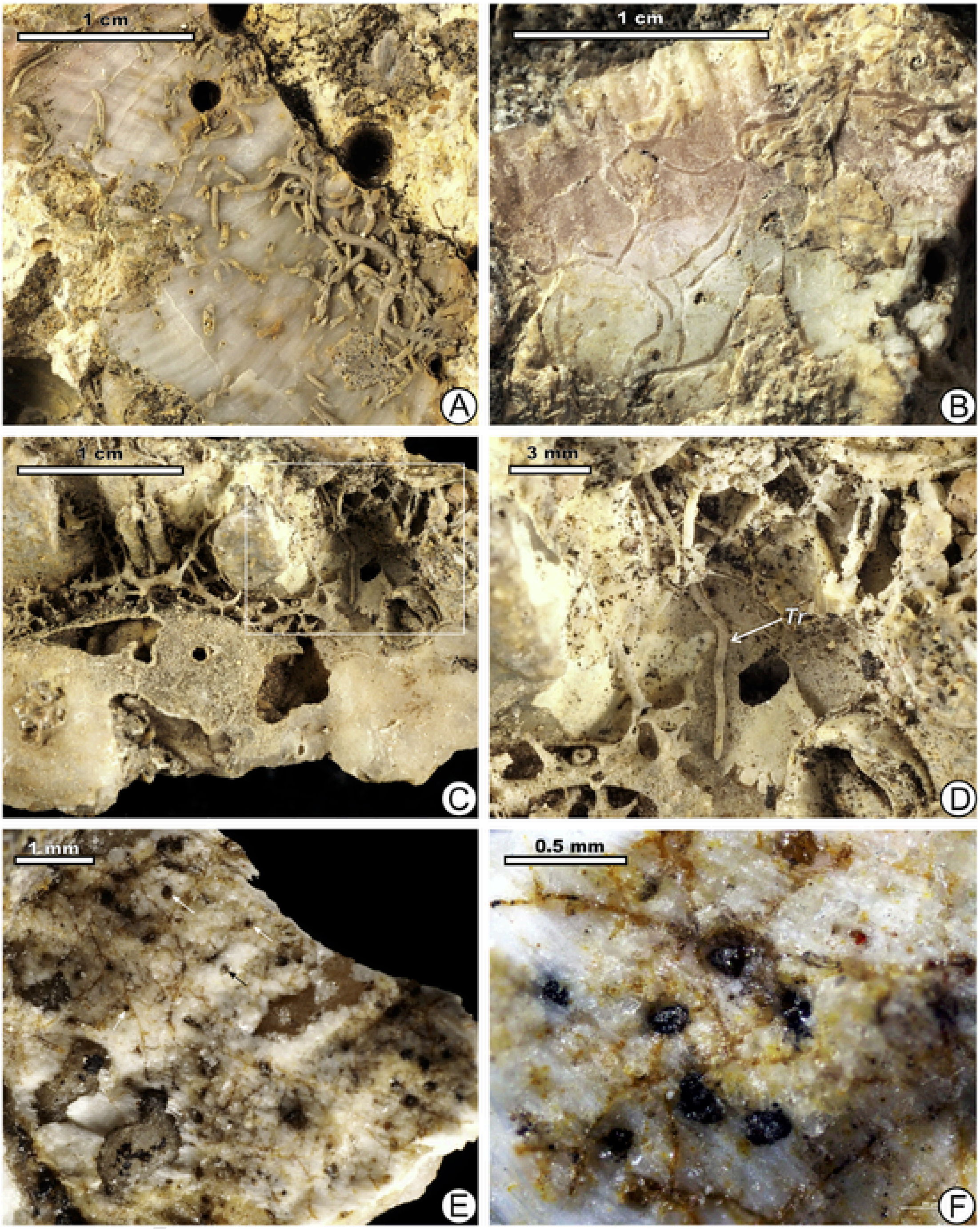


Fig. 13. Other borings from the Baía de Nossa Senhora section. **A.** *Talpina ramosa* in Bivalvia indet., INGUJ249P33. **B.** *Talpina ramosa* in *Spondylus* sp., INGUJ249P72. **C.** *Trypanites solitarius* in Bivalvia indet. INGUJ249P74. **D.** Closer view of *Trypanites solitarius* in Bivalvia indet., INGUJ249P74. **E.** *Iramena danica* in *Spondylus* sp., INGUJ249P111; arrows show zooid cavities. **F.** Closer view of *Iramena danica* in *Spondylus* sp. INGUJ249P111.

(*Caulostrepsis, Maeandropolydora*, partly *Trypanites*), sipunculid (some *Trypanites*), phoronid (*Talpina*) and other worms, and by ctenostome bryozoa (*Iramena*). The majority of the bioerosion trace fossils, especially the sponge borings are preserved as natural casts in molluscan shells, dominantly in bivalves. It can be assumed that the borings were transported in bioclasts from different locations within the island and that the borings and body fossils represent a time averaged association. The assemblage of borings points to the *Entobia* ichnofacies and accords with the rocky shore assemblage reported mostly from the Neogene of the Tethys, Paratethys and the eastern Atlantic coast realms, and much less from the western coasts of the Atlantic. Similar rocky shore assemblages are known since the Mesozoic of the “Old World” and possibly originated in the Tethys region. This supports the fact that the majority of the shallow-water marine organisms that presently occur in the Azorean islands are biogeographically related to the eastern Atlantic shores. This ancient colonisation of Santa Maria Island may have taken place from the east, namely from European shores and from the Webbnesian archipelagos of Madeira, Selvagens and Canaries (or from other islands that nowadays are seamounts), by sea currents that no longer exist, aided by easterly winds.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.palaeo.2021.110284.

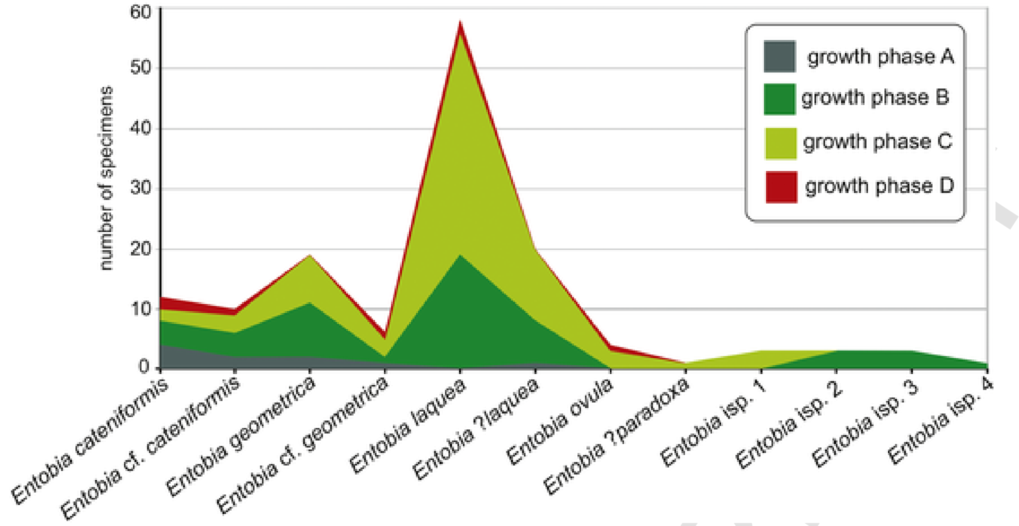


Fig. 14. Growth phase distribution of entobians in the Baía de Nossa Senhora section.

Table 1
Distribution of the identified ichnotaxa. Baía de Nossa Senhora, Santa Maria Island, Azores. The percentage refers to the whole number of specimens in the outcrop.

Ichnotaxa	Specimens	%
Entobia cateniformis	8	4.8
Entobia cf. *cateniformis*	6	3.6
Entobia geometrica	14	8.3
Entobia cf. *geometrica*	3	1.8
Entobia laquea	44	26.2
Entobia?laquea	14	8.3
Entobia ovula	3	1.8
Entobia?paradoxa	1	0.6
Entobia isp. 1	3	1.8
Entobia isp. 2	3	1.8
Entobia isp. 3	4	2.4
Entobia isp. 4	1	0.6
Caulostrepsis taeniola	3	1.8
Maeandropolydora sulcans	8	4.8
Maeandropolydora elegans	1	0.6
Maeandropolydora isp.	5	3.0
Gastrochaenolites lapidicus	17	10.1
Gastrochaenolites cf. *torpedo*	12	7.1
Gastrochaenolites isp.	5	3.0
Talpina ramosa	10	6.0
Trypanites solitarius	2	1.2
Iramena danica	1	0.6

Uncited references

Bromley and D'Alessandro, 1987
Bronn, 1837–1838
Hagenow and Von, 1840

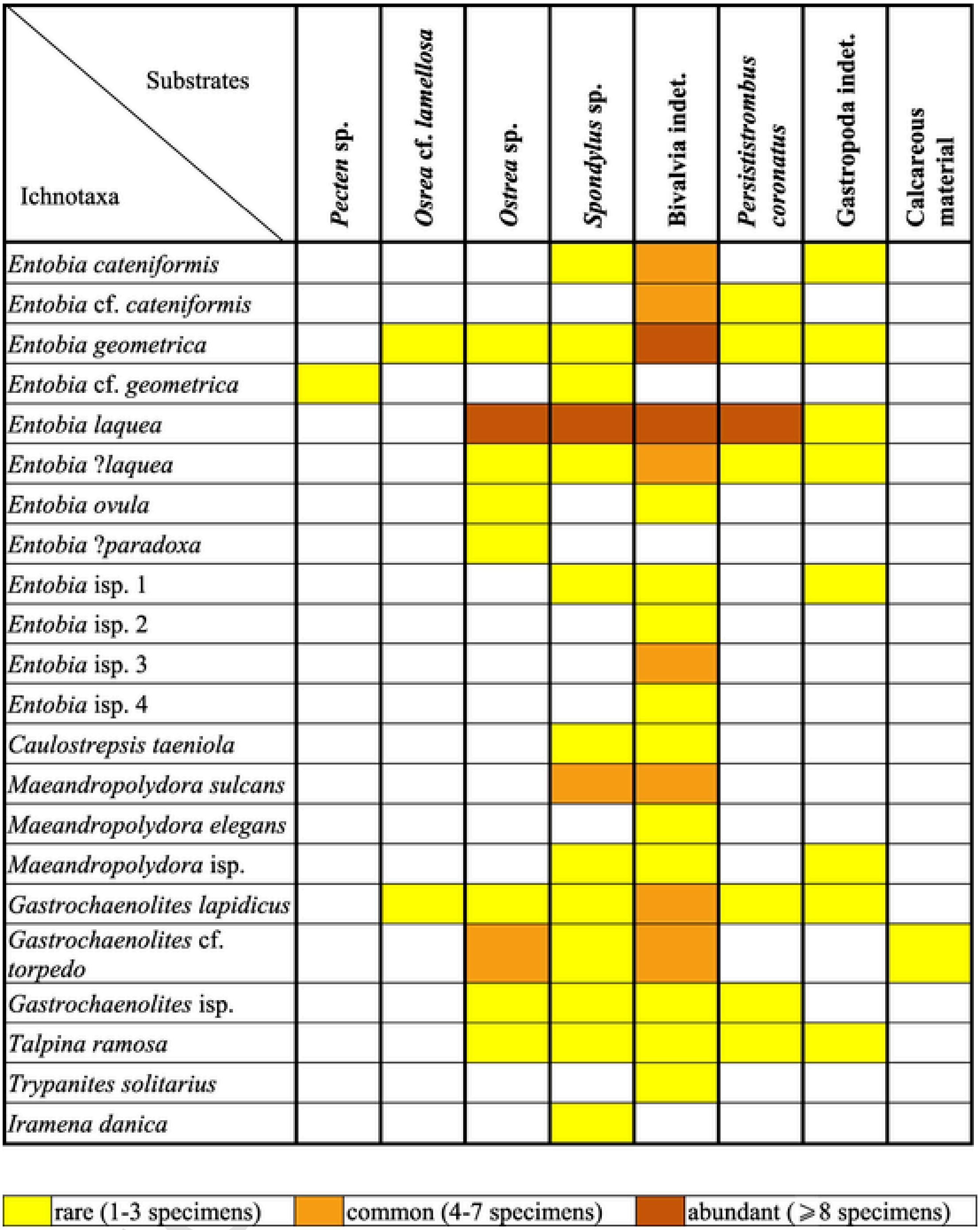
Declaration of Competing Interest

None.

Acknowledgements

This work was supported by FEDER funds through the Operational Programme for Competitiveness Factors – COMPETE, by National funds through FCT – Foundation for Science and Technology under the UID/Multi/04326/2013, UID/BIA/50027/2013, UID/BIA/00329/2013, 2015-2018, UID/BIA/00329/2019, FCT/UIDB/50019/2020 – IDL, and POCI-01-0145-FEDER-006821 projects, and by Regional funds through DRCT-M1.1.a/005/Funcionamento-C-/2016 (CIBIO-A). This work was also financed by FEDER in 85% and by Azorean Public funds by 15% through Operational Program Azores 2020, under the projects VR-PROTO (ACORES-01-0145-FEDER-000078) and AZORESBIOPORTAL –PORBIOTA (ACORES-01-0145-FEDER-000072). We thank the Direção Regional da Ciência, Tecnologia e Comunicações (Regional Government of the Azores), FCT (Fundação para a Ciência e a Tecnologia) and Câmara Municipal de Vila do Porto (Santa Maria Island, Azores) for financial support, and the Câmara Municipal de Vila do Porto for field assistance. We are grateful to the organizers and participants of several editions of the International Workshops "Palaeontology in Atlantic Islands" who helped with fieldwork (2002, 2005–2019). AU received additional support from the Jagiellonian University (DS fund). CSM is benefiting from a PhD grant M3.1.a/F/100/2015 from FRCT/Açores 2020 by Fundo Regional para a Ciência e Tecnologia (FRCT). SPA and RSR acknowledge their IF/00465/2015 and IF/01641/2015 research contracts funded by FCT. ACR was supported by a postdoctoral grant SFRH/BPD/117810/2016 by FCT. Rozália Fodor (Debrecen) helped to construct Fig. 7. We thank the Editor Thomas Algeo, Ana Santos and an anonymous reviewer for their critical remarks, which helped to improve the paper.

Table 2
Number of occurrences of the observed ichnotaxa according to the different substrates.



Substrates / Ichnotaxa	*Pecten* sp.	*Osrea* cf. *lamellosa*	*Ostrea* sp.	*Spondylus* sp.	Bivalvia indet.	*Persististrombus coronatus*	Gastropoda indet.	Calcareous material
Entobia cateniformis				🟨	🟧		🟨	
Entobia cf. *cateniformis*					🟧	🟨		
Entobia geometrica		🟨	🟨	🟨	🟫	🟨	🟨	
Entobia cf. *geometrica*	🟨			🟨				
Entobia laquea			🟫	🟫	🟫	🟫	🟨	
Entobia ?laquea			🟨	🟨	🟧	🟨	🟨	
Entobia ovula			🟨		🟨			
Entobia ?paradoxa			🟨					
Entobia isp. 1				🟨	🟨		🟨	
Entobia isp. 2					🟨			
Entobia isp. 3					🟧			
Entobia isp. 4					🟨			
Caulostrepsis taeniola				🟨	🟨			
Maeandropolydora sulcans				🟧	🟧			
Maeandropolydora elegans					🟨			
Maeandropolydora isp.				🟨	🟨		🟨	
Gastrochaenolites lapidicus		🟨	🟨	🟨	🟧	🟨	🟨	
Gastrochaenolites cf. *torpedo*			🟧	🟨	🟧			🟨
Gastrochaenolites isp.			🟨	🟨	🟨	🟨		
Talpina ramosa			🟨	🟨	🟨	🟨	🟨	
Trypanites solitarius					🟨			
Iramena danica				🟨				

🟨	rare (1-3 specimens)	🟧	common (4-7 specimens)	🟫	abundant (⩾8 specimens)

Table 3
Etology and producer organisms of the identified ichnotaxa. Baía de Nossa Senhora, Santa Maria Island, Azores. * – this bivalve produces *Gastrochaenolites torpedo* in the Azores.

Ichnotaxa	Ethological category	Producers
Entobia cateniformis	Domichnia	*Cliona vermifera*
Entobia cf. *cateniformis*	Domichnia	*Cliona vermifera*
Entobia geometrica	Domichnia	*Cliona celata*
Entobia cf. *geometrica*	Domichnia	*Cliona celata*
Entobia laquea	Domichnia	*Cliona viridis* *Pione vastifica* *Spiroxya heteroclita*
Entobia?laquea	Domichnia	*Cliona viridis* *Pione vastifica* *Spiroxya heteroclita*
Entobia ovula	Domichnia	*Pione vastifica* *Cliona glomerata* *Cliona schmidtii* *Cliona vermifera*
Entobia?paradoxa	Domichnia	*Cliona celata*
Entobia isp. 1	Domichnia	Clionaid Porifera
Entobia isp. 2	Domichnia	Clionaid Porifera
Entobia isp. 3	Domichnia	Clionaid Porifera
Entobia isp. 4	Domichnia	Clionaid Porifera
Caulostrepsis taeniola	Domichnia	*Polydora ciliata* *Lysidice ninetta*
Maeandropolydora sulcans	Domichnia	Spionid Polychaeta
Maeandropolydora elegans	Domichnia	Spionid Polychaeta
Maeandropolydora isp.	Domichnia	Polychaeta
Gastrochaenolites lapidicus	Domichnia	*Gastrochaena dubia* *Lithophaga* sp. *Hiatella* sp. *Parapholas* sp.
Gastrochaenolites cf. *torpedo*	Domichnia	*Leiosolenus aristatus* * *Lithophaga lithophaga* *Gastrochaena* sp.
Gastrochaenolites isp.	Domichnia	Bivalvia
Talpina ramosa	Domichnia	Phoronida
Trypanites solitarius	Domichnia	Sipunculida Acrothoracica Polychaeta
Iramena danica	Domichnia	Ctenostomata (*Penetrantia*, *Immergentia*)

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