Role of environmental change in rock-boring echinoid trace fossils

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ABSTRACT

Well preserved groove-borings related to the boring activity of regular sea urchins are preserved on Neogene rocks associated with rocky palaeoshores in a volcanic oceanic

island (Santa Maria, Azores archipelago) and a continental margin (Foz da Fonte, Central West Portugal).

The new trace fossil consists of a series of relatively deep grooves, with sinuous pathway and with a fairly uniform width along its trajectory. A series of forward oriented concave markings occur frequently inside the grooves, reflecting the movement direction of the producer. The trace fossil is designated as *Ericichnus* igen. n. with two new ichnospecies, *Ericichnus bromleyi* isp. n. and *Ericichnus asgaard* isp. n. *Ericichnus* igen. n. could have been produced by regular echinoids, similar to the extant echinometrid echinoid *Echinometra lucunter* (Linnaeus, 1758) for *E. bromleyi* isp. n. and similar to the echinid *Paracentrotus lividus* Lamarck, 1816 for *E. asgaard* isp. n. Ethologically, the compound trace fossil *Ericichnus* igen. n.-*Circolites* may correspond to an agrichnion-pascichnion and/or domichnion. Our study suggests that the new ichnospecies *E. bromleyi* may be used as a palaeoenvironmental tool, indicating the boring activity of termophile rock-boring echinoids in the fossil record.

Keywords: Echinoid bioerosion; *Ericichnus* igen. n.; non-sedimentary rocks, palaeorocky-shores; compound trace fossils; palaeoclimatic changes

1. Introduction

Echinoids are major components of marine benthic communities and play a critical role both in the production of carbonate sediments and as active bioeroders (e.g. Neumann, 1966; Bromley, 1975; Hoskin et al., 1986; Bak, 1994; Allouc et al., 1996; Mokady et al., 1996; Glynn, 1997; Chazottes et al., 2004). While grazing, sea urchins can scrape rocky or coral substrate covered by algae that act as a structuring force in coral reef environments. For example, Mills et al. (2000) estimated for the species

Echinometra mathaei Blainville, 1825 an average individual coral bioerosion of 0.32 $\text{CaCO}_3 \text{ g day}^{-1}$.

Numerous studies reported from the fossil record reveal structures that resulted from the bioerosive activity of regular sea-urchins, especially of those living on rocky shores (e.g., Radwański, 1969; Martinell and Domènech, 1986; Bromley and Asgaard, 1993; Mayoral and Muñiz, 1996; Gibert et al., 1998; Santos et al., 2008, 2011; Johnson et al., 2011) or boring on shell surfaces (e.g. Gibert et al., 2007; Radley, 2006; Santos and Mayoral, 2008). However, only two ichnotaxa described are related undoubtedly to the bioerosion activity of sea urchins: *Gnathichnus* Bromley, 1975 and *Circolites* Mikuláš, 1992. Yet, the ichnotaxon *Planavolites* Mikuláš, 1992, was tentatively assumed to be produced by chitons, gastropods and echinoids.

Gnathichnus is a star-shaped trace which is usually observed on skeletal remains, mostly on molluscan shells from the Middle-Upper Triassic to Recent (Fürsich and Wendt, 1977; Martinell and Domènech, 1981, 1986; Wilson, 2003; Radley, 2006; Santos and Mayoral, 2008). This grazing trace was likely imprinted by the five hard teeth of the feeding apparatus (Aristotle's lantern) of sea urchins, which allow them to scrape substrates covered by algae (Bromley, 1975).

Circolites is a cup-shaped boring first described from Lower Cretaceous materials at the Štramperk quarry in Moravia, Czech Republic (Mikuláš, 1992). However, *Circolites* is common on Neogene hard substrata, mainly limestone and calcarenite surfaces (Fürsich, 1979; Gibert et al., 1998; Santos et al., 2008; Johnson et al., 2011). The boring mechanisms used by the producers have been described in Holocene environments by John (1889 in Otter, 1932) and were interpreted as the abrading action of the teeth and spines of sea urchins.

The present study describes a new bioerosion structure that occurs on an unconformity over Upper Miocene (Messinian) bioclastic sandstone at Santa Maria Island (Azores Archipelago, Portugal) reflecting a rocky shore and on the unconformity of the Lower Miocene erosional surface on Cretaceous limestone reflecting a Burdigalian rocky shore, outcropping on the western coast of the Setúbal peninsula (Foz da Fonte, Central West Portugal).

The aim of this study is to focus on the identification, ichnotaxonomy, description, and interpretation of a new sea-urchin trace fossil. Compelling reasons to do so are twofold: (1) from an ichnotaxonomic point of view (first time that this structure is described from the fossil record); and, (2) to use this new bioerosion structure as proxy indicating the activity of termophile rock-boring echinoids in the fossil record.

2. Geographical and geological setting

The Azores archipelago (Portugal) is located in the middle of the North Atlantic, consisting of nine volcanic islands extending along 600 km with a direction NE-SW. “The Ichnofossil’s cave” outcrop is located on Santa Maria Island (the southernmost island of the Azores archipelago; Fig. 1).

In this location, the complete section exposed from bottom to top in the sea cliff is similar to the one seen in the nearby coastal area of Malbusca (500 m SE), composed of a 130 m thick sequence of submarine sheet flows, pillow-lavas and hyaloclastites intercalated with several tabular, fossiliferous biocalcarenitic beds, capped by subaerial lavas and the remains of a phreatomagmatic cone (Ávila et al., 2012). The basal submarine lavas and the first and main calcarenitic bed (between 16–25 m above sea level, asl, approximately) are considered part of the Touril Complex, whereas the lavas

and sediments above are assigned to the Facho-Pico Alto Volcanic Complex (Serralheiro et al., 1987; Serralheiro, 2003). Meireles et al. (2012) based on ostracods suggest a latest Miocene age for the calcarenitic beds of the Touril Complex in accordance with the age inferred by previous authors (Serralheiro et al., 1987; Serralheiro and Madeira, 1990; Serralheiro, 2003).

The herein called "Ichnofossil's cave" is a huge hollow carved by marine erosion in the sea cliff. The stratigraphic section exposed inside the "Ichnofossil's cave" is composed of seven beds, from bottom to the top (Fig. 2): (i) ~ 2 m of a reworked conglomerate/pillow breccia (Fig. 2, bed A); (ii) 0.6 m of a bioclastic, fossiliferous fine sandstone with *Arenicolites* isp., *Bichordites* isp., *Macaronichnus segregatis* Clifton and Thompson, 1978, *Dactyloidites otto* (Geinitz, 1849) (Figs. 4A-D) and *Circolites kotouzensis* Mikuláš, 1992. Some bivalve molluscs (*Manupecten pesfelis* (Linnaeus, 1758), *Spondylus* sp.) and large echinoids (*Clypeaster altus* (Leske, 1778) are present, although not common (Fig. 2, bed B); (iii) a horizontal stratified fine volcanoclastic sand 30 cm thick, with fine horizontal bedding and abundant fossil echinoids (*C. altus*), molluscs (*Spondylus* sp., *Bufonaria* cf. *marginata* (Gmelin, 1791), and Epitoniidae), the endemic barnacle *Zullobalanus santamariaensis* Buckeridge & Winkelmann, 2010 (Winkelmann et al., 2010) and fish vertebrae. Macrooids and rhodoliths also are present (Fig. 2, bed C); (iv) 2.5 to 4 m of foresets of volcanoclastic sand (reworked pyroclasts) with large scale cross bedding stratification, as a result of multiple events. This bed contains a few valves of *Ostrea* sp. (Fig. 2, bed D); (v) 0.5 m of compact limestone (Fig. 2, bed E) and a ~80 m thick pile of submarine basaltic lava flows, with abundant pillow lavas (Fig. 2, bed F); and (vi) a 0.5 m thick Pleistocene level located at about 8 m above present sea level (Fig. 2, bed G) corresponding to the last interglacial (MIS 5e) highstand that unconformably cuts the previously described Miocene sequence. This

deposit features a rolled pebble beach (with pebbles 5 to 40 cm in length) and contains abundant fossil molluscs (e.g., *Patella aspera* Röding, 1798). *Gastrochaenolites* isp. produced by *Myoforceps aristatus* (Dillwyn, 1817) can be seen on the ramp that connects the Miocene (facies B, Fig. 2) and the Pleistocene level (facies G, Fig. 2).

The Foz da Fonte site near Lisbon (Fig. 1) is a highly bioeroded hardground surface, which corresponds to a subhorizontal transgressive surface cut through a previously emerged topographic feature showing karstified carbonate relief (see Santos et al., 2010). The bioeroded surface is located about 10 m above present day mean sea level (Fig. 3). This surface, as well as the bioerosion structures affecting it, is Miocene in age and developed unconformably on the contact between Lower Cretaceous limestones (Albian age) below, and Lower Miocene conglomeratic and calcarenitic sediments above (Silva et al., 1995, 1999; Manupella et al., 1999; Santos et al., 2010).

The firstly described trace fossil is located on top of the bioclastic sandstone ("Ichnofossil's cave", bed B, Fig. 2) and the limestones (Foz da Fonte, Fig. 3), which represent the surfaces of former rocky shores. The beds on which the surfaces have been carved are bioturbated. Yet in the outcrop of the "Ichnofossil's cave" bioturbation is much more intense with *Arenicolites* isp., *Bichordites* isp., *Macaronichnus segregatis* and *Dactyloidites otto* (Figs. 4A-D) being partially infilled and preserved by the overlying volcaniclastic sediments (Figs. 4F-G). The Cretaceous limestones at Foz da Fonte are characterized exclusively by *Ophiomorpha nodosa* Lundgren, 1891 (Figs. 4E). To perform this study, the bioeroded hardgrounds were cleaned, and the bioerosion structures were identified and measured in detail.

3. Systematic palaeoichnology (by A. Santos and E. Mayoral)

Ichnogenus *Ericichnus* igen. n. Santos and Mayoral

Etymology From the Latin *ēricīus* (sea urchin).

Type ichnospecies *Ericichnus bromleyi* isp. n.

Diagnosis Grooves relatively deep, with sinuous pathway, with a width fairly uniform along its trajectory. Often they show points where the path is bifurcated reaching, in these cases, a width which can be the double of the normal diameter. Inside there are a number of lines or marks, more or less pronounced, with a concavity oriented in the animal's direction of movement.

Remarks The characteristics of *Ericichnus* igen. nov. are somewhat similar to those of the ichnotaxon *Planavolites* Mikuláš 1992 described from the Lower Cretaceous at the Štramberk quarry in Moravia (Czech Republic). However, *Ericichnus* igen. nov. and *Planavolites* differ substantially in their general structure and dimensions between 150 to 300 cm and 1 to 9.5 cm in length, respectively. *Ericichnus* igen. nov. is a system of grooves having concave lines oriented in the animal's direction of movement and presenting a bifurcation model very well defined. By contrast, *Planavolites* don't exhibit never these characteristics (Mikuláš 1992, pag. 307, Fig. 6). On the other hand, one of the most important distinctions between *Ericichnus* igen. nov. and *Planavolites* is the lack of hemispherical depressions associated with *Circolites kotoucensis* randomly distributed on the lateral margins of the grooves in the latter, for which there is no doubt that echinoids are the producers of *Ericichnus* igen. nov.

Ericichnus bromleyi isp. n. Santos and Mayoral

Figures 4F-G, 5-7

Derivation of name In honour of Richard Bromley, eminent ichnologist and tireless researcher in the search and study of the boring echinoids.

176 *Type material* All the material studied and illustrated here comes from the
177 "Ichnofossil's cave" (Santa Maria Island, Azores Archipelago, Portugal), and is Late
178 Miocene to Early Pliocene in age. The structures correspond to a highly complex
179 system of grooves recorded on the rocky surface. The type of the newly erected
180 ichnospecies is housed in the Collection of the Department of Biology of the University
181 of the Azores, Ponta Delgada (São Miguel Island, Portugal).

182 *Type locality* "Ichnofossil's cave", south of Santa Maria Island, Azores.

183 *Type horizon* Bioclastic sandstones. Touril Complex (See Serralheiro et al., 1987;
184 Serralheiro, 2003).

185 *Holotype* EM-UH/08-SM001 (Fig. 5A).

186 *Paratype* EM-UH/08-SM002 (Fig. 5C).

187 *Diagnosis* Grooves with a pathway defined by an apparently irregular system,
188 labyrinthine in aspect, which shows a pattern characterized by the repetition of two
189 different kinds of polygonal paths.

190 *Description* Series of elongated grooves relatively deep, with an average depth ranging
191 from 1.5 to 2 cm, and a width ranging from 1.8 to 5.3 cm. The grooves, characterized by
192 a wandering trajectory (apparently irregular), are interconnected when they are
193 numerous (i.e., high density) with frequent bifurcations that can have a width of up to
194 10 cm. (Figs. 5A-B). A number of lines or marks more or less prominent can be
195 observed inside the grooves, concave towards the direction of the groove progress,
196 which indicates the successive positions of the producer (sea urchin) and consequently,
197 the direction of its movement. The number of moves/positions varies from 12 to 15 for
198 grooves of 35 cm length.

Hemispherical depressions of cup-shaped borings, with a rounded contour, are randomly distributed on the lateral margins of the grooves, which correspond to the ichnotaxon *Circolites kotoucensis* Mikuláš, 1992 (Figs. 5-7).

The grooves form a network that increase in complexity with the groove density, and can cover an area of 3 to 4 m². A more detailed analysis of this geometric disposition reveals a pattern defined by two types of trajectories. The first model is represented by a groove network extending up to 3 m in length, and composed of small “modules” (patterns) of ~60 cm in length. These modules show a subrectangular pattern that repeats itself more or less regularly and sometimes in a symmetric way (Figs. 6A-B). The second model is more irregular, with a total length that can reach 1.5 m with the presence of smaller modules (~ 30 cm). The modules are characterized by a subtriangular pattern, which form loops, relatively close to each other. (Figs. 7A-B).

Remarks See remarks on the ichnogenus. Currently, the regular echinoid Echinometridae is the only known animal family with members capable of producing such large and prominent depressions or grooves when they forage for food. The species *Echinometra mathaei* (Blainville, 1825) produces many hemispherical depressions that correspond to *Circolites*, while *E. lucunter* (Linnaeus, 1758) is an active bioeroder that has an oval external exoskeleton that would fit perfectly in the observed grooves. The sea urchins *E. lucunter* adopt a sit-and-wait feeding strategy, firmly attached to the walls of the groove in order to capture drifting pieces of algae (McLean, 1967; Hunt, 1969). The foraging behaviour of *Echinometra* results in the production of deep grooves with complex networks, almost always intersecting with one another where the density of occupation is high (Asgaard and Bromley, 2006). This is in accordance with the presence of subrectangular patterns related with high density

of occupation by sea urchins. In the same way, the presence of subtriangular patterns is associated with a low density of occupation.

Krumbein and Van der Pers (1974) also noted that *Echinus esculentus* (Leach, 1942) follows a grazing behaviour on the substrate through a meandering course, which creates a fairly sinuous, shallow corridor, and a width equivalent to the diameter of the sea urchin. This groove takes on the ovoid and even cylindrical shape of the cross section of its own test.

The effect is that the groove is continually deepening to produce bridge structures and connections with other grooves, which are in this way, projected as branching. Our observations suggest that the grazing activity of *Echinometra lucunter* can produce canals that are very similar to the trace fossil identified.

Other echinometrids like *E. oblonga* (Blainville 1825), do not have a preferential direction of movement (Asgaard and Bromley, 2006). According to Russo (1977), *E. oblonga* is a rock-burrowing sedentary echinoid, frequently found in algal reefs and its distribution and abundance is significantly correlated with water flow over the reef and with detrital algae being deposited in its burrow. Such kind of trophism seems most likely to eliminate the possibility that *E. oblonga* was the producer of grooves similar to ours.

Echinoid material collected and studied by Madeira et al. (2011) from the Pleistocene fossiliferous outcrops of Santa Maria Island includes species of regular echinoids (*Sphaerechinus granularis* (Lamarck, 1816); *Arbacia lixula* Linnaeus, 1758; *Paracentrotus lividus*). Of these three species, only *P. lividus* is a rock-boring species able to erode cup-shape borings similar to *Circolites kotoucensis* found on the margins

of the described grooves. However, it does not produce traces with grooves. Thus, it is unlikely to be the potential producer of *Ericichnus bromleyi* isp. n.

Stratigraphic range Upper Miocene to Recent.

Ericichnus asgaardi isp. n. Santos and Mayoral

Figure 8A

Derivation of name In honour of Ulla Asgaard, a tireless scientist in the search and study of the boring echinoids.

Type material All the material studied and illustrated herein comes from Foz da Fonte, and is Early Miocene in age. The structures correspond to a simple pattern of a wide groove recorded on the rocky surface. The type material of these newly erected ichnospecies are housed in the E. Mayoral Neogene Bioerosion Collection at the University of Huelva, (Spain).

Type locality Foz da Fonte, Atlantic coast of the Setúbal Peninsula, central west Portugal.

Type horizon Lower Cretaceous (Albian) limestones (See Manupella et al. 1999; Santos et al., 2010).

Holotype EM-UHU/08-FzF001 (Fig. 8A).

Diagnosis Wide, deep groove with a lightly sinuous, simple to bifurcated pathway.

Description A simple groove, bifurcated in one edge, showing a gentle sinuous pathway. This groove is 2 m long, with 9 to 10 cm width and reaching 4.5 to 6.0 cm depth. Along the groove and in its margins are located several hemispherical depressions (up to 33 specimens) that correspond to *Circolites kotoucensis* (Figs. 8-9). The diameter of these depressions varies from 3.3 to 10.7 cm, with an average value of 5.8 cm. The section of the groove changes according to different sectors. Near the SE

edge (Section I-I', Fig. 8B) is U shaped and the bottom is flat. Towards the NW direction, the bottom is excavated to two levels leaving small shelves (Sections II-II' and III-III', Figs. 8B, 9E, G) and next to the NW edge (Section IV-IV', Figs. 8B, 9A, B) the U shape is more complex showing up to two terraces disposed to different heights just opposite one to another. The upper terraces are 3 to 3.5 cm deep, meanwhile the bottom of the groove can reach up from 1.5 to 2.5 cm below the first ones.

Remarks See remarks on the ichnogenus. Regular echinoid family Echinidae includes an active bioeroder, *Paracentrotus lividus*, which excavates shallow depressions or pits in the rock surface, often up from 5 to 10 cm deep (Otter, 1932; Trudgill, 1988). This sea urchin is largely confined to rock pools in the middle intertidal zone, but also occurs in the lower intertidal zone. The excavation is achieved by the mechanical abrading action of the teeth and spines, leaving a hemispherical pit (*Circolites*).

Trudgill et al. (1987) concluded that *P. lividus* is a major factor in pool deepening in the middle intertidal zone. These authors observed that some crevices and joints were widened for protection from wave action. Hence, pool deepening is followed by lateral widening that becomes more significant during the later stages of erosion, but disappears with urchins operating from the center of the exposed pools. This process is consistent with the characteristics observed in this new ichnospecies. A sequence of small pools was developed and widened along a joint oriented NW to SE according to the second more frequent set of regional crevices. Consequently, a protected runnel was produced to minimize desiccation during the few hours of subaerial exposure in the tidal cycle.

In our case, two or at least three generations of sea urchins are registered, as evidenced by the different terraces shown in cross sections. This reflects that re-exploitation of a

groove by different generations of sea urchins appears profitable since less energy is spending in beginning a new one. The oldest generations are related to the large *Circolites* located on the margin of the groove and situated in the higher most part of the same.

Stratigraphic range Lower Miocene to Recent.

4. Discussion

4.1. Record of Circolites in non-sedimentary substrates

Rocky intertidal communities exist in a mosaic of substrate types that may differ in a variety of ways from hard granite to softer sandstones. Surprisingly, the role of fossil sea urchins in comparison to others organisms like boring bivalves as bioeroders of non-sedimentary rocks (Santos et. al., 2012) has scarcely been studied.

To date, the presence of *Circolites* in sedimentary rocks is well known, and several studies have focused on the role that sea urchins play as bioeroders of coral substrates (e.g., Birkeland, 1989; Bak, 1994; Mokady et al., 1996; Carreiro-Silva and McClanahan, 2001). Yet, the same bioprocesses recorded in non-sedimentary rocky shores have seldom been studied. The oldest trace known so far is recorded by Johnson et al. (2014) for Miocene basalt boulders from São Nicolau Island in the Cape Verde (Table 1). *Circolites* also appears in basalt substrates from the Pleistocene (Santa Maria Island, Azores archipelago (Ávila et al., 2008b); Santiago Island (Baarli et al., 2013), and Sal Island (Cape Verde archipelago) (Table 1). Much less is known about *Circolites* on recent magmatic substrata and / or weathered rocks. Effectively, only a few observations were made in Ngaparou (Senegal) on thick ferruginous crusts (ironpans) (Allouc et al., 1996), in the Cape Verde Archipelago at the western coast of Sal Island, carved on tuffs (Ramalho et al., 2013), or at the southern coast of Santo Antão Island, in

basalts (Ramalho, 2011) (Table 1). The presence of *Circolites* in metamorphic rocks also is reported by Santos et al. (2011) from Upper Miocene marble boulders in South Spain and by Watkins (1990) from Pliocene marbles in Coyote Mountains (Salton, California, USA) (Table 1).

The large number of references concerning “cup-shaped borings”, “bore-holes”, “pits”, “pot-holes” or “thimble-shaped borings” both in plutonic and volcanic rocks as well metamorphic rocks in the Holocene is extensive (Table 1). The extensive nature of these data suggests this kind of bioerosive structure was overlooked in the fossil record as the presence of *Circolites* in non-sedimentary rocks may be not as rare as previously thought. In this case, the widespread characteristic feature of bioerosion in so many different substrate types may be related to the boring mechanisms of their producers, which is entirely mechanical and completely dependent on the strength of spines and teeth (John, 1889 in Otter, 1932). It appears that rock composition may not so dramatically limit the presence of echinoid borings in non-sedimentary rocks, as was previously thought.

4.2. *Ericichnus* record in the Holocene

As considered above, the presence of these kinds of boring systems is frequently observed in marine environments, nowadays (Fig. 10A) (McLean, 1967; Bromley, 1978; Grünbaum et al., 1978; Prager and Ginsburg, 1989; Asgaard and Bromley, 2008), and it is produced by sea-urchins. Nevertheless, little attention was paid to it and only the grooves made by *Diadema mexicana* from the Pacific coast of Costa Rica (Fischer, 1981) and Kona coast Hawaii (Grünbaum et al., 1978) by *Echinometra mathaei* have been described but never from an ichnotaxonomic point of view.. The research carried out in recent years in the Cape Verde archipelago enabled the discovery of the same

boring systems described herein, as *Ericichnus* igen. n. but with examples that are
 strictly Holocene in age. The borings are present in a horizontal surface of basaltic tuff
 in the western leeward coast of Sal (Fig. 10B). This horizontal surface lies between the
 lower supratidal and the mean level of the low tide in a surf bench. The locality
 represents an exposed setting covered by coralline algae. The algal turf usually present
 in the groove-shaped borings is completely scraped off and the surface of the grooves
 show a pale-coloured patina of the kind mentioned previously by Asgaard and Bromley
 (2008, Fig. 1A, pag. 283). The algal turf outside the borings is rarely grazed by the
 echinoids.

When found living within the borings, the producers have been identified as
Echinometra lucunter. In some grooves it is possible to find up to three or four
 individuals (Fig. 10C). This observation agrees with remarks by Hunt (1969) who
 observed non-aggressive behaviour between conspecifics, as opposed to other authors
 who reported agonistic behaviour between *E. lucunter* (Grünbaum et al., 1978) or *E.*
mathaei (Tsuchiya et al., 1991). The borings are relatively deep, with the result that its
 producers become virtually “submerged” within the borings. The borings typically show
 a length ranging from 15 to 25 cm and a width ranging from 5 to 10 cm. Some of the
 borings are interconnected but due to so high a density there are no visible patterns in
 the network, as shown by *Ericichnus* igen. n.

4.3. Palaeoenvironmental interpretation

The bioerosion features newly described herein represent traces produced on
 former rocky shores by echinoids adapted to life in the low intertidal zone. The current
 ichnofossil assemblages are preserved under the influence of low intertidal and shallow
 water zonation and are associated with an early stage of colonization on a stable

substrate. In fact, grazers such as sea urchins are an important source of disturbance in many hard substrate communities. They constantly expose bare substrate that may be colonised by other early successional boring and encrusting organisms and, thus prevent the development of a “mature” community of borers (Taylor and Wilson, 2003) and encrusters. In this context, the absence of remains from epilithobiont communities in the areas with bioerosion is related clearly to substrates exposed to high levels of grazing by echinoids, as suggested by the research of Breitburg (1985). According, only algal crusts, diatom/cyanobacterial films and short-lived filamentous algae became abundant. Also according to Tsuchiya et al. (1991), further colonization of the substrate by other benthic organisms occurs only after a long period of absence of *Echinometra mathaei* from the boring grooves.

Although primarily subtidal in nature, regular echinoids also inhabit wet areas of the intertidal zone beneath ledges or in tidal pools. This is consistent with the habits of present day rocky shore sea urchins. In effect, today, on the rocky shores of Foz da Fonte, regular echinoid communities of *Paracentrotus lividus* are responsible for bioerosion mainly at depths between 0 and –2 m. This is in agreement with what Martinell (1981) and Frantzis et al. (1992) described for the Mediterranean Sea, where the upper distribution limit of regular echinoids is determined by desiccation (Boudouresque and Verlaque, 2001). Also, in the Indian Ocean, *Echinometra mathaei* (Blainville, 1825) bores oval pits attributable to *Circolites* in coral reefs at the low tide line (Asgaard and Bromley, 2008, fig. 6). In agreement with such findings, the presence of these trace fossils in the studied areas records a coeval shoreline position.

4.4. Movement pattern analysis

Apart from palaeoichnological interests, this newly described trace fossil is of significance to the understanding of palaeoecological processes such as grazing that may regulate palaeocommunity structure. For example, the echinoid *Meoma ventricosa*, which thrives on the external platform of Florida in water up to 38 m deep, produces meander-like grooves on sandy substrata while searching for food at a rate of movement of 3 to 5 cm.h⁻¹. The grooves formed are 12 to 5 cm wide (Chesher, 1969) and their producers are thereby active disturbers of the benthos. This behaviour on sandy bottoms may be similar to that performed on hard substrates, although it may take months or even years for sea urchins to create the meanders entrenched in hard rock. In fact, Allouc et al. (1996) already established for the hemispherical depressions made by *Echinometra lucunter* an erosion rate of 1 mm/year in ferruginous crusts. On the other hand, Ogden (1977) reported displacements of a few centimeters a day for individuals of the same species when they graze the walls of the groove-shaped boring. Several studies point to an inverse relationship between food availability (algae) and rate of movement in many sea urchin species (Mattison et al., 1977; Andrew and Stocker, 1986; Luazon-Guay et al., 2006; Dumont et al., 2007).

A random-walk movement is the foraging strategy adopted for some non-boring sea urchin species, but some rock-boring species (e.g., *Diadema* spp.) adopt a homing behaviour by returning to their refuge after a foraging trip (Carpenter, 1984; Tuya et al., 2004). Sea urchins possess a limited sense of chemodetection and therefore change direction only over relatively short distances (Dumont et al., 2007) when they emerge from their hollows or borings to graze on algae.

From an ethologic and trophic point of view, the occurrences of *Circolites* and the newly described trace fossil *Ericichnus* would seem to indicate a multiplicity of roles that entail the activities of domichnion and / or agrichnion-pascichnion,

respectively. *Ericichnus* igen. n. reflects a combination of habits trapping drifting algae and farming endolithic algae within the dwelling boring (agrichnia), and simultaneously searching for food while moving (pascichnia). *Circolites* reproduces a dwelling structure where sea urchins are protected from predators and wave surge and where occasionally they act as macro-suspension feeders trapping organic material brought into the boring by the rising tide (Asgaard and Bromley, 2006). Hernández and Russel (2010) also attribute to these pits a more hospitable microhabitat by retaining water and moderating temperatures and desiccation during emersion at low tide.

Ericichnus igen. n. can be observed in exposed areas where, according to Mattison et al. (1977) and Konar (2000), population densities and probably, the length of grooves are related to wave exposure, because the sea urchins move much less to avoid dislodgement in high exposed areas. This would explain the two types of modules observed in figures 6 and 7.

4.5. *Ericichnus* igen. n. – *Circolites* an example of compound trace fossil

Trace fossils are often observed not fully isolated from others in the context of their surrounding matrix, but instead may comprise two or more different ichnological structures that grade directly one into another. These structures were formally defined and differentiated by Pickerill (1994) as compound trace fossils. According to Bertling et al. (2006) compound trace fossils arise from a behavioural change over time of a single trace producer. In this context, it is possible to demonstrate through this study an example of a compound trace fossil involving two ichnotaxa (*Ericichnus* igen. n. and *Circolites*). Intergradation of traces belonging to different ichnogenera is not grounds for synonymy (Bertling et al., 2006) and for this reason, the use of more than one

ichnotaxon becomes necessary to accurately the entire scenario (Ekdale and Bromley, 2001).

Different ichnological structures represent notably distinct producer behaviours (agrichnion-pascichnion and domichnion in the present case) by a single trace-making animal and therefore, may occur isolated. Both structures, assigned to different ichnotaxa, were produced by the same animal, a regular sea urchin that may be involved in different types of activities, perhaps during different ontogenetic stages of development. Hunt (1969) observed that cup-shaped borings are made by the juvenile *Echinometra* which do not yet have an elongated test shape as found in the adult animals. In turn, the adult animals are responsible for the large, groove-like borings produced when it bores slowly forward while grazing on algae. This is confirmed with experiments made by Hernández and Russel (2010), who observed that many sea urchins with identical food availability, such as *Echinometra mathaei*, *Strongylocentrotus droebachiensis*, *S. purpuratus* or *Paracentrotus lividus*, change their morphology during growth owing to the microhabitat conditions occupied (presence or absence of a cavity).

Details regarding both the morphology and behaviour of sea urchins can be provided from such a compound trace fossil. *Ericichnus* igen. n. indicates the movement of the animal while grazing, and *Circolites* indicates the size and shape of the animal's test.

4.6. *Ericichnus bromleyi* isp. n. as a palaeoenvironmental tool

Nowadays, three species of shallow-dwelling sea urchins inhabit the shores of the Azores Islands: *Sphaerechinus granularis*, *Arbacia lixula* and *Paracentrotus lividus*. Fossil representatives of these species are found from the last interglacial (MIS 5e)

Pleistocene deposits of Santa Maria Island (Madeira et al., 2011). Despite extensive work on the Upper Miocene to the Lower Pliocene and Upper Pleistocene outcrops of Santa Maria, no fossils of *Echinometra* spp. have so far been found. According to Kroh (2004) the extremely poor fossil record of this genus is related to the low preservation potential of its skeleton in the intertidal and the general lack of sedimentation in this environment.

In the Atlantic Ocean, the genus *Echinometra* is restricted to tropical waters, with mean monthly winter temperatures above 20° C (Kroh, 2004). Presently, *Echinometra lucunter* is an amphi-Atlantic species reported from the Western Atlantic (from North Carolina south to the Caribbean Region and the Gulf of Mexico, Bermuda) and the Eastern Atlantic (from the northwestern African coasts south to Senegal and the Gulf of Guinea) (Asgaard and Bromley, 2006).

Authors have reported the local disappearance of thermophile marine molluscs that inhabited Azorean shores during the last interglacial extirpated due to changes in temperatures related to the onset of the last glaciations farther to the north (Ávila et al., 2008a, 2009). Madeira et al. (2011) also reported the occurrence in the Miocene of Santa Maria Island of thermophile echinoids such as the extinct *Clypeaster altus* and the extant *Echinoneus* cf. *cyclostomus* Leske, 1778 and *Eucidaris tribuloides* (Lamarck, 1816); none of the extant species occur nowadays in the Azores. Thus, this pattern of local disappearances of thermophile Miocene species may be considered as the result of climatic cooling during the Pliocene and Pleistocene. The possible existence of *Echinometra* spp. in the littoral of Santa Maria Island during the Late Miocene to Early Pliocene, which is inferred from the new compound trace fossil *Ericichnus* igen. n.-*Circolites*, is thus another example of a thermophile taxon that locally disappeared from

the Azores islands as a consequence of the decreasing sea surface temperatures associated with Pliocene and Pleistocene climatic changes.

5. Conclusions

The main conclusions of this study can be summarized as follows:

1) The record of a new type of bioerosive structure is related to the boring activity of regular sea urchins on a volcanic oceanic island (Santa Maria, Azores Archipelago) and in the context of a continental margin (Foz da Fonte, Central West Portugal).

2) This newly described trace fossil is designated as *Ericichnus* igen. n. with two new ichnospecies, *Ericichnus bromleyi* isp. n. and *Ericichnus asgaardi* isp. n. The trace consists of a series of grooves relatively deep, with a sinuous pathway. The width is fairly uniform along its trajectory and within there are preserved a number of concave forward marks, showing the producer's direction of the movement.

3) Both types of grooves (*Ericichnus bromleyi* isp. n. and *Ericichnus asgaardi* isp. n.) occur in association with *Circolites kotoucensis*, located on the margins, inside or near the groove. In this context, *Ericichnus* igen. n.- *Circolites* provide an example of a compound trace fossil.

4) The most likely producer of *Ericichnus bromleyi* isp. n. may have been a regular echinometrid echinoid close to *Echinometra lucunter* (Linnaeus, 1758), whereas for *E. asgaardi* isp. n. the producer may have been an echinid close to *Paracentrotus lividus* Lamarck, 1816.

5) From an ethological point of view, the resulting compound trace fossil *Ericichnus* igen. n.- *Circolites* is interpreted as an agrichnion-pascichnion and / or domichnion.

6) The occurrence of *Ericichnus bromleyi* isp. n.- *Circolites* as a compound trace fossil may be applied as a proxy to recognize the activity of thermophile rock-boring echinoids in the fossil record.

7) The possible existence of *Echinometra* spp. from the Upper Miocene of Santa Maria Island constitutes a further example of an echinoid thermophile taxon that has locally disappeared from the Azores as a consequence of climatic changes during the Pliocene and Pleistocene.

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798 Figure Captions

799 **Fig. 1.** Geographical location of the studied areas in Portugal: "Ichnofossil's cave"
800 (Santa Maria Island, Azores Archipelago, Portugal) and Foz da Fonte (Central
801 West Portugal).

802 **Fig. 2.** General stratigraphical view of the "Ichnofossil's cave" outcrop. A) Reworked
803 conglomerate/pillow breccia. B) Bioclastic, highly bioturbated, fossiliferous
804 sandstone. Black arrows indicate the position of *Ericichnus bromleyi* igen. n. isp.
805 n. C) Horizontal stratified brick red fine volcanoclastic sand (reworked pyroclasts),
806 with abundant fossil remains. D) Foresets of volcanoclastic sand (reworked
807 pyroclasts) showing a great scale cross bedding stratification. E) Compact marine
808 limestone. F) Submarine basaltic lava flow. G) Rolled pebble beach with abundant
809 fossil molluscs (Pleistocene, MIS 5e).

810 **Fig. 3.** Detailed view of the Foz da Fonte outcrop. Cretaceous limestone surface with
811 borings of *Gastrochaenolites* isp. (black arrows) and *Ericichnus asgaard* isp. n.
812 (white arrows). (Hammer scale = 30 cm).

813 **Fig. 4.** Paleoichnological features of the substrates. A) *Arenicolites* isp. in the Miocene
814 bioclastic sandstone at the "Ichnofossil's cave". B) *Bichordites* isp. preserved as
815 epirelief on top of the Miocene bioclastic sandstone at the "Ichnofossil's cave". C)
816 *Macaronichnus segregatis* Clifton and Thompson, 1978 in full relief on the
817 Miocene bioclastic sandstone at the "Ichnofossil's cave". D) *Dactylodites otto*
818 (Geinitz, 1849) in full relief on top of the Miocene bioclastic sandstone at the
819 "Ichnofossil's cave". E) Longitudinal cross section of *Ophiomorpha nodosa*
820 Lundgren, 1891 in the Cretaceous limestone at Foz da Fonte. F) General view of

Ericichnus bromleyi igen. n. isp. n. at the “Ichnofossil’s cave” showing the contact between the bioeroded surface and the overlying volcanic ash (Va) that cover and fossilize it. G) Close-up view of *Ericichnus bromleyi* igen. n. isp. n. (E) and *Circolites kotoucensis* (C) infilled by volcanoclastic sand. White arrows represent the contact between the bioeroded surface and the overlying volcanoclastic sand.

Fig. 5 A-D. *Ericichnus bromleyi* igen. n. isp. n. on the bioeroded surface of the “Ichnofossil’s cave”. A) Detail of the holotype EM-UHU/08-SM001 on the field. B) Interpretative scheme showing the trajectory of the grooves with the movement direction (thin black arrows) and the successive position of *Circolites* (thick black arrows). Several cross sections are represented: (1) normal section, (2) expanded section in the bifurcating point, (3) *Circolites* section. C) Close-up view of *Ericichnus-Circolites* igen. n. structures. Paratype EM-UHU/08-SM002. D) Schematic plan of the former picture, detailing the resting trace of the sea urchin (*Circolites*) and the beginning of the groove (*Ericichnus bromleyi* isp. n.) with the movement direction.

Fig. 6. A) Plan view of the bioeroded surface from the “Ichnofossil’s cave” showing high density grooves of *Ericichnus bromleyi* igen. n. isp. n. partially infilled by the overlying volcanoclastic sand. (Hammer scale = 30 cm). B) Schematic plan view showing the grooves pathway characterized by a repeated pattern of several subrectangular modules (subrectangular pattern).

Fig. 7. A) Plan view of the same bioeroded surface at the “Ichnofossil’s cave” showing low density grooves of *Ericichnus bromleyi* igen. n. isp. n. B) Plan view showing the grooves pathway characterized by a repeated pattern of subtriangular modules (subtriangular pattern).

Fig. 8. *Ericichnus asgaardi* igen. n. isp. n. on the bioerored surface of Foz da Fonte outcrop. Holotype EM-UHU/08-FzF001. A) Plan view of the grooves on the field. B) Diagram showing the outline of *E. asgaardi* igen. n. isp. n. including the location of *Circolites* (circles with dashed lines) into and out of the grooves. Squares 1 to 8 pointed the area of the *Circolites* inside *Ericichnus* igen. n. The close-up views of these squares are presented in the Figure 9. Sections I-I' and IV-IV' indicates the cross section of the groove with different levels of terraces.

Fig. 9. Close-up views of squares 1-8 from Figure 8 showing location of different *Circolites* inside the large *Ericihnus asgaardi* isp. n. A) Detail of square 1. Large *Circolites* on the upper first terrace of the main groove. B) Detail of square 2. *Circolites* at two different levels, upper (white arrow) and lower (black arrow). C) Detail of square 3. Three specimens of highly eroded *Circolites* (black arrows) on bottom. D) Detail of square 4. Incomplete *Circolites* in two terraces, upper (white arrows) and lower (black arrow). E) Detail of square 5. *Circolites* in the margin of the upper part of the groove. F) Detail of square 6. Two specimens of large incomplete *Circolites* (black arrows) on the bottom of the groove. G) Detail of square 7. Two incomplete *Circolites* in the margin (white arrows). H) Detail of square 8. Four *Circolites* (white arrows) in both margins of the end of the groove. (All scale bar: 10 cm).

Fig. 10. A) Groove borings made by *Echinometra mathaei* observed on vesicular basalts on ex-situ boulders of Kailua-Kona shores (Big Island, Hawaii). B) Groove borings made by *Echinometra lucunter* on a surf bench of basaltic tuff in Rabo de Junco (western coast of Sal Island, Cape Verde). C) Grup of *Echinometra lucunter* specimens inside the groove borings at Rabo de Junco (western coast of Sal

869 Island, Cape Verde). D) Holocene *Circolites* on basalt at Ponta Fiura (North coast
870 of Sal Island, Cape Verde). E) Pleistocene *Circolites* on basalt at Costa da Fragata
871 (Sal Island, Cape Verde). F) Pleistocene *Circolites* on phonolite at Porto da Furna
872 (Brava Island, Cape Verde).

873

874 **Table Captions**

875

876 **Table 1** Ichnologic record of *Circolites* in non-sedimentary rocky shores and non-
877 natural substrates.

878

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Table
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	Lithology	Age	Outcrop	Authors
Igneous (Plutonics)	Granite	Holocene	Sant Feliú de Gírxols (NE Spain)	Martinell (1981)
	Coarse granite	Holocene	Bay of Croisic (Brittany, France)	Lory (1855 in Otter, 1932)
	Coarse crystalline granite	Holocene	Coast of Brittany (France)	Cailliaud (1856 in Otter, 1932)
Igneous (Volcanics)	Basalt	Holocene	São Miguel Island (Azores, Portugal))	John (1889 in Otter, 1932)
	Basalt	Holocene	Ponta Fiura (N coast of Sal Island, Cape Verde)	present paper (Fig. 10D)
	Basalt	Holocene	Punta San Francisco (Pacific coast of Costa Rica)	Fischer (1981)
	Basalt	Holocene	St. Helena Island (British Overseas Territories)	Cailliaud (1805 in Otter, 1932)
	Basalt	Holocene	Kona (Hawaii)	Grünbam et al. (1978)
	Basalt	Holocene	Easter Island (Chile)	Hubbard et al. (2003)
	Basalt	Pleistocene	Ponta do Atum (Santo Antão Island, Cape Verde)	Ramalho et al. (2010)
	Basalt	Pleistocene	Costa da Fragata (Sal Island, Cape Verde)	present paper (Fig. 10E)
	Basalt	Pleistocene	Ponta das Bicudas (Santiago Island, Cape Verde)	Baarli et al. (2013)
	Phonolite	Pleistocene	Porto da Furna (Brava Island, Cape Verde)	present paper (Fig. 10F)
	Basalt	Pleistocene	Praïnhã (Santa Maria Island, Azores, Portugal))	Ávila et al. (2008b)
	Basalt	Miocene	Castilhano (São Nicolau Island, Cape Verde)	Johnson et al. (2014)
Metamorphic	Mica schist	Holocene	The Black Ledges (Nantucket Island, Canada)	Fewkes (1890a)
	Marble	Pliocene	Coyote Mountains (Salton, California, USA)	Watkins (1990)
	Marble	Upper Miocene	Resinera (S Spain)	Santos, Mayoral, Bromley (2011)
	Ferruginous crusts	Holocene	Ngaparou (Senegal)	Allouc et al. (1996)

Igneous/Metamorphic		Holocene	Guaymas Harbor (Mexico)	Fewkes (1890b)
Non Natural substrates	Steel pipes	Holocene	Pacific Coast of California (USA)	Irwin (1953)

Table I. Ichnologic record of *Circolites* in non-sedimentary rocky-shores and non-natural substrates.