Extreme habitat adaptation by boring bivalves on volcanically active palaeoshores from North Atlantic Macaronesia

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Abstract

Extensive bivalve borings are described in detail for the first time from basalt rockgrounds in the North Atlantic volcanic islands of Macaronesia. They occur on a Middle Miocene rocky shore of a small islet of Porto Santo (Madeira archipelago of Portugal), as well as on Plio-Pleistocene rocky shores on Santiago (Cape Verde archipelago). A basalt substrate is widely penetrated by clavate-shaped borings belonging to the ichnogenus *Gastrochaenolites* interpreted as dwelling structures of suspension-feeding bivalves. Some of these borings still retain evidence of the alleged trace-makers preserved as body fossils, while others are filled with their casts. The ichnofossil assemblage present on these bioeroded surfaces belongs to the *Entobia* ichnofacies. Recognition of *Gastrochaenolites* borings in volcanic rocks provides useful palaeoenvironmental information regarding an expanded strategy for hard-substrate colonization. Preliminary results from fieldwork in the Cape Verde Islands indicate that such borings are more widespread through Macaronesia than previously thought.

Key words Bioerosion, Bivalve borings, *Gastrochaenolites*, Endolithic communities, volcanic rocks, Macaronesia islands.

Introduction

The study of rock-boring organisms is paramount to the identification and interpretation of marine palaeoenvironments denoted by hard substrates. Using mechanical and/or chemical means to bore the substrate, these organisms are capable of degrading large volumes of rock in intertidal to subtidal settings (Neumann 1966; Chazottes et al. 1995; Pari et al. 1998). This is accomplished by employing specialized functional and morphological adaptations related to their unique mode of life (Evans 1968; Ahr and Stanton 1973; Stanley 1970; Kleemann 1990). Such benthic organisms are generally referred to as euendoliths (Golubic et al. 1981). They penetrate lithified substrates and excavate permanent dwelling structures (domichnia) below the surface (Ekdale and Bromley 2001).

Euendoliths developed specialized life strategies and ethological responses dependent on physical properties reflecting different environmental variables including substrate consistency, food availability, energy conditions at the depositional interface, water depth and salinity (Goldring 1995). Among these, the main factor influencing substrate colonization by marine boring organisms is the degree of consolidation of the substrate itself (Goldring and Kaźmierczak 1974).

The type of hard substrate occupied by specific euendoliths is determined by the organism’s method of cavity formation. Hence, mechanical borers tend to occur in a wider range of substrates than those that use a chemical agent to penetrate rock (Wilson and Palmer 1992). The remarkable ability of some bivalves to bore into various mineralized and organic substrates, mechanically and/or chemically, is well documented (Turner 1969). Such substrates include biogenic materials (shell, wood, bone, e.g., Kříž and Mikuláš 2006; Mikuláš et al. 2006; Santos and Mayoral 2008), lithified substrates (different rocks, from sedimentary to volcanic, of varying hardness, e.g., Masuda 1968; Kleemann 1973; Allouc et al 1996; Mikuláš et al. 2002; Tapanila et al. 2004; Carmona et al. 2007), and even anthropogenic materials such as PVC (polyvinyl chloride), ABS (acrylonitrile butadiene styrene) and concrete (e.g., Lam 2000; Jenner et al. 2003).

Dwelling structures resulting from the boring activity of bivalves commonly show an overall clavate shape with a broadly rounded base and a narrowing neck (Kelly and Bromley 1984) and, therefore, are usually assigned to the ichnogenus *Gastrochaenolites* Leymerie, 1842. Bivalves also may produce boring structures attributable to other ichnogenera, such as *Teredolites* Leymerie, 1842, *Petroxestes* Wilson and Palmer, 1988 and *Phrixichnus* Bromley and Asgaard, 1993. Although bivalve borings identified as *Gastrochaenolites* are fairly common in sedimentary substrates, especially in carbonate lithologies, very few studies have provided information on the penetration of igneous or metamorphic rocks other than marble (e.g. Santos et al. 2011a).

The discovery of numerous well preserved and clearly identifiable fossil borings left in basalt by endolithic bivalves at the Miocene rocky shore of Ilhéu de Cima, a small islet of Porto Santo in the Madeira archipelago, Portugal (Fig. 1), was thus unexpected. It represents a new and important source of information regarding the limits of hard-substrate penetration and colonization in such unusual environments. The present report further elaborates on this discovery briefly reported in Santos et al. (2011b).

From the extensive literature on ancient rocky shores reviewed by Johnson (2006), the only previous example of *Gastrochaenolites* in volcanic rocks comes from the Japanese Miocene near Sendai (Masuda 1968). More recently, Haga et al. (2010) reported *in situ* occurrence of *Lithophaga* in volcanic substrate from the early middle Miocene Moniwa Formation of northern Honshû (Japan). Previously these borings were interpreted as fossilized sea-snake eggshells or possibly as the fossilized pupal chambers of a coleopteran insect (Haga et al. 2010). Bivalves attributed to *Petricola carditoides* (Conrad, 1837) from the Upper Pleistocene of Baja California (Mexico) also are known to occupy deep borings in coastal andesite rocks (Zwiebel and Johnson 1995), although it is believed this species with a nestling habit did not make the borings but took advantage of pre-existing domichnia.

This paper documents the extensive and well preserved occurrence of bivalve-produced *Gastrochaenolites* bioerosional structures in a Middle Miocene active volcanic island rocky-shore on Ilhéu de Cima. We aim to: (1) unequivocally demonstrate the presence of bivalve borings in basaltic substrates; and (2) characterize the ecological and geological parameters controlling the production and preservation of these trace fossils. We also hope to promote palaeoichnological research on volcanic island rocky shores, as exemplified by the preliminary results of fieldwork in the Cape Verde archipelago.

Location and geological setting

The volcanic Madeira archipelago (Portugal) is located 420 km west off the shores of Morocco in the North Atlantic Ocean. Porto Santo is an outlying island located 50 km northeast of the main island of Madeira (Fig. 1). No more than 41 km^2 in area, Porto Santo is a relatively old and deeply eroded island. Based on evidence from surrounding bathymetry, it is evident that the emerged part of Porto Santo occupies today only about a third of its former area (Santos et al. 2011b; Johnson et al. 2011a). Erosion has removed most of the subaerial volcanic units that once constituted the accreted circumference of the island, disclosing earlier stages of its development, and revealing the transition between submarine and subaerial volcanic formations in which shallow marine fossiliferous sedimentary beds may be found (Cachão et al. 2003).

Ferreira (1996) produced a geological map of Porto Santo, including its various satellite islets. The second largest is Ilhéu de Cima with a perimeter of approximately 3 km and maximum elevation of 115 m. The islet is presently separated from the main island of Porto Santo, to the northeast, by a shallow channel merely 350 m wide. Fossiliferous sedimentary beds occur in several places around the islet related to the transition between two major volcanic units: a trachytic to basaltic submarine basal volcanic complex with ages ranging from 18.8 to 13.5 Ma; and a subaerial alkali basaltic to hawaiitic complex dated between 14 and 10.2 Ma (Ferreira 1985). Based on calcareous nannofossil assemblages at Lombinhos on the east side of Porto Santo, Cachão et al. (1998) correlated the sedimentary units there with the Middle Miocene, lower Serravallian Stage (Calcareous Nannofossil biozone CN4 of Okada and Bukry 1980). A comparable age of about 14 to 15 Ma is projected for sedimentary intercalations with volcanic rocks on Ilhéu de Cima.

According to Schmidt and Schmincke (2002, p. 605), the northeastern end of Ilhéu de Cima across from Porto Santo preserves foreset-bedded, steeply dipping pillow breccias overlain by, but connected with, horizontal flows interpreted as subaerial eruptions that entered the sea as a lava delta. Considered together with the diverse range of fossil-rich carbonates intercalated with volcanic deposits on the north and west sides of the island, it appears that Ilhéu de Cima was a separate island at least during part of its Miocene history. The study site is located at a place locally known as Poio Pequeno, approximately 150 m SE of the only landing place on the islet (Figs. 1, 2) at an elevation 4 m above mean sea level.

Methods

Sample quadrates 0.5×0.5 m divided into twenty-five units of 10 × 10 cm each were deployed on the vertical face and top horizontal surface of the exposed rocky palaeoshore to collect quantitative data on body and trace-fossil content preserved *in situ* on the basalt surface and to map distributional patterns (Fig. 3). In total, five adjoining grid samples were recorded. The full survey entailed the coverage of an area 2.30 m by 0.5 m (1.15 m^2). The bioerosional structures within these grid samples were identified, counted and measured. The remains of bioeroding and encrusting organisms were identified and tallied. Bioerosional structures were measured using digital callipers. Composition of the ichnocoenosis was determined on the basis of these data.

Palaeontological analysis

Census Data

The area around the study site at the Poio Pequeno is shown in Figure 3a. An interpretational scheme for the preserved rocky palaeoshore from which census data were collected and the actual placement of census quadrats is shown in Figure 3b. The scheme is drawn with reference to the local geological setting, which includes the basaltic palaeoshore surface overlain by an ash-lapilli level draped by a subsequent lava flow (also basaltic). The flat sub-horizontal surface at the top of the Miocene rocky shore is exposed over a full metre (Fig. 4), while the vertical relief on the preserved shore face amounts to no less than 1.3 m (Fig. 5).

Patterns in spatial distribution among both bivalve borings and associated encrusting epibiota preserved on the vertical and on the top sub-horizontal basalt surface of the study area are tabulated in Table 1. The encrusting epibiota on the rocky-shore wall included several organisms such as the bivalve *Ostrea* sp., and barnacles (*Balanus* sp.), all represented by *in situ* remains. The existence of this community of sclerobionts is further evidence of the existence of a lithified substrate. Encrusting *Ostrea* sp. are limited to the lower part of the vertical wall (between 30 cm to 50 cm) represented by only four specimens (Fig. 5). In contrast, individual specimens of *Balanus* sp. span almost the entire surface between 0.1 to 1.2 m, with most (seven) preserved in the lowermost sector (Fig. 5). On the top sub-horizontal surface there remains no evidence of an encrusting epibiota (Fig. 4).

Carbonate crusts were found to cover approximately 27% of the total surface area (Figs. 4, 5). Almost two-thirds of the study surface was exposed as bare basalt (73%). An unknown portion of bare basalt in the census may have been stripped of its carbonate crust and/or other distinguishable macrofossils as a result of Recent erosion. Nevertheless, the spatial distribution of remaining body and trace fossils still reveals a marked vertical zonation pattern (Table 1).

Gastrochaenolites is distributed all over the vertical and top sub-horizontal surface (Figs. 4, 5). Borings into the vertical and top sub-horizontal surfaces are consistently oriented perpendicular to them. A close-up photo of the outcrop gave sufficient resolution to count the borings in the entire grided area of 1.15 m^2.

Gastrochaenolites density on the exposure basalt surface (82%, 174 specimens) exceeds that on the carbonate crust (18%, 39 specimens) (Figs. 4, 5). The density of borings is higher on the vertical surface of the study area (162 specimens) than on the top sub-horizontal surface (51 specimens) (Table 1). Results show an average of 79 borings per sample quadrate (0.25 m^2) on the vertical surface and 25 borings on the top sub-horizontal surface (Table 1).

Description of the borings

The first report on bivalve borings in volcanic rocks at Poio Pequeno (Ilhéu de Cima, Porto Santo) was produced by Santos et al. (2011b). These authors identified *Gastrochaenolites lapidicus* Kelly and Bromley, 1984 penetrating the basaltic substrate to a maximum depth of 4.5 cm. They also noted the presence of *Gastrochaenolites torpedo* Kelly and Bromley, 1984 affecting algal crusts and patchy colonial corals encrusted on basalt, and extending all the way through into the rocky substrate below. Further analysis of these structures has revealed more morphological details and an additional ichnospecies identification to add to the previous report by Santos et al. (2011b).

The only trace fossil genus found on the irregular basaltic rocky surface at Poio Pequeno is *Gastrochaenolites* preserved in concave epirelief on the bioeroded surface (circular cross-section) and casts of this boring. In some examples, the borings contain the body fossil of the trace-producer organism preserved in life position (Fig. 6a). Most *Gastrochaenolites* perforations on the study surface show partial to nearly complete erosion of the original boring (Fig. 6b). In a few cases, however, *Gastrochaenolites* borings are entirely preserved in the form of casts (Fig. 6c). Coarse granular aggregates of calcite occur in the lower parts of some borings, but usually they are simply filled with micro-granular calcium carbonate (Fig. 6b). The diameter of the borings varies from 0.8 to 3 cm, with an average value of 1.6 cm (n = 213). None of these borings were observed to intercept one another.

Morphological analysis of the bioerosional structures under study reveals the presence of both *Gastrochaenolites lapidicus* and *G. ornatus* Kelly and Bromley, 1984. *Gastrochaenolites* ichnospecies were identified on the basis of the shape and sculpture of the distal part of the clavate boring. The borings of both ichnospecies show a short, blunt rounded base. The inner basal surface of the borings is smooth in *Gastrochaenolites lapidicus* and, in some cases, where the preservation of the borings is good enough, a calcareous wall lining of uniform thickness (reaching at least 1.3 mm) remains intact, although partially and slightly recrystallised (Fig. 6d). Unlike *Gastrochaenolites lapidicus*, *G. ornatus* bears circular bioglyphs (*sensu* Kelly and Bromley 1984) in the deepest, distal, part of the cavity. These bioglyphs consist of grooves arranged in concentric whorls around the periphery of the perforation (Fig. 6e). The combination of a prominent bioglyph and the general club-shape of these borings is diagnostic of *Gastrochaenolites ornatus* and is reported here for the first time from Poio Pequeno. Some of the *Gastrochaenolites* borings are covered by a thin calcareous crust (Fig. 6f).

Presence of tracemakers

There is no doubt that the Poio Pequeno bioerosion structures described and discussed here represent the boring activity of endolithic bivalves on basalt and, moreover, from an ethological point of view, to dwelling structures (domichnia) of suspension-feeding bivalves. This assignation is based on the fact that bivalve shells occur as body fossils preserved *in situ* within the *Gastrochaenolites* (Fig. 6a). Generally, the bivalve specimens were fragmented and the shell walls recrystallised. However, the shell sculpture is often retained, showing characters typical of the families Pholadidae and Mytilidae (Fig. 6a). Identification at the generic level is more difficult because some of the necessary morphologic features are not preserved or cannot be seen in the fossil material.

Substrate analysis

Macroscopically, the rock on which the bioeroded surface occurs is a basaltic reddish-brown breccia produced by the drag of a basic volcanic flow over the pre-existing palaeotopography. Microscopically, the rock shows a micro-porphyritic vesicular texture. There are needle-shaped microphenocrystals of plagioclase, in some cases with preserved fluid orientation, together with small (max. 60 µm) opaque oxides and altered olivine (Fig. 7a). The matrix has no glass and is mainly composed of plagioclase with small (6 to 10 µm) abundant opaque oxides and common small crystals (~4 µm) of a more or less titaniferous augite pyroxene (Fig. 7b-c). According to Table 2, the substrate could be classified as a trachybasalt with less than 52% of SiO_2.

The heterogeneous macroscopic colouration of the rock is mainly due to an asymmetric concentration of vesicles relative to the matrix. The matrix has distinct lighter/darkish tones due to an uneven distribution of plagioclase relative to opaque oxides (Fig. 7d). The vesicles are completely filled by the crystallization of diagenetic calcium carbonate (most probably calcite) (Fig. 7e).

Other occurences in Macaronesia

Preliminary fieldwork on Santiago Island (Cape Verde archipelago) allows the identification of two Plio-Pleistocene outcrops with substrate bioeroded by boring bivalves (Fig. 1). The Tarrafal outcrop, located near the town of the same name in the northwest part of Santiago Island, features a bioeroded limestone overlain by a coarse-grained, rhodolithic limestone with angular to subrounded basalt boulder. The surface corresponds to an unconformity at the contact between the older limestone and the breccia (Fig. 8a). Borings are common on the upper surfaces of the boulders as well as on the limestone. The recognized trace fossil assemblage is basically composed of the bivalve boring *Gastrochaenolites* isp. Average diameter of the observed borings is 8 mm. *Gastrochaenolites* isp. appear perpendicular to the surface and are filled with the overlying rhodolithic sediment (Fig. 8b).

The other outcrop exhibiting bioerosion structures on a basalt substrate occurs at Ponta da Bicuda located 3 km east of Praia in the southeastern part of Santiago Island. This example corresponds to a horizontal surface of a basaltic rocky shore. Bivalve borings are common on the upper horizontal surface affecting *Siderastea* sp. and *Millepora* sp. corals (Fig. 8c), as well as on the vertical surface of basalt (Fig. 8d). The distal portions of *Gastrochaenolites* isp. are easily identified. These borings are oriented perpendicularly to the bored surface and show diameters ranging between 5.5 and 8 mm. Usually, on the basalt substrate the borings are filled with cemented carbonate (Fig. 8d). In a few examples the borings still contain the body fossil of the trace-producing bivalve inside (Fig. 8d).

Discussion

Substrate nature implications

It is well documented that the vast majority of all marine borings are found in sedimentary carbonate substrates (Taylor and Wilson 2003), which are softer and, therefore, more susceptible to both mechanical and chemical bioerosion than igneous and metamorphic rocks. Nevertheless, clavate-shaped borings reported at Poio Pequeno (Madeira archipelago, Portugal), and also from Santiago Island (Cape Verde), fit within the ichnogenus *Gastrochaenolites*. Occurrences of bivalve body-fossils *in situ* within the *Gastrochaenolites* structures leave no doubt about the nature of these borings. Discovery of individuals belonging to the family Pholadidae, as well as the Mytilidae (Lithophaginae), demonstrates that both were members of the boring bivalve community on volcanic rocks. This was well documented for the Recent black date mussel *Lithophaga nigra* (d'Orbigny, 1853), belonging to the Mytilidae, by Fang and Shen (1988) who proved that it is not a chemical borer, as previously believed (Yonge 1955, Kleemann 1980), but a mechanical borer. Fang and Shen (1988) mentioned modifications in both their internal morphology as well as in their external shell configuration, which allows *Lithophaga* spp. to bore into very hard lithologies. A modern example of *Lithophaga curta* (Lischke, 1784) boring into andesite rocks at Cape Manazuru, central Japan, was reported by Masuda and Matshushima (1969). McHuron (1976) also noted that some modern borers, such as *Penitella penita (*Conrad, 1837*)*, are capable of penetrating a wide spectrum of lithologies with varying hardnesses, ranging from stiff clay to olivine basalt. However, there is always the possibility that at least one of these body fossil types presented at Poio Pequeno may represent a nestler species.

Along the modern Pacific coast of Costa Rica, Fischer (1981) described some examples of polychaetes, sea-urchins, and basalt-boring snapping shrimps that bioeroded modern volcanic substrates. According to Fischer (1981), all the bioeroding organisms mentioned above require mechanical means to penetrate basalt, often by exploiting the differences in mineral hardness and crystal boundaries in the rock. In this regard, Johnson et al. (2010), who described an example of borings found in quartzite, suggested that the basalt could have been previously softened by microendolithic organisms such as fungi, since they are well known in basaltic glass (McLoughlin et al. 2008; Montague et al. 2007). According to McLoughlin et al. (2008), it appears that chemolithoautotrophs, which employ Fe and Mn oxidation, are plausible candidates for bioerosion of basaltic glass.

In this context, it is probable that the same circumstances also apply to basaltic substrates. The volcanic substrate with the borings found at Poio Pequeno on Ilhéu de Cima differs from the superseding homogeneously compact and dark basaltic lava flows on account of its vesicular nature, which may have resulted from a precocious volcanic alteration facilitated by intense activity of oxidizing hydrothermal fluids. This is indicated by the alteration of all olivine crystals into reddish iddingsite, with larger opaque crystals having red margins. Also, most pyroxenes were altered to yellow-green FATs (Ca, Fe^{3+}, Al-rich fassaitic clinopyroxenes), after the manner described by Munhá et al. (1991). This type of volcanic alteration may have facilitated the bioerosion of lithophagous bivalves, having most likely initiated their colonization of the substrate after it was softened by chemolithoautotrophic organisms.

The encrusting epibiota clearly preferred surfaces covered by a carbonate crust, as opposed to the boring bivalves, which appear on both types of substrate surfaces. Nevertheless, *Gastrochaenolites* occur in great numbers on basalt and in a several cases it can be demonstrated that the initial settlement was directly on basalt and not on the calcareous crust present on the surface (Fig. 6F). Obviously, if a more suitable substrate was lacking, the type of altered basalt found at Poio Pequeno sufficed.

Palaeoecological implications

The presence of *Gastrochaenolites* borings on this substrate is ecologically significant because it signals the novel possibilities opened up by an endolithic lifestyle for both the producer and secondary inhabitants. As Pinn et al. (2008) clearly demonstrated, several modern species of Pholadidae (*Pholas dactylus* Linnaeus, 1758, *Barnea candida* Linnaeus, 1758, and *B. parva* (Pennant, 1777) are habitat modifiers with a subsequent influence on intertidal biodiversity. It has further been suggested by Pinn et al. (2008) that these species are allogenic ecosystem engineers (defined as organisms that modify the environment through their behaviour and activity). This factor significantly increases the topographical complexity and, consequently, the species richness of the habitat. In this context, an extreme palaeoenvironment such as an active volcanic coast with hydrothermal activity could attract boring bivalves that acted as opportunistic organisms to modify and, at the same time, promote substrate colonization by other species, thus playing an important role in community structuring.The interstitial space observed on the volcanic substrate would provide an increased amount of "living space" for certain taxa of colonizers, such as the endolithic bivalves, thus increasing the total area available for larval settlement.

The bivalve borings from these examples in volcanic rocks exhibit the same morphological characters as others present in sedimentary substrates. However, differences concerning *Gastrochaenolites* density are evident. The more easily penetrated substrates normally have a boring community with the highest density (e.g. Lewy 1985; Watkins 1990; Domènech et al. 2001; Santos et al. 2008; Johnson et al. 2011b). In most of the harder substrates, i.e. greywacke, basalt or calcareous arkose, the density of borers is very low (McHuron 1976).

Physical properties of the substrate and the volcanic environment, namely lava input, control this ichnofacies, which depends on lithified, exposed substrates. The ichnofossil assemblage was preserved under the influence of intertidal to subtidal conditions and belongs to the *Entobia* ichnofacies (Bromley and Asgaard 1993). This colonization implies a certain period of time during which neither significant erosion, nor deposition, took place.

This Ichnofacies, characterized by domichnial borings of bivalves in basalt, signifies an adaptive strategy for macro-invertebrates to bioeroding hard substrates. The paucity of basaltic rocky shores preserved and recognized in the geological record, and the fact that bivalves bore mostly into carbonates, accounts for the unusual nature of this discovery. It remains to be determined how widespread the phenomenon may be, or how far back in geological time it might be traced.

Conclusions

The main conclusions regarding *Gastrochaenolites* trace fossils on a basalt rockground from a volcanic active Middle Miocene shoreline at Poio Pequeno (Ilhéu de Cima, Porto Santo Island, Madeira archipelago, Portugal) can be summarized as follows:

(1) Contrary to conventional thought, boring bivalves as group appear to have broad niches and can exploit a wide range of substrates. Discovery of individuals belonging to the family Pholadidae, as well as the Mytilidae (Lithophaginae), demonstrates that both were members of the boring bivalve community on volcanic rocks.

(2) The ichnofossil assemblage present on the bioeroded basalt surface at Poio Pequeno is entirely formed by *Gastrochaenolites* borings. This indicates a bivalve-dominated community assigned to the *Entobia* ichnofacies.

(3) These borings represent an important source of new information regarding strategies for the use of hard substrates.

(4) By identifying the role played by dominant habitat modifiers (such as boring bivalves), it is possible to learn just how some natural communities in stressful habitats depend on their presence.

(5) The presence of *Gastrochaenolites* at Poio Pequeno (Ilhéu de Cima, Porto Santo, Madeira) and Santiago Island (Cape Verde) are only the first confirmed examples from the North Atlantic domain of volcanic islands across Macaronesia, and represent the first detailed reports of the ichnospecies *Gastrochaenolites lapidicus* and *G. ornatus* from a basaltic substrate.

(6) Occurrences of *Gastrochaenolites* on basalt substrates in the Cape Verde islands indicate that they are more widespread than previously thought.

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Figure Captions

Fig. 1 Maps at various scales for the Madeira archipelago, Porto Santo with its satellite islets, and Ilhéu de Cima, and Santiago Island (Cape Verde), with stars showing locations of the study sites

Fig. 2 General view of the locality where *Gastrochaenolites* borings are present on the Miocene rocky shore at Poio Pequeno (Ilhéu de Cima, Madeira archipelago, Portugal)

Fig. 3 a Detail of the bioeroded rocky palaeoshore outcrop at Poio Pequeno. **b** Schematic cross-section of the outcrop showing the location of two *census* stations (A-B) on the horizontal top surface of the rocky palaeoshore and three stations (C-E) on the rocky palaeo-shoreface that is vertical with respect to the basalt basement and other deposits of the Miocene rocky shore. The area that was used in the census covers a total of 1.15 m^2

Fig. 4 Bivalve borings and spatial distribution of associated encrusting epibiota mapped on the horizontal top surface of the rocky palaeoshore at Poio Pequeno (Madeira archipelago, Portugal)

Fig. 5 Bivalve borings and spatial distribution of associated encrusting epibiota mapped on the vertical wall on the rocky palaeoshore at Poio Pequeno (Madeira archipelago, Portugal)

Fig. 6 Presence of *Gastrochaenolites* borings on the vertical wall of basalt at Poio Pequeno. **a** Several borings include trace-fossil producers organisms preserved in life position. Mytilidae (white arrow), Pholadidae (yellow arrow). **b** Bioeroded surface showing partial to nearly complete erosion of the original *Gastrochaenolites* filled with carbonate. **c** *Gastrochaenolites lapidicus* cast. **d** *Gastrochaenolites* cast showing the calcareous wall lining (white arrow). **e** *Gastrochaenolites ornatus* showing typically concentric sculpturing (bioglyphs). **f** *Gastrochaenolites* cast eroded and covered by a thin calcareous crust (black arrows)

Fig. 7 Microphotographs of thin-sections showing the basaltic matrix of the outcrop with bioerosion at Poio Pequeno. **a** Microporphyritic basalt with needle-shaped microphenocrystals of plagioclase with fluidal orientation; crossed nicols. **b** Iddingsite (alteration of olivines); parallel nicols. Same scale as A. **c** Fassaitic pyroxene. Parallel nicols. **d** Opaques oxidized. Parallel nicols. Same scale as A. **e** Vesicles replenished with carbonates. Crossed nicols. Same scale as 7 a

Fig. 8 a Bioeroded limestone surface overlain by a medium coarse-grained, rhodolithic limestone with angular to subrounded basalt boulder at Tarrafal outcrop (Santiago Island, Cape Verde). **b** *Gastrochaenolites* isp. on a basalt boulder with boring filled with the overlying rhodolithic sediment at the Tarrafal outcrop. **c** Upper horizontal basalt rocky palaeoshore at Ponta da Bicuda (Santiago Island, Cape Verde) with corals affected by *Gastrochaenolites*. **d V**ertical rocky palaeo-shoreface at Ponta da Bicuda showing borings filled with cemented carbonate (white arrow) and remnants of the trace-producer inside a boring in the basaltic substrate (black arrow)

Table Captions

Table 1 Density of bivalve borings and associated encrusting epibiota on the basaltic Miocene rocky-shore at Poio Pequeno (Ilhéu de Cima, Madeira archipelago, Portugal)

Table 2 Main geochemical characteristics of the basaltic rocky shore at Poio Pequeno (Ilhéu de Cima, Madeira archipelago, Portugal)

Figure 1

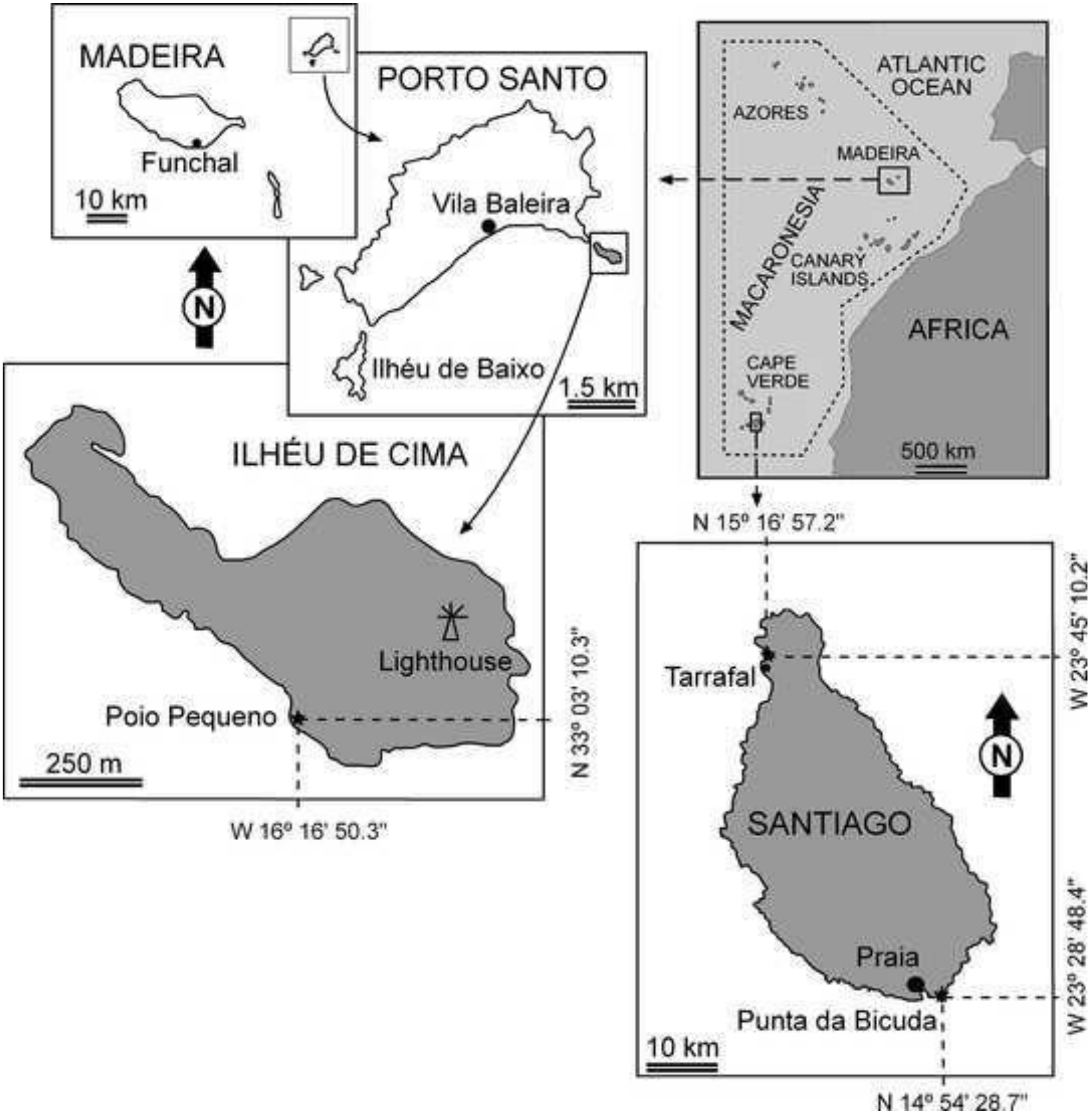
MADEIRA
Funchal
10 km
PORTO SANTO
Vila Baleira
Ilhéu de Baixo
1.5 km
ATLANTIC OCEAN
AZORES
MADEIRA
MACARONESIA
CANARY ISLANDS
AFRICA
CAPE VERDE
500 km
N
ILHÉU DE CIMA
Lighthouse
Poio Pequeno
250 m
N 33º 03' 10.3"
W 16º 16' 50.3"
N 15º 16' 57.2"
W 23º 45' 10.2"
Tarrafal
N
SANTIAGO
Praia
Punta da Bicuda
10 km
W 23º 28' 48.4"
N 14º 54' 28.7"

Figure 2

Figure 4

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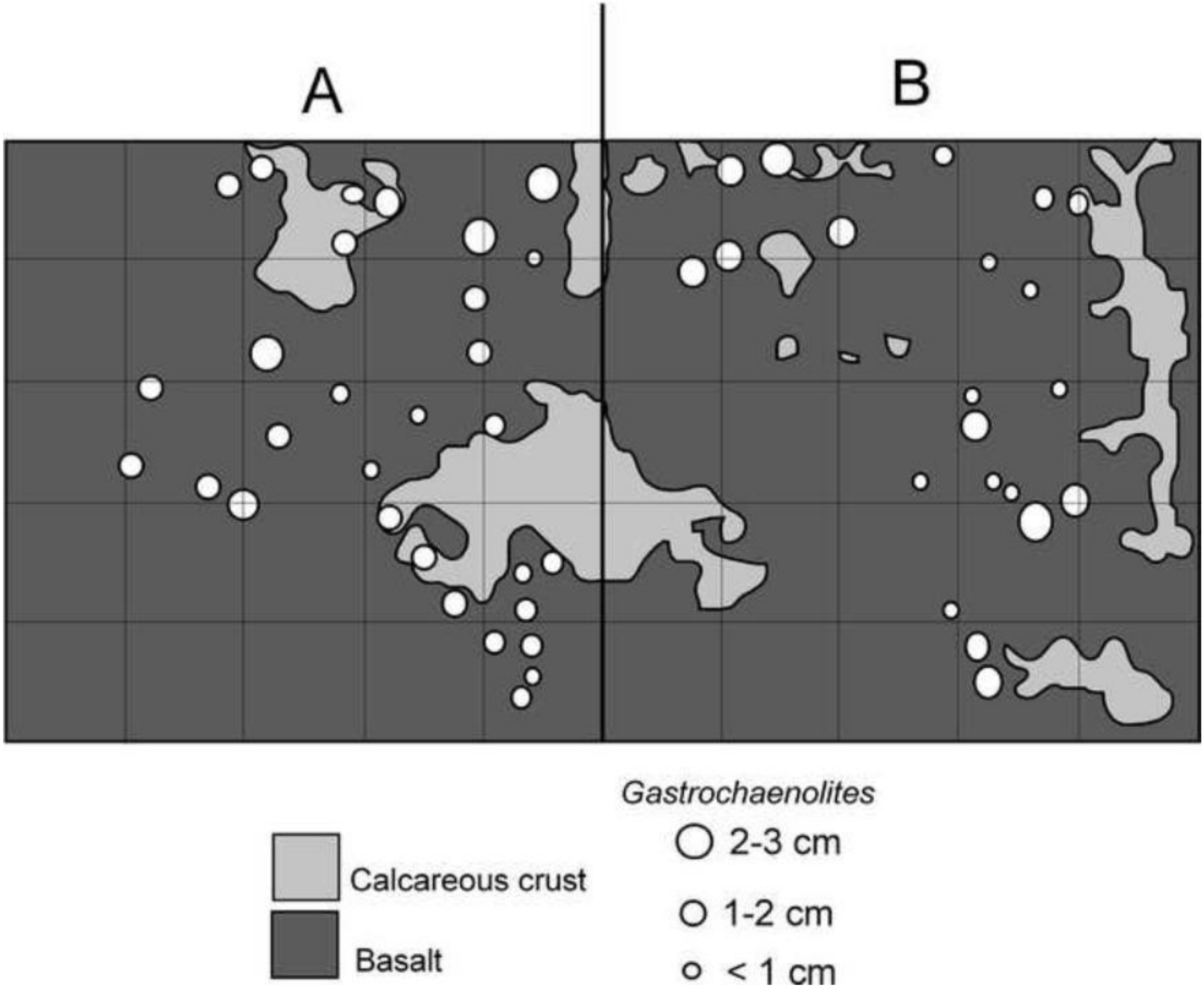

Figure 5

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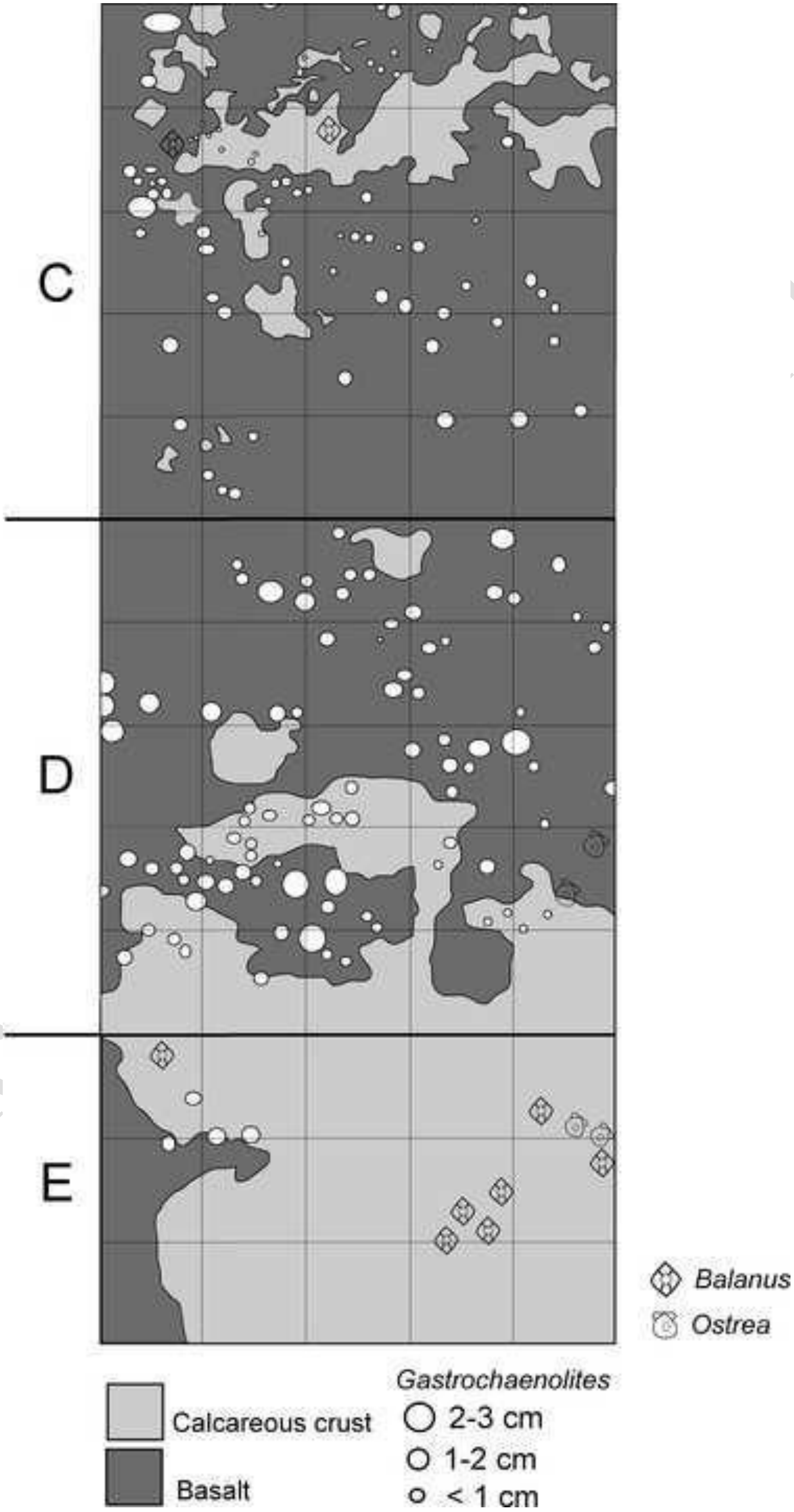

Figure 3

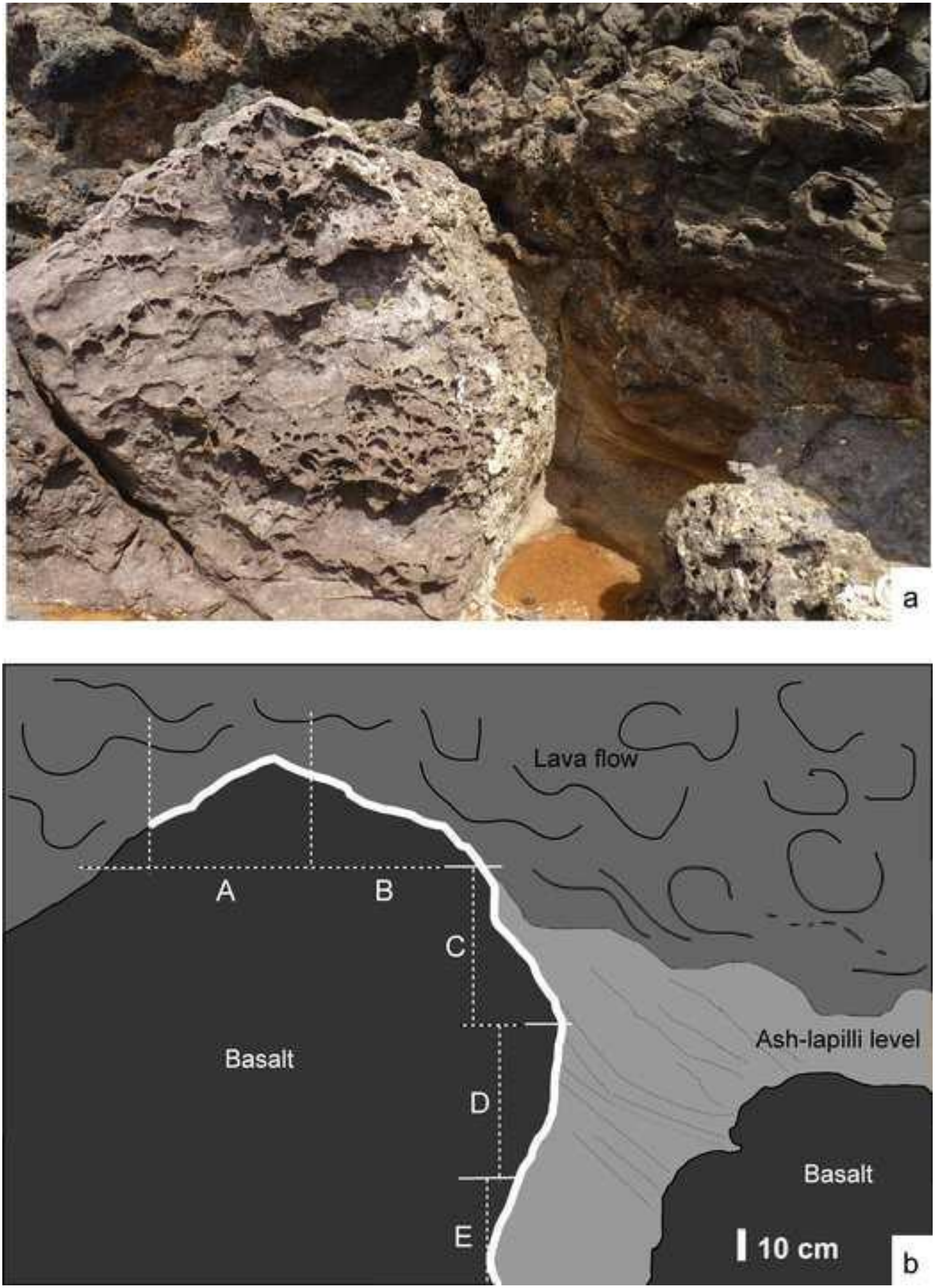

Figure 6

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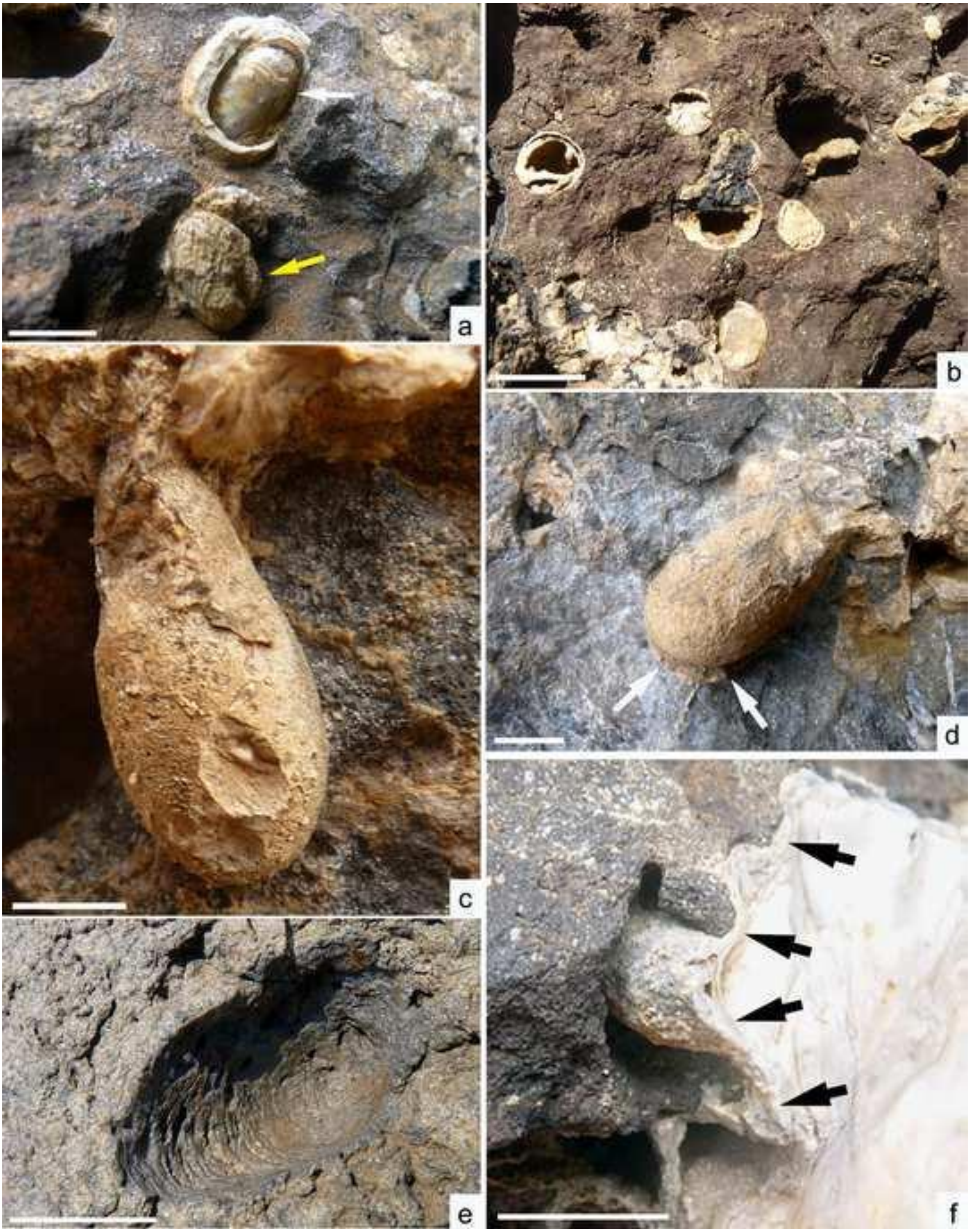

Figure 7

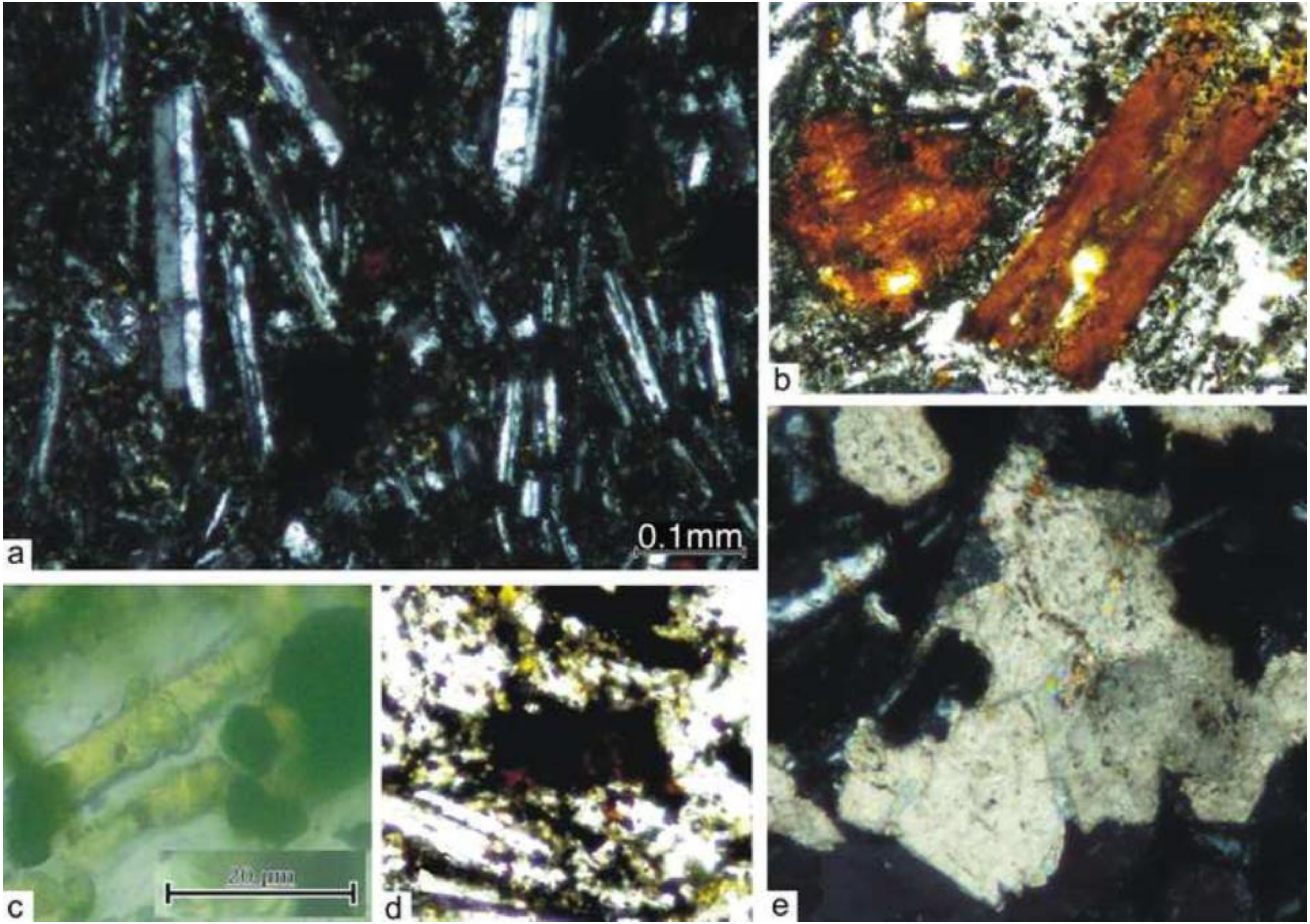

Figure 8

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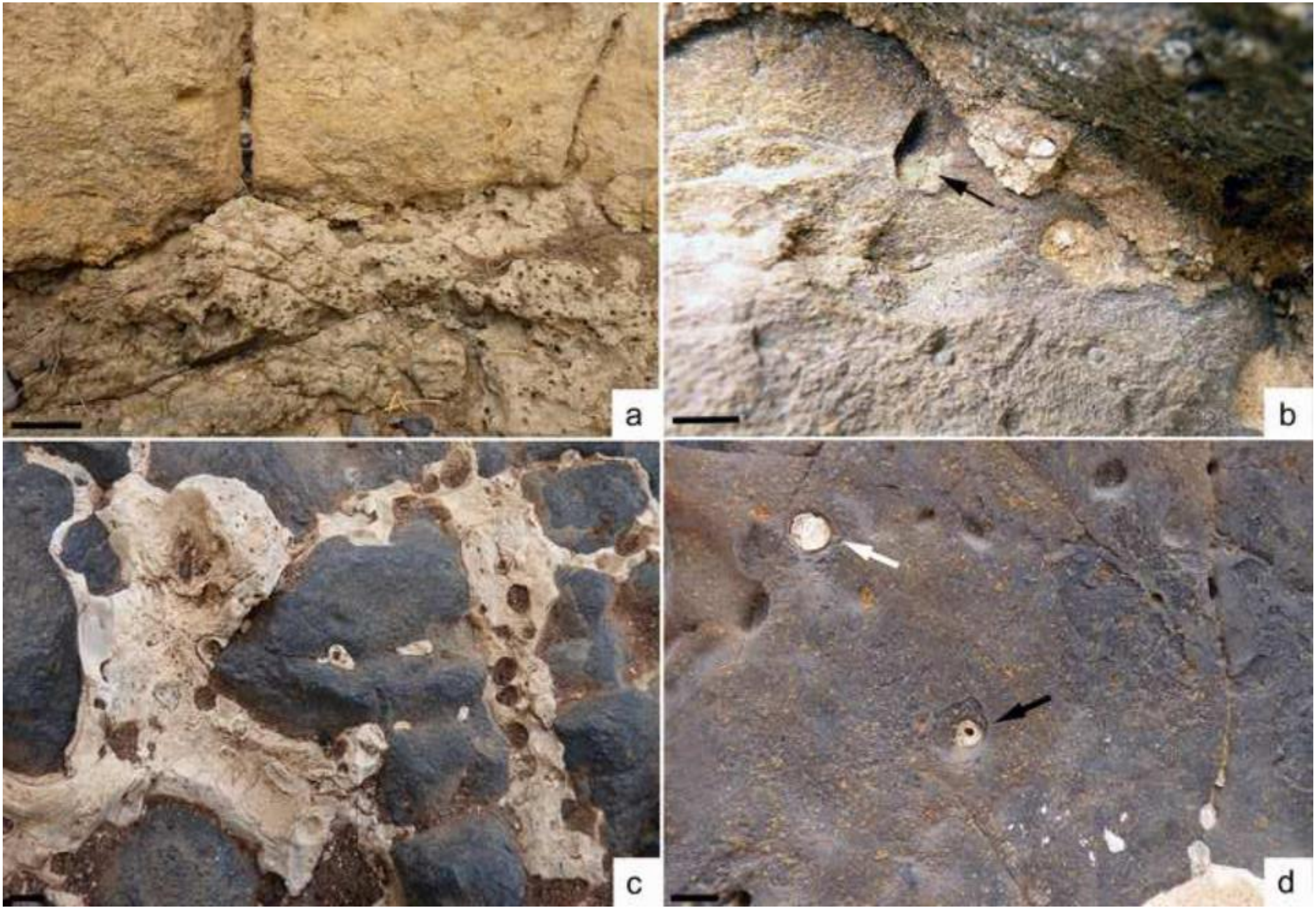

Table 1

	Centimetres (cm)	Sample/ Quadrat (0.5 × 0.5 m)	Rocky-shore biota			
			Balanus sp.	*Ostrea* sp.	*Gastrochaenolites* isp.	Calcareous crust (%)
Sub-horizontal top surface	0-50	**A**			**30**	**12**
	50-100	**B**			**21**	**14**
Vertical surface	80-130 (top)	**C**	**2**		**70**	**16**
	30-80	**D**		**2**	**88**	**30**
	0-30 (base)	**E**	**7**	**2**	**4**	**87**

Table 2

Rocky-shore	substrate
Element	**Percentage**
SiO_2	49.732
CaO	9.327
FeO	8.769
Na_2O	4.527
AL_2O_3	17.919
K_2O	1.283
MnO	0.171
MgO	3.905
F	0.107
SO_3	0.01
TiO_2	2.609
Cr_2O_3	0.015
P_2O_5	0.832
BaO	0.047
SrO	0.086
NiO	0.013