Acta Geologica Polonica, Vol. 61 (2011), No. 3, pp. 243–264

The fossil echinoids of Santa Maria Island, Azores (Northern Atlantic Ocean)

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ABSTRACT:

Madeira, P., Kroh, A., Cordeiro, R., Meireles, R. and Ávila, S.P. 2011. The fossil echinoids of Santa Maria Island, Azores (Northern Atlantic Ocean). *Acta Geologica Polonica*, **61** (3), 243–264. Warszawa.

In the relatively young archipelago of the Azores, fossiliferous deposits are restricted to the oldest island (Santa Maria), mainly from Late Miocene–Early Pliocene deposits, and a few from the Pleistocene. Echinoid material collected from these deposits comprises mainly disarticulated skeletal material (primary spines and coronal fragments) and a few complete tests. The taxa present in the Upper Miocene to Lower Pliocene beds comprise *Eucidaris tribuloides*, *Echinoneus* cf. *cyclostomus*, *Clypeaster altus*, *Echinocyamus pusillus*, *Echinocardium* sp. 1, *Echinocardium* sp. 2, *Schizobrissus* sp. and undetermined spatangoids. The spatangoids and *E.* cf. *cyclostomus*, are new records for the Miocene–Pliocene strata of the island. The material collected from Upper Pleistocene outcrops (MISS 5e) included three regular echinoid species, *Sphaerechinus granularis*, *Arbacia lixula* and *Paracentrotus lividus*. The two latter species are recorded for the first time from the Pleistocene deposits of the island. Compared to the older deposits, the Pleistocene record represents a very narrow range of environments and is basically restricted to deposits associated with an ancient rocky shore. Moreover, the conspicuous presence of taxa typical of tropical seas in the Mio-Pliocene sediments contrasts with the Pleistocene and modern echinoid fauna, which is warm temperate in composition.

Key words: Northeastern Atlantic; Azores; Santa Maria Island; Late Miocene–Early Pliocene; Late Pleistocene; MISS 5e.

INTRODUCTION

The Azores is one of the most remote archipelagos of the North Atlantic. This relatively young oceanic island system is composed of nine volcanic islands and several islets, located midway between the North American and European shores. Reports on marine fossiliferous outcrops are restricted to the oldest island of Santa Maria (Lat. 37º 23' N; Long. 24º 45' W), mostly from deposits of Late Miocene to Early Pliocene age and from a few Pleistocene deposits (Madeira *et al.* 2007). Exceptionally, very small fossiliferous deposits from the Late Miocene–Early Pliocene are also known from the islet of Formigas, 30 km NE of Santa Maria (Zbyszewski *et al.* 1961b; Abdel-Monem *et al.* 1975).

The fossiliferous deposits of Santa Maria Island have long attracted the attention of researchers, and several studies devoted to the fossil faunas were published, particularly on the fossil malacofauna (García-Talavera 1990; Callapez and Soares 2000; Ávila *et al.*

2002, 2009; for older references see Madeira *et al.* 2007). However, the Neogene echinoid fauna of Santa Maria is poorly known. The list of reported species remained almost unchanged in over 150 years of palaeontological research on the island. In the first publications (e.g., Bronn 1860a; Mayer 1864 and Cotter 1892) a total of three echinoid species were reported from the Mio-Pliocene outcrops: *Eucidaris tribuloides* (Lamarck, 1816), *Echinocyamus pusillus* (O.F. Müller, 1776) and *Clypeaster altus* (Leske, 1778). The last addition was *Prionocidaris avenionensis* (Des Moulins, 1837) (but see remarks below under *Eucidaris tribuloides*) by Ferreira (1955), making a reported total of four species from the older outcrops of Santa Maria. *Sphaerechinus granularis* (Lamarck, 1816) reported by Callapez and Soares (2000), is the only record from the Pleistocene outcrops.

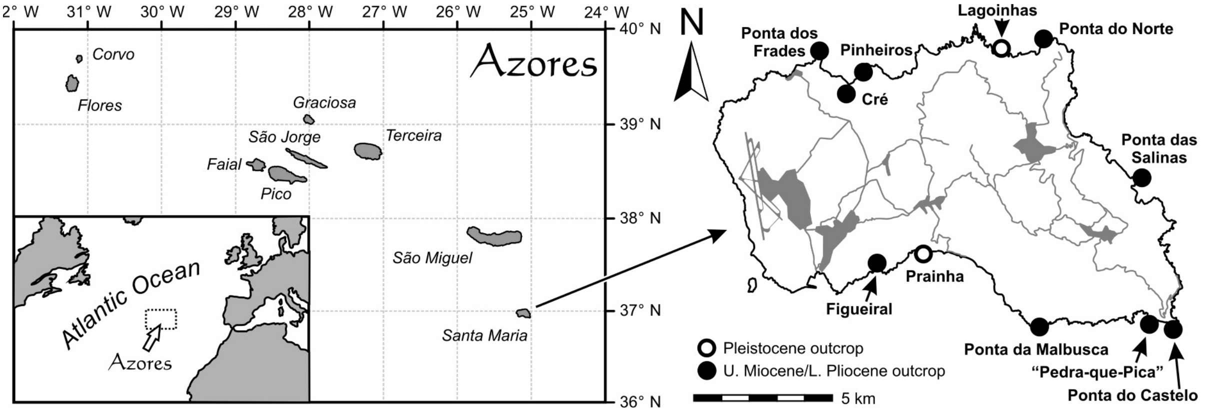
The rediscovery of the fossiliferous outcrops made during the international workshops "*Palaeontology in Atlantic Islands*" (2002, 2005–2009), and the retrieval of new echinoderm fossil specimens, clearly shows that this subject is in need of revision.

STUDY AREA

Santa Maria is a relatively small island, with an area of 97 km^2 and a maximum length of 16.8 km (França *et al.* 2003). Radiometric (K-Ar) analysis has shown that this most south-eastern island of the Azores began its rise above the sea at a maximum estimate of 8.12 Ma (Abdel-Monem *et al.* 1975). The sedimentary deposits are exposed mainly along coastal sections and up valleys, rarely extending higher than 200 m above the present sea level. These deposits consist of sedimentary layers intercalated by volcanic material, and are represented by limestone, breccia, sandstone, conglomerate and subaerial deposits (Agostinho 1937; Ferreira 1955; Mitchell-Thomé 1974). Pure calcareous units are rare and poorly developed, being restricted to thin beds of bioclastic rud- and wackestone in most outcrops (Madeira *et al.* 2007). These deposits were grouped in two basic units by Serralheiro *et al.* (1987, 1990) and Serralheiro (2003): the Touril Complex and the Facho-Pico Alto Complex. The older fossiliferous outcrops studied here fall in the second group. Recent Sr-isotope data by Kirby *et al.* (2007) and biostratigraphic data by Janssen *et al.* (2008) dated them as Early Pliocene (Zanclean), although a Latest Miocene age cannot be completely ruled out. Pleistocene marine fossiliferous deposits are locally exposed on the north and south coasts of the island, consisting mainly of poorly consolidated bioclastic sands resting either on a layer of algal crust or directly on basaltic marine terraces. Recent dating estimates by Ávila *et al.* (2008a) suggest that the Pleistocene outcrops of Santa Maria Island correspond to Marine Oxygen Isotope Substage 5e (MISS 5e), with an absolute age of 130–120 ky.

A review of the palaeontological research on the island can be found in Madeira *et al.* (2007). Further details on the litho- and bio-stratigraphy of the Miocene–Pliocene outcrops can be found in Kirby *et al.* (2007), Janssen *et al.* (2008) and Kroh *et al.* (2008). Detailed descriptions of the Pleistocene fossiliferous deposits can be found in Ávila *et al.* (2002, 2009, 2010) and Ávila (2005).

The echinoid material was collected from six locations scattered along the coastal areas of Santa Maria (Text-fig. 1): Cré, Ponta dos Frades, "Pedra-que-Pica", Ponta da Malbusca, Ponta do Castelo, Praia do Calhau (Praia Formosa) and Lagoinhas. The outcrop names used herein are based on the geological map by Serralheiro *et al.* (1987) and, with few exceptions, are consistent with the historical studies (see Table 1).



Text-fig. 1. Locations of Upper Miocene/Lower Pliocene and Pleistocene outcrops studied. Inset (left hand side) shows the position of Santa Maria Island. For coordinates and alternate names of the outcrops see Table 1

Outcrop	Location	Other names
Cré	N 37° 0'3.76", W 25° 8'10.78"	Bocca do Crè; Forno do Cré; Furna da Cré; Casa da Cré; Escarpa da Cré; Pedreira dos Frades
“Pedra-que-Pica”	N 36°55'48.37", W 25°1'29.23"	
Ponta da Malbusca	N 36°55'46.10", W 25°4'8.14"	Forno da Cré; Furna da Cré; Boca da Cré; Ponta da Piedade
Ponta do Castelo	N 36°55'43.93", W 25°0'58.35"	Ponta da Maia
Ponta dos Frades	N 37°0'41.67", W 25°8'44.68"	-
Ponta das Salinas*	N 36°58'22.97", W 25°1'43.38"	Feiteirinhas; Feteirinha
Ponta do Norte*	N 37°0'57.76", W 25°3'50.80"	
Pinheiros*	N 37°0'21.45", W 25°7'48.87"	Pinheiras
Figueiral	N 36°56'53.82", W 25°7'40.31"	-
Prainha	N 36°57'7.46",W25°6'17.89"	Praia Formosa
Lagoinhas	N 37°0'47.05",W25°4'58.23"	-

(*) historical outcrops from which we were unable to collect new material

Table 1. Reported fossiliferous outcrops of Santa Maria islands, their location, and other names used in the literature (for references see Madeira *et al.* 2007)

MATERIALS AND METHODS

All of the specimens were collected during the International Workshops “*Palaeontology in Atlantic Islands*”, held in Santa Maria Island, in June 2002, 2006, 2007 and 2008. Individual echinoid specimens were collected from the surface by bed-to-bed collecting. Additionally, beds with suitable lithology were subject to bulk sampling. These bulk samples were treated with H_2O_2 and processed by wet sieving. Both whole specimens and fragments were picked from the residues using a binocular microscope. The specimens are deposited in the fossil collection of the Department of Biology of the University of the Azores (DBUA-F collection).

Abbreviations

DBUA-F – fossil collection of the Department of Biology of the University of the Azores, Ponta Delgada, São Miguel Island, Azores, Portugal; MG-LNEG – Museu Geológico (Laboratório Nacional de Energia e Geologia, Lisbon), Portugal; NHMW – Natural History Museum of Vienna, Vienna, Austria;

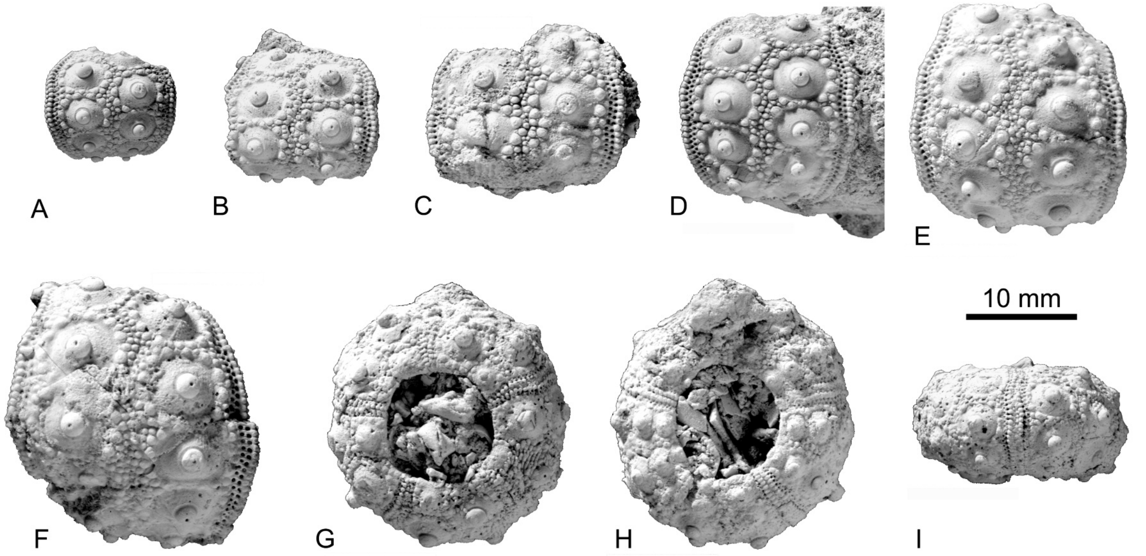
TL – Test length; TD – Test diameter; % TL – Percentage of the test length; % TD – Percentage of the test diameter.

SYSTEMATIC PALAEONTOLOGY
(following Kroh and Smith 2010)

Class Echinoidea Leske, 1778
Subclass Cidaroidea Smith, 1984
Order Cidaroida Claus, 1880
Family Cidaridae Gray, 1825
Genus *Eucidaris* Pomel, 1883

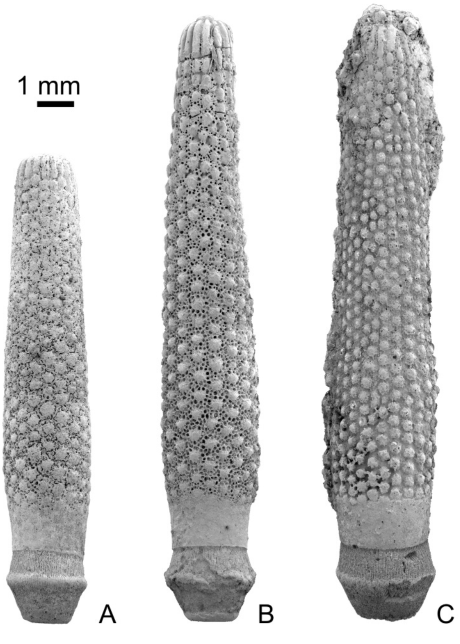
Eucidaris tribuloides (Lamarck, 1816)
(Text-figs 2A–I, 3A–C)

1816. *Cidaris tribuloides*; Lamarck, p. 56.
1862. *Cidaris ?tribuloides* Lmk.; Bronn *in* Reiss, p. 47, pl. 1, fig. 20 [3 spines].
1864. *Cidaris tribuloides*. Lamarck; Mayer, p. 11.
1898. *Cidaris tribuloides* Lamarck; Koehler, pp. 7–9
1928. *Eucidaris tribuloides* (Lamarck.); Mortensen, pp. 400–408, fig. 119; pl. 41, figs 9–16; pl. 48, fig. 1; pl. 73, fig. 1; pl. 86, fig. 16 [cum syn].
1955. *Cidaris avenionensis* Desmoulins; Ferreira, p. 15; pl.10, fig. 71 [misidentification].
1961. *Cidaris tribuloides*, Lamarck; Ferreira, pp. 532–533; pl. 1, fig. 5; pl. 2, fig. 11.
1961a. *Eucidaris trïbuloides*, Lam.; Zbyszewski, Ferreira and Assunção, p. 14.
1962a. *Cidaris tribuloides*, Lam.; Zbyszewski and Ferreira, p. 224.
1962a. *Eucidaris tribuloides*, Lam.; Zbyszewski and Ferreira, p. 226, 231.
1962b. *Cyathocidaris avenionensis* Desm.; Zbyszewski and Ferreira, p. 251. [following the misidentification of Ferreira, 1955]
1962b. *Cidaris tribuloides* Lam.; Zbyszewski and Ferreira, p. 251, pl. 1, figs 7–8.
1976. *Cyathocidaris avenionensis* Desm.; Mitchell-Thomé, p. 89. [following the misidentification of Ferreira, 1955]
1976. *Eucidaris tribuloides* Lamarck; Mitchell-Thomé, p. 89.



Text-fig. 2. *Eucidaris tribuloides* (Lamarck, 1816); A – DBUA-F 343-1; B – DBUA-F 455; C – DBUA-F 272; D – DBUA-F 305; E – DBUA-F 448; F – DBUA-F 346; G-I – DBUA-F 445. A, E and G-I from Ponta da Malbusca, B-D and F from Pedra-que-Pica

MATERIAL: Late Miocene–Early Pliocene: a single complete specimen from Ponta da Malbusca (DBUA-F 445); 32 corona fragments from Cré (three fragments; DBUA-F 444), "Pedra-que-Pica" (23 fragments, DBUA-F 107-4, 272, 305, 346, 352, 367, 448, 449, 450, 451, 452, 453, 455 and 461-1) and from Ponta da Malbusca (four fragments, DBUA-F 335, 336, 343-1 and 343-3); three primary spine fragments from Cré (DBUA-F 443), "Pedra-que-Pica" (one complete spine, DBUA-F290; 102 fragments, DBUA-F 266-2, 274, 290, 454, 456), Ponta da Malbusca (32 fragments, DBUA-F 192-14, 250-2, 343-5, 446 and 447), and Ponta do Castelo (four complete spines, DBUA-F294-1; 35 fragments, DBUA-F 266-02, 345-5 and 442).



Text-fig. 3. *Eucidaris tribuloides* (Lamarck, 1816); A – DBUA-F 446-1 (Ponta Malbusca); B – DBUA-F 456-1 (Pedra-que-Pica); C – DBUA-F 294-1 (Ponta do Costelo)

DESCRIPTION:

Corona – Apart from one complete corona from Ponta Malbusca (DBUA-F 445), the specimens usually comprise a full interambulacrum and adjoining half ambulacra. The ambulacra are narrow, with a sinuous, double row of marginal tubercles (one on each plate). In the ambital region of larger specimens (TH > 15 mm) a small internal tubercle is added on each plate. The pores are C1 isopores (*sensu* Smith 1978). Each interambulacral plate is bordered by 7 to 9 ambulacral plates ambitally.

Each interambulacral plate bears one large, non-crenulate, perforate primary tubercle, the areole of which takes up the whole plate height. Adorally the areoles are confluent, ambitally adjoining areoles are separated by a narrow band of tubercles. The scrobicular tubercles are distinctly larger than the other secondary tubercles. The latter are generally rare in small specimens, but increase in number during growth. In the largest specimens observed (TH ~ 25 mm) there are up to two rows of secondary tubercles interradially (per interambulacral plate), forming a moderately wide median zone. In small specimens the median zone is narrow. In the sole whole corona observed (DBUA-F 445, TD 19.4 mm), peristome diameter and apical region are subequal and c. 8.5 mm wide (~ 44 % TD).

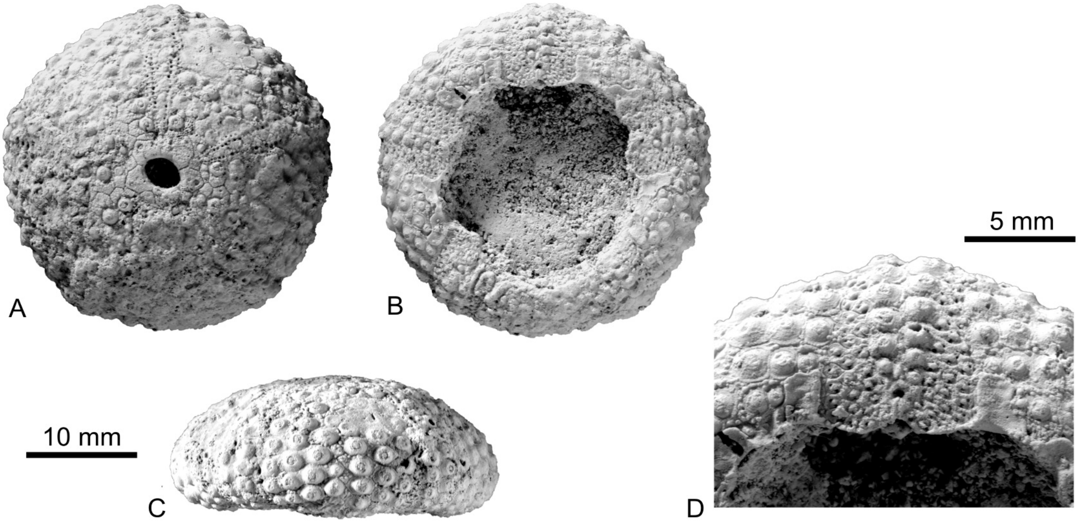
Primary spines – Numerous primary spines have been found in most of the outcrops studied. They are up to 21 mm in length, but most lie in a range from 11 to 17 mm. They are slightly widened just above the collar, giving the spines a stout appearance. The ornamentation consist of small nodulae arranged in vertical rows (22 to 26), forming a uniform surface. No thorns or spikes are formed. The acetabulum has a non-crenulate margin, the milled ring is finely striated, and both the collar and the neck are short. At the distal end a blunt point is developed, the most distal nodulae forming low ridges and a weakly developed crown with a small central projection. Traces of the original coloration, namely a coarse brown to lilac horizontal banding, are commonly still visible. Cross sections reveal a thick cortex layer and a comparatively small medulla.

REMARKS: Comparisons of the abundant fossil material from Santa Maria Island with extant specimens of *Eucidaris tribuloides* in the NHMW collection confirm that they are conspecific. This also confirms earlier reports of that species by Bronn (*in* Reiss 1862), Mayer (1864) and others. The occurrence of this species in the Early to Middle Miocene of the Mediterranean, although mentioned by Philippe (1998, pp. 46–48, p. 274, pl. 4, figs 16–18), is doubtful (see Kroh 2005, p. 8). There, another species of *Eucidaris* occurred, namely *E. zeamays* (Sismonda, 1842). It differs from *E. tribuloides* in its smaller size, well separated areoles, narrower median zone, and spines coarsely ornamented by whorls of thorns.

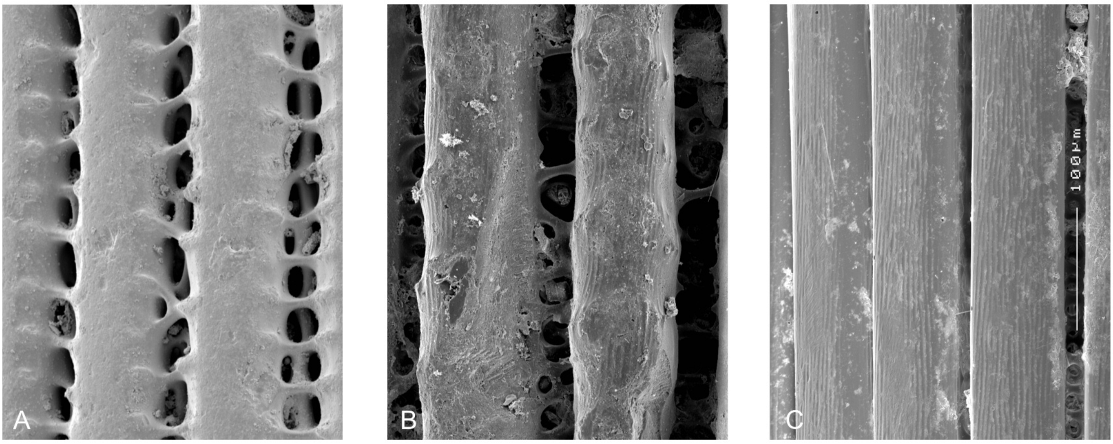
E. desmoulinsi, described by Borghi (1999, pp. 110–111, pl. 3, figs 1–9, pl. 5, figs 1–2) from the Italian Pliocene, closely resembles the specimens collected in Santa Maria, particularly regarding spine size and ornamentation.

Ferreira (1955, p. 15, pl. 10, fig. 71) reported the presence of some small and poorly preserved spines of "*Cidaris avenionensis* Desmoulins" [now *Prionocidaris avenionensis* (des Moulins, 1837)], in the Santa Maria fossil collection of Serviços Geológicos de Portugal (now allocated to the Geological Museum, in Lisbon). We were unable to trace the original specimens in the Portuguese collection. However, based on Ferreira's illustrations, the referred spines are very similar to the ones here described and assigned to *E. tribuloides*, with no indication of the ornament series of thorns seen typically in *Prionocidaris avenionensis* (compare Philippe 1998, pp. 34–42, pl. 1, pl. 3, figs 1–19; Kroh and Nebelsick 2003, figs 3f–g). We thus dismiss the record of *P. avenionensis* from the Azores as misidentification, especially as this species is restricted to the Burdigalian and Early Langhian elsewhere (Philippe 1998, p. 42).

OCCURRENCE: This species was reported from the Late Miocene–Early Pliocene of Santa Maria Island, from the outcrops of Figueiral (Bronn *in* Reiss 1862; Mayer 1864; Zbyszewski and Ferreira 1962a, b), Ponta da Malbusca (Bronn *in* Reiss 1862; Mayer 1864; Zbyszewski and Ferreira 1962a, b), Ponta das Salinas (Mayer 1864; Zbyszewski and Ferreira 1962a, b) and Cré (Ferreira 1961; Zbyszewski and Ferreira 1962b). This species is also known to occur in the Pleistocene of the Caribbean islands (Donovan 2003) and also the Bermuda Archipelago (Olson and Hearty 2009). At present, this species occurs in tropical waters of the East Atlantic, in the Guinea Gulf and Cape Verde Islands (see Kroh and Mooi 2010 for more extensive distribution records). In the Western Atlantic, it occurs in the warmer waters of the American coasts, from South Carolina (USA) to Northern Brazil, including the



Text-fig. 4. *Arbacia lixula* Linné, 1758; DBUA-F 271 (Pleistocene of Praia do Calhau)



Text-fig. 5. Microstructure of echinoid spines from the Pleistocene of Lagoinhas (bulk sample DBUA-F LH06-7): A – *Arbacia lixula* Linné, 1758; B – *Sphaerechinus granularis* (Lamarck, 1816); C – *Paracentrotus lividus* (Lamarck, 1816)

Caribbean archipelagos. It can be found in small crevices on coral reefs, under rocks and boulders in back reef lagoon areas, though it is particularly abundant in turtle grass beds, from the littoral to a depth of 450 m (Schultz 2005). Koehler (1898, pp. 7–9) reported this species (= *Cidaris tribuloides* Lamarck) from the Azores, based on a single specimen dredged from the Pico-Faial Channel at 130 m depth, a record that later surveys failed to confirm.

Subclass Euechinoidea Bronn, 1860b
Echinacea Claus, 1876
Order Arbacioida Gregory, 1900
Family Arbaciidae Gray, 1855
Genus *Arbacia* Gray, 1835

Arbacia lixula Linnaeus, 1758
(Text-figs 4A–D, 5A, 6A)

1758. *Echinus lixula*; Linnaeus, p. 664.
1935. *Arbacia lixula* (Linnaeus); Mortensen, pp. 566–572; pl. 70, fig. 13; pl. 87, figs 11–12 [cum syn.]

MATERIAL: Pleistocene of Prainha: one complete corona from (DBUA-F 271); 6 corona fragments (DBUA-F 354); Pleistocene of Lagoinhas: 22 corona fragments (DBUA-F 327; 438); numerous primary spines fragments (DBUA-F 149-7; 438).

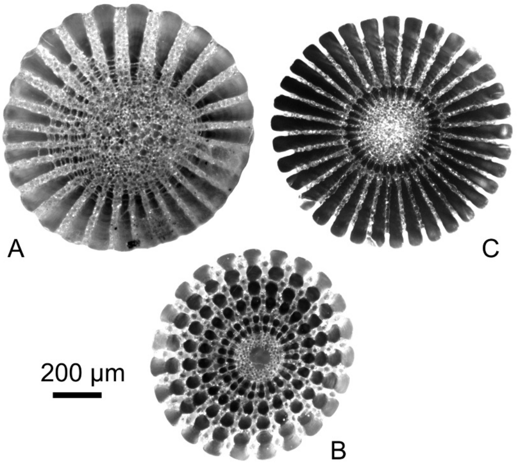
DESCRIPTION:

Corona – The complete corona is c. 29 mm (DBUA-F 271) in horizontal diameter. In profile, the corona is flattened, test height 52 % TD. Apical disc dicyclic, enclosing an oval periproct with maximum width 3.5 mm. Genital and ocular plates are almost devoid of tubercles, the remaining surface covered by epistromal ornament. The ambulacra are formed by trigeminate plates of the arbacioid compound type. The ambulacral pores belong to the C1 type (*sensu* Smith 1978) and form more or less straight, vertical rows. Each ambulacral plate bears one large primary tubercle. On adapical plates, however, these are less distinct.

Ambitally and orally the interambulacra bear large, multiple subequal primary tubercles in horizontal rows. Up to four imperforate, non-crenulate tubercles per plate are present at the ambitus. Secondary tuberculation is generally sparse, but plates are covered by epistromal ornament in between the tubercles. On the two most adapical plates in each interambulacral column there are no primary tubercles along the interradial suture. A pronounced naked zone, however, is not formed. Peristome large (55.9 % TL in DBUA-F 271), with ambulacra expanding adorally forming phyllodes facilitating enlarged pore pairs.

Primary spines – Primary spine fragments associated with the test fragments could be attributed to *Arbacia* based on their surface microstructure (Text-fig. 5A) and cross sections (Text-fig. 6A) and on comparison with extant material. The wedges on the surface of the spines are typically finely jagged, and the furrows between the ridges show the irregular mesh that fills most of the cross section of the spines (Text-fig. 6A).

REMARKS: The features outlined above enable confident assignment of the fossil material from Santa Maria to the genus *Arbacia*. The lack of a pronounced naked zone in the adapical interambulacra suggests attribution to *A. lixula*, which still occurs in the area. This species has not previously been reported from the Santa Maria fossil fauna.



Text-fig. 6. Cross sections of echinoid spines from the Pleistocene of Lagoinhas (bulk sample DBUA-F LH06-7): A – *Arbacia lixula* Linné, 1758; B – *Sphaerechinus granularis* (Lamarck, 1816); C – *Paracentrotus lividus* (Lamarck, 1816)

OCCURRENCE: On Santa Maria Island *A. lixula* was present in both Pleistocene outcrops, Lagoinhas (north shore) and Prainha (south shore). This species occurs presently in shallow waters (0–40 m depth) of the Mediterranean and adjacent Atlantic waters to the Gulf of Guinea, including the archipelagos of the Azores, Madeira, Canaries and Cape Verde (Mortensen 1935; Schultz 2005). In the western Atlantic, it is also known to occur in Brazil (Schultz 2005), which represent a genetically distinct population (Palumbi and Lessios 2005). Together with *Paracentrotus lividus*, it is one of the most conspicuous echinoid species of the Azorean shallow-waters, commonly forming dense patches on the rocky shores of the islands (Marques 1983; Morton *et al.* 1998). Despite its common occurrence throughout the Lusitanian Province today, fossil records of *Arbacia lixula* are rare. To our knowledge, fossil *A. lixula* has only been reported from the Lower Pleistocene ("Post-pliocene/Piano Siciliano") of the Livorno area in western Italy and the Pleistocene of Madeira (Stefanini 1911; under the name *A. pustulosa*, a junior synonym of *A. lixula*). Based on these occurrences, Mortensen (1935, p. 572) concluded that *A. lixula* had migrated from the Atlantic to the Mediterranean in "post-glacial" times (at that time the absolute dating of the glaciation periods was poorly known).

Order Camarodonta Jackson, 1912
Infraorder Echinidea Kroh and Smith, 2010
Family Parechinidae Mortensen, 1903
Genus *Paracentrotus* Mortensen, 1903

Paracentrotus lividus (Lamarck, 1816)
(Text-figs 5C, 6, 7)

1816. *Echinus lividus*; Lamarck, p. 50.
1943b. *Paracentrotus lividus* (Lamarck); Mortensen, pp. 157–168, pl. 17, figs 2–3; pl. 22, figs 1–9; pl. 57, figs 1–3, 11, 12, 20. [cum syn.]

MATERIAL: Pleistocene of Lagoinhas: one test fragment (DBUA-F 327-1), numerous primary spine fragments (DBUA-F 149-7).

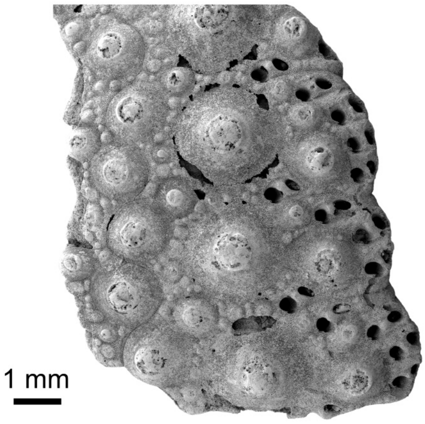
DESCRIPTION:

Corona – Coronal material is represented by a single fragment of a supraambital ambulacrum only. This fragment consists of polygeminate ambulacral plates (4 or 5 pores per plate respectively), which belong to the echinoid compound type. The pores are P2 type pores (*sensu* Smith 1978). They are arranged in arcs, forming oblique rows, separated by secondary tubercles. The tubercles are imperforate and non-crenulate, each ambulacral plate bears one primary tubercle and several secondary tubercles.

Primary spines – Though much more common that the coronal material, they are usually highly fragmented. The spines have a glassy smooth uniform appearance, with the wedges joining closely together (Text-fig. 5C). The wedges have a very fine longitudinal striation and extend deep into the spine, reducing the irregular meshwork to the centre of the cross section, with no central cavity (Text-fig. 6C).

REMARKS: Albeit fragmentary, the present specimen can clearly be assigned to the genus *Paracentrotus*, based on the characters of the aboral ambulacrum. Comparison with extant material of *P. lividus* from the Mediterranean and the Northern Atlantic showed a high degree of similarity.

Another species of this genus occurs at present in the Atlantic, *P. gaimardi* (reported from the Brazil, Angola and Eloby Islands of the Gulf of Guinea; Mortensen 1943b, p. 168). This species was described by Mortensen (1943b), who stated that the only significant difference between these two species was the radiating striation on the apical disc, albeit *P. lividus* tended to attain bigger sizes than *P. gaimardi*. The fossil specimens do not preserve the features used for distinguishing *P. lividus* and *P. gaimardi*. However, comparing the extant geographical ranges of both species, *P. lividus* being a common element of the extant Azorean fauna, is the most likely candidate. Thus, until new data allows further comparisons, we assume that the remains found at Lagoinhas belong to this later species.



Text-fig. 7. *Paracentrotus lividus* (Lamarck, 1816), ambulacral test fragment (DBUA-F 327-1, Lagoinhas)

OCCURRENCE: In the Pleistocene of Santa Maria, it is only known from the locality of Lagoinhas. *P. lividus* is a rock-boring shallow water species (0–100 m depth) presently known to occur in the Mediterranean and in the Northeast Atlantic from Ireland and the English Channel southwards to the Western Sahara, including the archipelagos of Azores, Madeira, Canaries and Cape Verde (Schultz 2005; Kroh and Mooi 2010). *P. lividus*, together with *A. lixula*, is one of the most conspicuous grazers of the Azorean shallow-water rocky shores today (Marques 1983; Morton *et al.* 1998). *P. lividus* has been reported fossil from the Pleistocene of the Moroccan Atlantic coast (Néraudeau and Masrour 2008), Northern Italy (Airaghi 1898 as "*Strongylocentrotus draebachiensis* [sic!]", Borghi 1995), Morocco (Pomel 1887), Sicily (Checchia-Rispoli 1907), and the Portugal mainland (Callapez 2000), as well as from the Late Pliocene ("Astian") of Greece (Marcopoulou-Diacantoni 1967). There is also a tentative record (*Paracentrotus* aff. *lividus*) from the Messinian of north-west France (Néraudeau *et al*. 2003).

Superfamily Odontophora Kroh and Smith, 2010
Family Toxopneustidae Troschel, 1872
Genus *Sphaerechinus* Desor, 1856

Sphaerechinus granularis (Lamarck, 1816)
(Text-figs 5B, 6B)

2000. *Sphaerechinus granularis* (Lamarck, 1822); Callapez and Soares, p. 314.

MATERIAL: Pleistocene of Prainha: one corona fragment (DBUA-F 482-3); Pleistocene of Lagoinhas: numerous primary spine fragments (DBUA-F 149-7).

DESCRIPTION:
Corona – The coronal material is represented solely by one heavily eroded ambulacral fragment of c. 15 mm size. The ambulacral plates are polygeminate, with four pores belonging to the P1 type (*sensu* Smith 1978), forming a more or less regular arc. Each plate bears a primary tubercle and one to two secondary tubercles. The tubercles are apparently non-crenulate and imperforate.
Primary spines – Although heavily eroded, traces of an irregular rugose microstructure can be seen on the surface ridges of the primary spines (Text-fig. 5B). The cross section (Text-fig. 6C) shows pronounced, beaded wedges, followed by a dense meshwork, and at the centre a small irregular cavity.

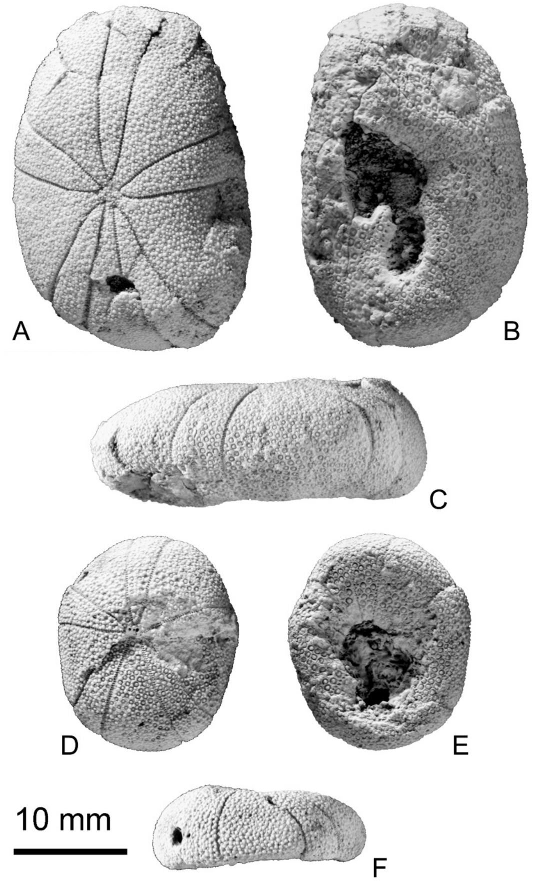
REMARKS: Despite the highly fragmentary nature of the material, comparison with extant specimens enables confident assignment of the fossil material from Santa Maria to *Sphaerechinus granularis*.

OCCURRENCE: On Santa Maria Island it was known only from the Pleistocene outcrop of Lagoinhas (Callapez and Soares 2000). At present, this species is known to occur on rocky shores (0–100 m) of the Mediterranean and in the Northeast Atlantic southwards to the Gulf of Guinea (including the archipelagos of the Azores, Madeira, Canaries and Cape Verde) and to the Channel Islands (Schultz 2005). *S. granularis* is common on the Azorean rocky sublittoral. Though preferring deeper waters (Marques 1983), it is not uncommon to spot them in the first few metres in sheltered areas (Azevedo *et al.* 1994). *S. granularis* appears to be a relatively recently evolved species, its fossil record being restricted to a few occurences reported from the Pleistocene of Calabria, southern Italy (Seguenza 1880; Airaghi 1900), Morocco (Pomel, 1887) and Sicily (Checchia-Rispoli 1907).

Irregularia Latreille, 1825
Order Echinoneoida H. L. Clark, 1925
Family Echinoneidae L. Agassiz and Desor, 1847
Genus *Echinoneus* Leske, 1778

Echinoneus cf. *cyclostomus* Leske, 1778
(Text-figs 8A–F, 9A–C)

MATERIAL: Late Miocene–Early Pliocene of "Pedra-que-Pica": two complete coronas (DBUA-F 439 and 440) and seven fragments (DBUA-F 108-7, 441); Late Miocene–Early Pliocene of Ponta da Malbusca: two fragments (DBUA-F 193-33, 343-2); Late Miocene–Early Pliocene of Ponta do Castelo: one specimen (DBUA-F 438).

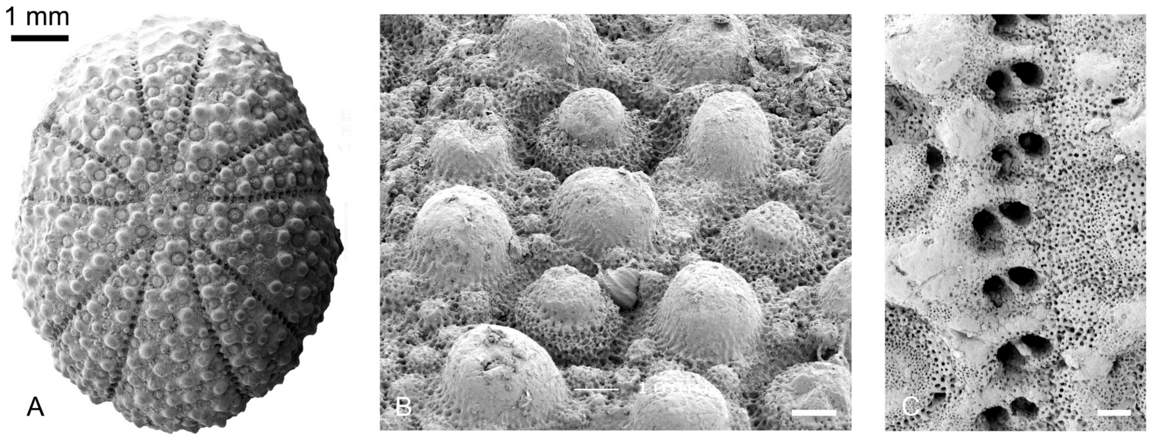


Text-fig. 8. *Echinoneus* cf. *cyclostomus* Leske, 1778; A-C – aboral, oral and lateral view of DBUA-F 439; D-F – aboral, oral and lateral view of DBUA-F 440 (both from Pedra-que-Pica)

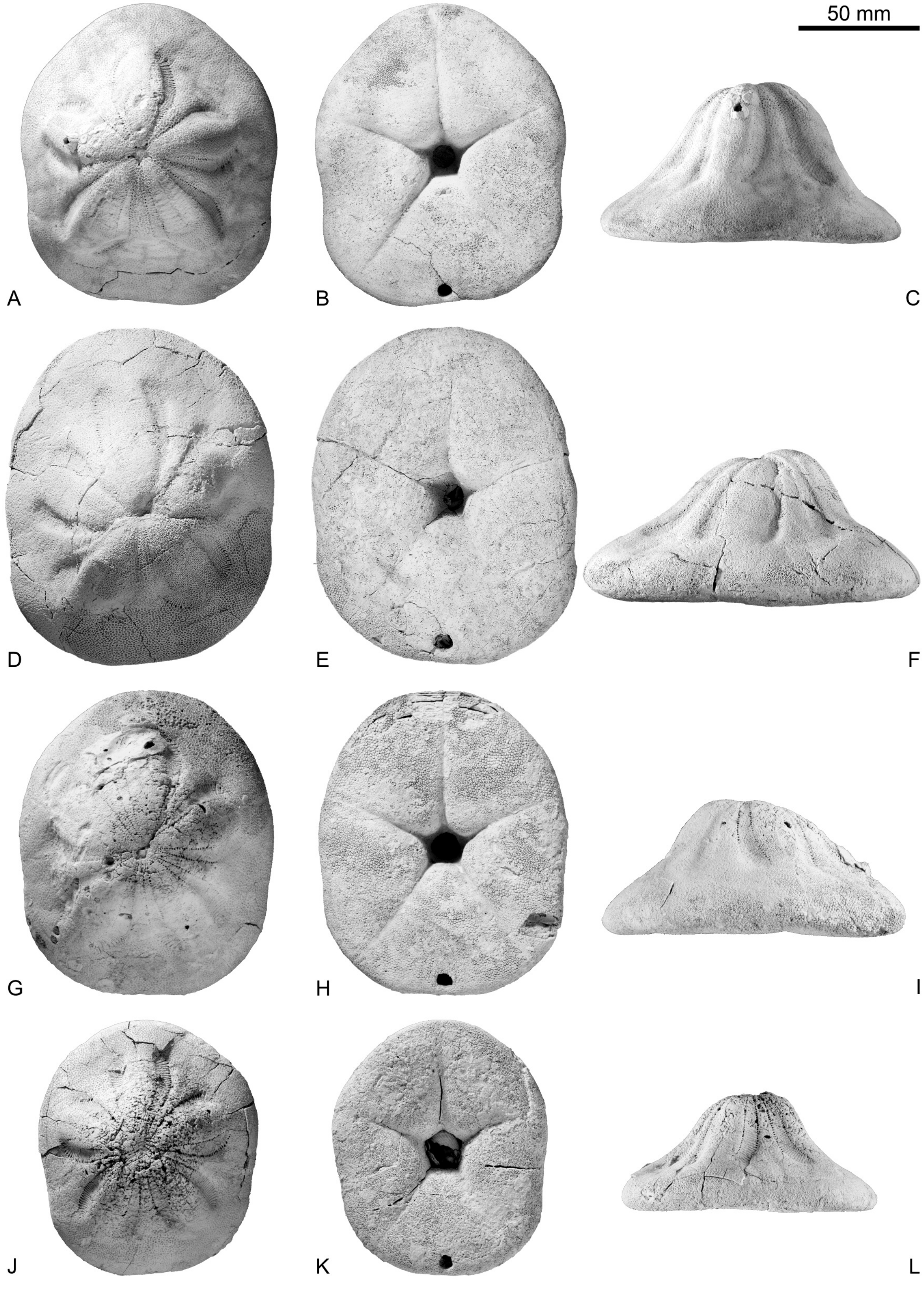
DESCRIPTION: Most specimens are fragmentary and/or crushed. The complete coronas available range from 7.5 to 30.8 mm test length. The shape of the corona is ovoid, with the maximum width lying posteriorly (small specimens) to centrally (larger specimens). In profile the corona is flattened, the maximum height lying subcentrally. The apical disc (varying between 42 and 51% TL from the anterior margin) is tetrabasal and bears four circular genital pores; only the smallest of the complete specimens (DBUA-F 438) lacks them. Surprisingly, the gonopores in the largest specimen (DBUA-F 439, TL 30.8 mm) are very small.

The ambulacra are non-petaloid with small, closely spaced partitioned isopores adapically. Adorally the pores are strongly oblique, less closely spaced and arranged in weak arches of three. The poriferous zones are distinctly depressed and very narrow, being clearly visible also in worn specimens. Both the aboral and oral sides are densely covered by small imperforate, non-crenulate primary tubercles. In between the primary tubercles large nodulae ("glassy tubercles" *sensu* Westergren 1911) are present on the aboral surface. Miliary and secondary tubercles are interspersed between these nodulae and the primaries, filling the remaining space. On the oral side the tubercles are separated by narrow ridges with few secondary and miliary tubercles but lacking glassy tubercles. In the largest specimen (Text-figs 8A–C; DBUA-F 439), the tubercle size varies according to the position on the corona, the oral tubercles being distinctly larger (2 times) than the aboral ones. The peristome is irregularly oval and strongly oblique (elongated along the 2-V axis). The periproct lies fully on the oral side, in between the peristome and the posterior margin and is elongated antero-posteriorly. Both peristome and periproct show distinct allometric growth, being comparatively larger in juveniles than in adult specimens (periproct: 30 vs. 21 % of TL).

REMARKS: Remains of members of the genus *Echinoneus* are commonly reported from Oligocene to Pleistocene deposits of the Caribbean (Donovan 1993, p.



Text-fig. 9. *Echinoneus* cf. *cyclostomus* Leske, 1778; A – aboral view of DBUA-F 438 (Ponta Malbusca); B-C – aboral tuberculation (B) and ambital ambulacral pores (C) DBUA-F 441 (Pedra-que-Pica). Scale bar of B and C equals 100 µm



Text-fig. 10. *Clypeaster altus* (Leske, 1778); A-C – aboral (A), oral (B), and left lateral (C) view of DBUA-F 155 (Ponta Malbusca); D-F – aboral (D), oral (E), and left lateral (F) view of DBUA-F 214 (Pedra-que-Pica); G-I – aboral (G), oral (H), and right lateral (I) view of DBUA-F 223 (Pedra-que-Pica); J-L – aboral (J), oral (K), and left lateral (L) view of DBUA-F 431 (Ponta Malbusca)

382; Donovan and Veale 1996, pp. 633–635; Dixon and Donovan 1998, p. 104; Donovan 2001, p. 183; Simpson 2001, p. 34; Donovan *et al.* 2005, pp. 106–107). Most occurrences, however, consist of single finds of comparatively poorly preserved specimens. On Santa Maria, however, *Echinoneus* is rather common. Despite the fragmentary nature of the test, three nearly complete, albeit crushed coronas could be recovered from "Pedraque-Pica" and Ponta da Malbusca.

When compared to extant *Echinoneus cyclostomus*, a large number of similarities are apparent. Differences observed concern the size of the gonopores in the largest of the fossil specimens (DBUA-F 439) and the apparent high variability of the aboral tubercle size. Despite the monograph of Westergren (1911) the intraspecific variability and possible ontogenetic effects on tubercle size are still poorly understood in *Echinoneus*. Thus we prefer to name the fossil material of Santa Maria in open nomenclature until it can be compared with the wide size range of extant *E. cyclostomus*.

OCCURRENCE: On Santa Maria, *E.* cf. *cyclostomus* was found in the outcrops of Ponta da Malbusca, "Pedraque-Pica" and Ponta do Castelo. Elsewhere, *E. cyclostomus* is known from the Jamaican Pleistocene (see references above) and from the Early Pliocene of Egypt (Ali 1985). *E. cyclostomus* Leske, 1778 has been reported to live cryptically under rocks, boulders or in burrows in the warm tropical coastal waters of the West Indies, from the Bahamas to Tobago, on Ascension Island, but not in Western Africa. It is also found in the Indo-Pacific, along the eastern African coast from Zanzibar to Natal, from Madagascar to Hawaii and Easter Islands, and from Japan to Northern Australia and Lord Howe Island (it is not known from the west coast of America) (Schultz 2005). *E. cyclostomus* does not occur in the Azores today.

Microstomata Smith, 1984
Order Clypeasteroida L. Agassiz, 1835
Suborder Clypeasterina L. Agassiz, 1835
Family Clypeasteridae L. Agassiz, 1835
Genus *Clypeaster* Lamarck, 1801

Clypeaster altus (Leske, 1778)
(Text-figs 10A–L)

1862. *Clypeaster ?altus* Lmk.; Bronn *in* Reiss, pp. 46–47.
1864. *Clypeaster altus.* Linné. (*Echinus*); Mayer, p. 12.
1892. *Clypeaster altus*, Lamarck; Cotter, p. 259.
1955. *Clypeaster altus* Lamarck; Ferreira, p. 16, pl. 9, figs 66, 69; pl. 10, figs 70, 73; pl. 11, fig. 76.
1961. *Clypeaster altus*, Lamarck; Ferreira, pp. 539–540; pl. 4, figs. 22, 23, 28, 29.
1961a. *Clypeaster altus*, Lam.; Zbyszewski, Ferreira and Assunção, p. 14.
1962a. *Clypeaster altus*, Lam.; Zbyszewski and Ferreira, p. 219, 231.
1962b. *Clypeaster altus* Lam.; Zbyszewski and Ferreira, p. 251, pl. 2, fig. 21.
1976. *Clypeaster altus* Klein; Mitchell-Thomé, p. 88.
1976. *Clypeaster altus* Lamarck; Mitchell-Thomé, p. 89.

MATERIAL: Late Miocene–Early Pliocene of "Pedraque-Pica": two specimens (DBUA-F 214, 223); Late Miocene–Early Pliocene of Ponta da Malbusca: two specimens (DBUA-F 155, 431).

Additionally, two fragments from Ponta da Malbusca (DBUA-F 355, 457) are tentatively attributed to *C. altus*

DESCRIPTION: The corona is large (commonly > 110 mm TL), antero-posteriorly elongated and has a subpentagonal to angular outline. The margin is slightly indented in interambulacra 1 and 4 and straight or slightly convex in the other interambulacra. The maximum width lies anterior of the apical disc, where ambulacral columns IIa and IVb reach the ambitus. Posteriorly ambulacral columns Ib and Va are nearly as wide. In profile the corona is high (usually between 45 and 55 % TL), trapezoid, with a (usually) thick, tumid ambitus and a domed petaloid area. The maximum height usually coincides with the adapical parts of the interporiferous zones of petals I and V. The oral surface is flattened, only the most adoral parts being steeply inclined towards the peristome, thus forming a narrow, deep infundibulum.

The apical disc is monobasal, with a large central madreporite of stellate shape and five gonopores varying from circular to oval (radially elongate). In some specimens the gonopores lie directly at the edge of the madreporite, in others they occupy a more distal position. A similar variation in gonopore position is observed in the extant *C. rosaceous* (A. Kroh, unpublished data).

The petals are straight and bear large elongate isopores. Adjacent pore pairs are separated by narrow ridges with a single row of up to nine primary tubercles. The distal parts of the poriferous zones curve towards the midline of the petals, but do not reach the perradial suture, the petals thus being widely open distally. The interporiferous zones are strongly inflated, the poriferous zones slightly depressed. Trailing podia *sensu* Mooi (1989, e.g. fig. 28a) are not observed.

The tuberculation consists of closely spaced primary tubercles in sunken areoles and dense miliary tuberculation on the remaining surface. Tubercle density is highest on the interporiferous zones of the petals and the ambitus, lowest adapically in between the petals. Tubercle size is largest on the oral surface, leaving only narrow ridges in between.

The peristome is large, subcircular and lies deeply sunken in a narrow infundibulum with steep, almost vertical walls. The subcircular periproct lies inframarginally in interambulacrum 5, close to the posterior margin (usually 2.5 to 3 mm away from it in specimens > 100 mm TL).

Apart from the general double-walled nature of the clypeasteroid corona, the internal support system in the Santa Maria specimens consists of few massive pillars, leaving a large body cavity in between the walls of the infundibulum and the ambitus. Additionally, the small fragments (DBUA-F 355; DBUA-F 457) show a similar double-walled construction and similar tubercle morphology and distribution.

REMARKS: *Clypeaster* fragments observed in some of the outcrops are tentatively attributed to this species due to the fact that they show consistent morphological features. There is no evidence for the occurrence of a second species of *Clypeaster* on Santa Maria.

OCCURRENCE: This species was reported from the Late Miocene–Early Pliocene of Santa Maria, from the fossiliferous outcrops of Pinheiros (Bronn *in* Reiss 1862; Mayer 1864; Ferreira 1961; Zbyszewski and Ferreira 1962a), Ponta da Malbusca (Ferreira 1961; Zbyszewski and Ferreira 1962a, p. 231; Zbyszewski and Ferreira 1962b), Figueiral (Ferreira 1961; Zbyszewski and Ferreira 1962b) and Ponta do Norte (Ferreira 1961; Zbyszewski and Ferreira 1962b). This species is only known from the fossil record, ranging from the Middle Miocene (Serravallian) to Early Pliocene. It is widely distributed in circum-Mediterranean countries, occurring in Algeria, France, Crete, Corsica, Italy, Sardinia and Spain (see Rose and Wood 1999; Néraudeau *et al*. 2001 and references therein).

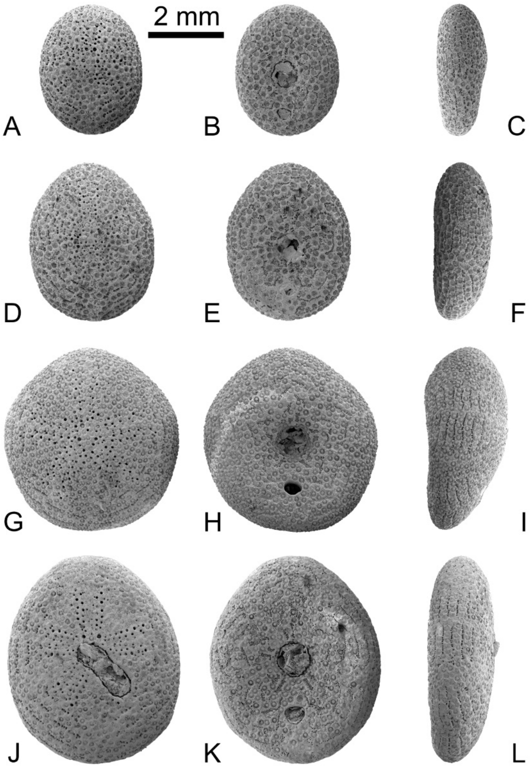
No species of this genus are known to occur presently in the Northeastern Atlantic and on the Mediterranean coasts. Clypeasterids are confined to the tropical and subtropical coasts of all continents (Mortensen 1948). In general, they prefer sandy bottoms, feeding on the interstitial fauna, e.g., foraminifera and small molluscs (Mortensen 1948).

Suborder Scutellina Haeckel, 1896
Infraorder Laganiformes Desor, 1847
Family Fibulariidae Gray, 1855
Genus *Echinocyamus* van Phelsum, 1774

Echinocyamus pusillus (Müller, 1776)
(Text-figs 11A–L)

1862. *Echinocyamus minimus* Girard; Bronn *in* Reiss, p. 46.
1864. *Echinocyamus pusillus.* Müller (Spatangus); Mayer, p. 12.
1955. *Echinocyamus pusillus* Mull.; Ferreira, p. 14.
1961. *Echinocyamus pusillus* Muller; Ferreira, p. 535, pl. 4, fig. 25.
1961a. *Echinocyamus pusillus* Mull.; Zbyszewski, Ferreira and Assunção, p. 14.
1962a. *Echinocyamus pusillus* Müll; Zbyszewski and Ferreira, p. 226.
1962b. *Echinocyamus pusillus* Muller; Zbyszewski and Ferreira, p. 251.
1976. *Echinocyamus pusillus* Müller; Mitchell-Thomé, p. 89.

[Remark: Only references relating to fossil Azorean specimens have been included in the synonymy list above. For a full synonymy of extant *E. pusillus* the reader is referred to Mortensen (1948).]



Text-fig. 11. *Echinocyamus pusillus* (Müller, 1776); A-C – aboral (A), oral (B), and left lateral (C) view of DBUA-F 432-2 (Cré); D-F – aboral (D), oral (E), and left lateral (F) view of DBUA-F 343-3-2 (Ponta Malbusca); G-I – aboral (G), oral (H), and left lateral (I) view of DBUA-F 343-3-1 (Ponta Malbusca); J-L – aboral (J), oral (K), and left lateral (L) view of DBUA-F 432-5 (Cré)

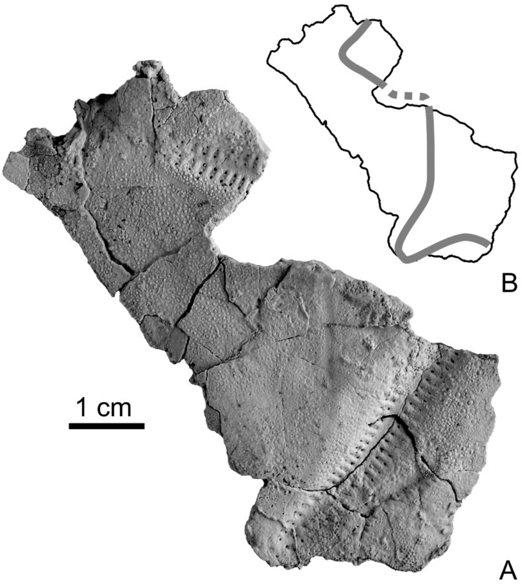
MATERIAL: Late Miocene–Early Pliocene of Cré: 10 specimens (DBUA-F 432); Late Miocene–Early Pliocene of "Pedra-que-Pica": four specimens (DBUA-F 434); Late Miocene–Early Pliocene of Ponta da Malbusca: 67 specimens (DBUAF 372); Late Miocene–Early Pliocene of Ponta do Castelo: one specimen (DBUA-F 433).

DESCRIPTION: Test very small, usually less than 8 mm. Outline oval (anterior-posteriorly elongated) to egg-shaped. Maximum width lying slightly posteriorly, ranging from 69 to 100 % TL (mean 83.6 %). In profile the test is low arched, the maximum height coinciding with the apical disc.

The apical disc lies slightly anterior of the centre (34–43 % TL, from the anterior margin). Four genital pores are present; the distance between the posterior genital pores are 0.4 mm, on average. The ocular pores are small, being indistinct in most specimens (due to the poor preservation). A single circular hydropore is present, lying roughly at the centre of the apical disc.

The ambulacra are petaloid, consisting of 4 to 7 strongly oblique pore pairs in each column. The frontal petal is the longest; the paired petals are subequal in length. The poriferous zones diverge. Outside the petals only accessory pores (micro-unipores) are present, which form distinct arcs along the adoral plate sutures. The tuberculation is homogeneous and consists of primary tubercles in sunken areoles, with a dense miliary tuberculation occupying the remaining surface. The peristome is located subcentrally on the oral surface and varies considerably in size (from 9 to 21 % of TL in diameter). It is slightly sunken, subcircular and its posterior margin is distinctly depressed in most specimens. The periproct is usually about half as wide as the peristome, and generally less than 10% of TL in width. It is transversally elongated and lies approximately halfway between the peristome and the posterior margin.

REMARKS: Two other similar *Echinocyamus* taxa are known to occur in the deeper waters of the Azores, *E. scaber macrostomus* Mortensen, 1907 and *E. grandiporus* Mortensen, 1907. In contrast to these species, however, *E. pusillus* has relatively well developed petals. This is also true for the specimens studied here, which show consistently larger pore numbers than the ones presented by Mortensen (1907, pp 28–39) for *E. scaber? grandiporus* and *E. macrostomus* of similar sizes. Another diagnostic feature in which *E. pusillus* differs significantly from the deep water species is the smaller distance between the posterior genital pores (Mironov and Sagaidachny 1984; Mironov 2006). In the Santa Maria specimens, the distance between the posterior genital pores never exceeds 0.6 mm, well inside the range given by Mironov (2006) for this species.

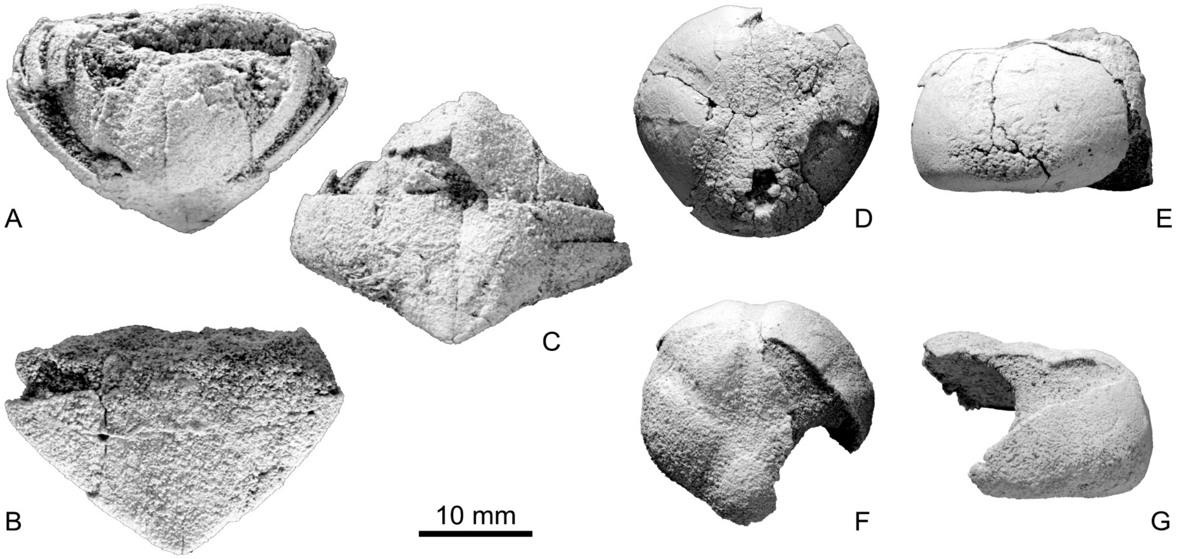


Text-fig. 12. *Schizobrissus* sp.; A – aboral test fragment; B – outline and peripetalous fasciole pathway; DBUA-F 381 (Pedra-que-Pica)

OCCURRENCE: On Santa Maria Island *E. pusillus* was reported from Figueiral (Bronn *in* Reiss 1862; Mayer 1864; Zbyszewski and Ferreira 1962a; Zbyszewski and Ferreira 1962b). This species is a common element of the fauna of soft bottom (coarse sands/fine gravels) marine environments (0–1,250 m depth) in the Northeastern Atlantic and the Mediterranean, from Iceland, Norway, the North Sea and the western Baltic Sea to West Africa. It is known to occur presently in Azorean waters. *E. pusillus* has been commonly reported fossil from European and North African deposits of Early to Middle Miocene age onwards, but the oldest records may be based on misidentifications (see discussion in Kroh 2005, p. 77, 81–82). Confirmed records of *Echinocyamus pusillus* are known from the Pliocene (e.g. Borghi 1993; Néraudeau *et al.* 2003) and Pleistocene from the Mediterranean and the North Sea Basin.

Atelostomata von Zittel, 1879
Order Spatangoida L. Agassiz, 1840
Suborder Brissidina Stockley *et al.*, 2005
Family Brissidae Gray, 1855
Genus *Schizobrissus* Pomel, 1869

Schizobrissus sp.
(Text-figs 12A–B)



Text-fig. 13. *Echinocardium* sp. 1 (A-C) and *Echinocardium* sp. 2 (D-G); A-C – aboral (A), oral (B), and posterior view of DBUA-F 370 (Ponta Malbusca); D-E – aboral (D) and left lateral (E) view of DBUA-F 980-1 (Ponta dos Frades); F-G – aboral (F) and right lateral (G) view of DBUA-F 980-2 (Ponta dos Frades)

MATERIAL: a single aboral corona fragment collected from Upper Miocene to Lower Pliocene deposits at "Pedra-que-Pica" (DBUA-F 381).

DESCRIPTION: The only available specimen is a large aboral fragment (length 77 mm, test thickness 1.3 to 2 mm) preserving the distal parts of petals IV and V and part of interambulacra 4 and 5. The petals are moderately sunken and feature large, elongate isopores (interporiferous area approx. 1.5 to 2 times pore diameter). The imporiferous zone is nearly as wide as a single poriferous zone. The ends of the petals are blunt and flexed anteriorly. The poriferous zones converge slightly, but do not form a lanceolate shape. Petal V is bent twice within 15 mm from its distal tip. As far as preserved, the aboral tuberculation seems homogenous outside the peripetalous fasciole. Within it, small groups of larger tubercles situated at the interradial/adapical half of the plates occur in interambulacrum 5. The course of the peripetalous fasciole is shown in Text-fig. 12B.

REMARKS: Although highly fragmentary, only a limited number of spatangoids come into consideration for the present specimen. Its considerable size, as well as the shape and structure of the petals combined with the tuberculation and presence of a peripetalous fasciole, rule out many groups. Most likely candidates are found within the family Brissidae, namely the genera *Brissus*, *Meoma* and *Schizobrissus*. Based on direct comparison with extant material, we rule out *Brissus* because of its tendency to form lanceolate petal tips in large specimens (at least in *B. unicolor* Leske, 1778), its deeply indented peripetalous fasciole in interambulacra 1 and 4 and its narrow imporiferous zones. Additionally, the kink observed in distal petal V is very similar to the kinks/bends found frequently in the posterior petals of *Meoma ventricosa* (Lamarck, 1816) and in various species of *Schizobrissus*. While *Meoma* and *Schizobrissus* are closely similar, and have been considered as synonyms at times (Chesher 1970), it is possible to differentiate between the two genera (Lachkhem and Roman 1995). In species of *Meoma* there is only a weak frontal notch and the petals extend almost to the ambitus, whereas *Schizobrissus* has a deep frontal notch and much shorter petals. The fragment studied here clearly shows that the petals were comparatively short, terminating in the flattened aboral portion of the test above the ambitus. In fragments of extant *Meoma ventricosa* they terminate close to the ambitus, where the test is already distinctly curved. We thus conclude that our specimen is more correctly assigned to S*chizobrissus* than to *Meoma*. Owing to the nature of the specimen, a specific identification is impossible at this time without additional material.

OCCURRENCE: "Pedra-que-Pica", Santa Maria Island, Azores. At present, no representatives of either the genus *Meoma* or the genus *Schizobrissus* (extinct) are known from Azorean waters.

Superfamily Spatangidea Fischer, 1966

Family Loveniidae Lambert, 1905
Genus *Echinocardium* Gray, 1825
Echinocardium spec. 1
(Text-figs 13A–C)

MATERIAL: A fragmentary corona collected from Upper Miocene to Lower Pliocene deposits at Ponta da Malbusca (DBUA-F 370).

DESCRIPTION: The single available specimen is a crushed fragment preserving the posterior end of the corona. The corona is very thin (~ 0.7 mm thick) and fragile. The posterior paired petals are slightly sunken, widen towards the apex, and bear conjugate isopores. The posterior part of the plastron ends in a pointed process bearing a diamond-shaped subanal fasciole. The periproct lies high on the posterior face, is oval (vertically elongated) and appears to have been overhung by a small "hood" (post-mortem distortion makes it difficult to confirm this). Aboral tuberculation, as far as preserved, appears to have been uniform at least in the posterior half of the corona.

REMARKS: Although highly fragmentary, the specimen from Ponta da Malbusca can clearly be assigned to the genus *Echinocardium* based on the characteristic shape of the posterior face and the structure of the posterior petals. A specific identification, however, is impossible without additional material. Today, *E. cordatum* (Pennant, 1777) and *E. flavescens* (Müller, 1776) occur in the area.

OCCURRENCE: On Santa Maria Island, only known from the Upper Miocene/Lower Pliocene of the Ponta da Malbusca outcrop.

Echinocardium spec. 2
(Text-figs 13D–G)

MATERIAL: Two partially preserved coronas collected from Upper Miocene to Lower Pliocene deposits at Ponta dos Frades (DBUA-F 980).

DESCRIPTION: The specimens available are small, with a test length of about only 21 mm. The corona is very thin and fragile. The outline is distinctly heart-shaped and slightly wider than long. The frontal notch is narrow and quite shallow. In profile, the test is high (c. 70 % of TL) and rectangular, with a vertically truncated posterior end.

The apical disc is ethmolytic with four gonopores. The petals are confluent, slightly sunken and widen towards the apex. The frontal ambulacrum is distinctly, but not deeply sunken adapically and bears a single row of moderately widely spaced partitioned isopores in each column. The periproct lies high on the posterior face and is oval, vertically elongated.

REMARKS: The two specimens from Ponta dos Frades are much smaller than the Ponta da Malbusca specimen and lack the pronounced subanal projection present in that specimen. It thus appears that at least two species of *Echinocardium* were present in the Late Miocene/Early Pliocene of the Azores. In terms of shape and outline they are very similar to *E. flavescens*, but do exhibit a sunken frontal ambulacrum adapically. They differ from *E. cordatum* in their small and rather widely spaced pores of adapical ambulacrum III.

OCCURRENCE: On Santa Maria Island, known only from the Late Miocene–Early Pliocene of the Ponta dos Frades outcrop.

Spatangoida indet.

MATERIAL: Upper Miocene to Lower Pliocene of Ponta da Malbusca (two fragments, DBUA-F 188-18; 343-4) and Upper Miocene to Lower Pliocene of "Pedra-que-Pica" (six fragments, DBUA-F 458; 459).

DESCRIPTION: The material is composed of heavily eroded small interambulacral fragments (less than 18.2 mm TL). They are relatively thick and bear perforated and crenulated tubercles arranged in a dense uniform pattern. A small fragment of about 9 mm TL (DBUA-F 458) bears two rows of large, elongate symmetrical isopores.

REMARKS: The highly fragmentary nature of the material, largely lacking diagnostic characters, renders a more refined identification futile. It is not clear whether the fragments represented one or more spatangoid species. Based on the thickness of most fragments, it is unlikely that they derive from one of the *Echinocardium* species described above, instead they could be fragments of *Schizobrissus*, but this cannot be substantiated.

DISCUSSION

Systematics and Biogeography

The material collected from the fossiliferous outcrops of Santa Maria Island comprises a total of 11 different taxa. The Upper Miocene to Lower Pliocene fauna includes one species of regular echinoid (*Eucidaris tribuloides*) and several irregular taxa, such as *Echinoneus* cf. *cyclostomus*, clypeasteroids (*Clypeaster altus* and *Echinocyamus pusillus*) and corona fragments of spatangoids (*Echinocardium* sp. 1, *Echinocardium* sp. 2, *Schizobrissus* sp. and undetermined spatangoids). *E. cyclostomus* and the spatangoids are new records from the Miocene/Pliocene of Santa Maria, thus significantly increasing the echinoid diversity reported from that time slice on the island. The material collected from the Pleistocene outcrops (Lagoinhas and Prainha) includes three regular echinoid species, *Arbacia lixula*, *Paracentrotus lividus*, and *Sphaerechinus granularis*; the two former species are new records for the Pleistocene deposits of the island.

The extant shallow-water fauna reported from the Azores archipelago comprises a total of 14 echinoid species (Pereira 1997). Only two species of echinoids are common to both the Mio-Pliocene fauna of Santa Maria Island and the Recent fauna of the Azores, *i.e., Eucidaris tribuloides* and *Echinocyamus pusillus*. However, the presence of *E. tribuloides* in the extant fauna of the Azores, based on a single report by Koehler (1898, pp. 7–9), is questionable. *E. tribuloides* typically occurs in the tropical parts of the Atlantic. As shown by Lares and McClintock (1991), when exposed to temperatures of 18ºC this species shows a low growth rate and delayed gametic development, thus it is unlikely that it could maintain viable populations in the colder waters of the Azores, where the sea surface temperatures show an annual average of 19ºC, ranging from 14ºC to 24ºC (Santos *et al.* 1995). Together with *E. tribuloides*, other typically tropical taxa found in the Santa Maria Mio-Pliocene but absent from the extant Azorean fauna (*E. cyclostomus*, *Clypeaster altus* and *Schizobrissus* sp.), may represent examples of local disappearance of thermophilic species due to a series of cooling events starting in the mid-Pliocene and continuing in the Pleistocene (Raffi and Monegatti 1993; Landau *et al.* 2007). The echinoids are yet another group of animals that increases the number of taxa which are believed to have disappeared from the Azores during the Pleistocene climatic deterioration: molluscs (Ávila 2005; Ávila *et al.* 2008b, 2009; Janssen *et al.* 2008), brachiopods (Kroh *et al.* 2008) and crustaceans (Winkelmann *et al.* 2010). This is consistent with the disappearance of these taxa from the North Atlantic and the Mediterranean, in which the absence of representatives of these genera on the present European and Northwest African coasts clearly contrasts with the rich Miocene fauna for the same regions (see Mortensen 1948; Chesher, 1970; Lessios *et al.* 1999; Kroh 2007). On the other hand, the presence in the Azorean Upper Miocene to Lower Pliocene of *E. pusillus*, typically a temperate species, tells us that the environmental conditions of the Azorean islands at the Miocene/Pliocene boundary did not restrict the presence of temperate species.

All the echinoid species present in the Pleistocene of Santa Maria represent relatively modern taxa (Mortensen 1943a, b; Smith 1988). The oldest of the genera, *Arbacia*, dates back to the Late Oligocene (Cooke 1941), and it is believed that *A. lixula* diverged from the American *A. punctulata* only about 3–5 million years ago (Metz *et al.* 1998). The fossil record of *A. lixula* from Santa Maria is in fact the oldest record of this common extant species. The fossil record of *Paracentrotus* extends to the Late Miocene (Mortensen 1943b), and no records of *Sphaerechinus* are known prior to the Pliocene (Mortensen 1943a). It is clear that, in terms of faunal affinities, the Pleistocene fauna shows no apparent differences regarding what is generally accepted for the Azorean extant fauna, *i.e.* a close relationship to the faunas of the Northeastern Atlantic and Mediterranean coasts (e.g. Wirtz and Martins 1993; Santos *et al.* 1995; Ávila 2000, 2005).

Ecology

The Miocene echinoid fauna found on Santa Maria Island is dominated by irregular echinoids that typically live in soft bottom environments (spatangoids, clypeasteroids and *Echinoneus*), with the exception of *Eucidaris tribuloides*, which preferentially lives epifaunally on hard substrates. The presence of ecologically incompatible faunal elements may be explained by transport, as illustrated by Nebelsick (1992). Moreover, the detected dominance of irregular taxa may be explained by their preferred palaeoenvironments for, as noted by Smith (1984), irregular echinoids are potentially more prone to be preserved in the fossil record, because they live in environments of active sedimentation, in contrast to many regular euechinoids which live in areas of active erosion. Additionally, the fragmentary nature of the echinoid remains in the Santa Maria Miocene/Pliocene fossil record may testify as well that they may have spent some time decomposing on the ocean floor, before being incorporated in the sediment. Very few complete coronas were found, and most of these belong to the clypeasteroids, a group of irregular echinoids with a robust skeleton and thus a high preservation potential (Seilacher 1979; Smith 1984; Donovan and Portell 1996). Their tests are a frequent presence in the fossil record of high energy palaeoenvironments (see Nebelsick and Kroh 2002) and are the main reason why they are often preserved accumulated in coquinas (Smith 1984).

The diversity of echinoids and environments preserved in the Miocene/Pliocene deposits of Santa Maria differs markedly from that shown by the Pleistocene fossil record of the island. As pointed out by Donovan (2003), Pleistocene faunas tend to be closely related to the living biota of any area, and the Azorean Pleistocene is no exception (a similar conclusion was reached for the Pleistocene Azorean marine molluscs by Ávila *et al.* 2009). This is particularly the case, since the Pleistocene fossil record is usually highly selective in terms of palaeoenvironments exposed (only deposits from the uppermost subtidal and intertidal are currently accessible – environments which are prone to erosion and not usually preserved from older periods).

The three echinoid species identified from the Pleistocene outcrops of Santa Maria are the most conspicuous echinoids of the extant Azorean shallow waters (Marques 1983; Azevedo *et al.* 1994). They are typically found in the first few metres of the rocky shores of the archipelago, similar to the palaeoenvironmental settings preserved in the Pleistocene fossil record (see Ávila *et al.* 2009), thus making these echinoids the most likely species to occur in the Pleistocene fossil record of the islands. On the other hand, this may also be the reason for the apparent low echinoid diversity (e.g., deeper Pleistocene sediments are currently unknown to occur onshore), making it difficult to find taxa living in slightly deeper settings such as brissids and diadematoids.

Dispersal and Colonization

As truly oceanic islands, the Azores were never connected to continental land masses. The great distances from nearest the continental shores (2,000 km from the Portuguese mainland) may represent a problem to many benthic species. However, all echinoid species present in the Pleistocene outcrops are known to have long planktotrophic larval stages, and thus can be considered to have had a great dispersal potential (Pedrotti and Fenaux 1992; Emlet 1995). The colonization of these islands is believed to have been made through chance-event dispersal for the majority of species, albeit for some at least this probably occurred during glacial terminations (short periods of time when sea-surface currents and favourable winds may have provided “windows of opportunity”; see Ávila 2005; Carine 2005; Ávila *et al.* 2009). Additionally, the abundant seamounts present between the Azores and the European and African mainland may have acted as “stepping stones” particularly at times of low sea level, promoting the dispersal of benthic taxa with planktotrophic larvae.

In his review of the faunal history of the Atlantic islands, Briggs (1975) postulated that the lack of endemism in the Azores was due to the Pleistocene glacial episodes, which had wiped out the older Azorean fauna. Recent palaeontological studies do not support this idea, showing that several species of molluscs endemic to the Azores persisted in the archipelago (see Ávila *et al.* 2008a, b). Species solely restricted to shallow sand bottoms, however, were indeed heavily affected by lowstands during glacial episodes when sea level dropped below the shelf break of the islands (Ávila *et al.* 2008b). Our limited data also show that, so far as echinoids are concerned, the fauna of the Azorean rocky shores in the Pleistocene was identical to the modern rocky shore fauna in the area. However, the echinoid taxa reported here from the Pleistocene outcrops of Santa Maria all have long-lived planktotrophic larval stages today and are thus unlikely to develop endemic offshoots. Modern examples of shallow water echinoids investigated genetically (e.g. *Arbacia* – Metz *et al.* 1998, *Diadema* – Lessios *et al*. 2001) do show active gene flow over considerable distances.

CONCLUSIONS

In terms of general patterns, the fossil echinoid faunas from the Santa Maria Island outcrops reflect the overall Neogene faunal history of the North Atlantic. The conspicuous presence of species with tropical affinities in the Upper Miocene to Lower Pliocene fossil record, contrasts with a more temperate fauna present in the Pleistocene, which in turn is similar to the extant fauna in the Azores. Moreover, and similarly to what happens nowadays, the fossil echinoids from Santa Maria Island also support biogeographical relationships with the Northeastern Atlantic and the Mediterranean, in both the Miocene/Pliocene-boundary interval and the Pleistocene.

The low diversity of palaeoenvironments preserved in the sedimentary record of Santa Maria, particularly in the Pleistocene deposits, explains the low diversity of the echinoid fauna these in these time slices. This is particularly true if we consider that, in spite of the sampling effort (including bulk sampling) made since 1998, no other classes of echinoderms were collected. This is possibly related to diagenetic dissolution, which is prone to affect smaller-sized disarticulated elements of asterozoans, crinoids and holothurians more strongly than larger-sized echinoid remains. Nonetheless, the seven new records show that the specific richness of the echinoid fauna of Santa Maria Island was largely underestimated and should prove a valuable aid to future biogeographic studies in the Northeastern Atlantic.

Acknowledgements

Critical reviews and constructive comments from Alexander Mironov and a second, anonymous reviewer are gratefully acknowledged. We are grateful to the organizers and participants of the International Workshops "*Palaeontology in Atlantic Islands*" who helped in the fieldwork. We also thank the Direcção Regional da Ciência e Tecnologia (Regional Government of the Azores), Direcção Regional do Ambiente e do Mar (Regional Government of the Azores), FCT (Fundação para a Ciência e Tecnologia) of the Portuguese Government for financial support, and we thank the Clube Naval de Santa Maria and Câmara Municipal de Vila do Porto for field assistance. Fabrizio Lirer (Instituto Ambiente Marino Costiero, Napoli) kindly provided information on Italian Pleistocene stratigraphy.

P. Madeira was supported by grant SFRH/BD/61146/2009 (FCT – Fundação para a Ciência e Tecnologia) of the Portuguese government, and by the SYNTHESYS Project http://www.synthesys.info/, which is financed by European Community Infrastructure Action under the FP6 and FP7 programmes.

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Manuscript submitted: 2nd December 2010
Revised version accepted: 15th August 2011