Neogene echinoids from the Cayman Islands, West Indies: regional implications

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The first fossil echinoids are recorded from the Cayman Islands. A regular echinoid, *Arbacia*? sp., the spatangoids *Brissus* sp. cf. *B. oblongus* Wright and *Schizaster* sp. cf. *S. americanus* (Clark), and the clypeasteroid *Clypeaster* sp. are from the Middle Miocene Cayman Formation. Test fragments of the mellitid clypeasteroid, *Leodia sexiesperforata* (Leske), are from the Late Pleistocene Ironshore Formation. Miocene echinoids are preserved as (mainly internal) moulds; hence, all species are left in open nomenclature because of uncertainties regarding test architecture. All Miocene taxa are recorded from single specimens apart from the 27 assigned to *Brissus*. *Schizaster* sp. cf. *S. americanus* (Clark) is compared to a species from the Oligocene of the south-east USA. *Brissus* sp. cf. *B. oblongus* is close in gross morphology to a taxon from the Miocene of Malta. *Leodia sexiesperforata* is identified from fragments with confidence, being the only extant Antillean sand dollar with elongate ambulacral petals that is limited to carbonate substrates. The Miocene echinoids of Grand Cayman, although of limited diversity, are mainly comprised of genera common in comparable mid-Cenozoic carbonate environments.

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1. INTRODUCTION

In a region renowned for its fossil faunas, it is surprising to note that echinoids have hitherto not been recorded from the rock record of the Cayman Islands in the Greater Antilles (Fig. 1). The first echinoid fossils were only discovered by B.J. and his graduate students in 1995 and further specimens have been slow to accumulate.

Apart from any biogeographic significance, these echinoids are also noteworthy for being mainly from the Miocene. This interval was called the ‘age of echinoids’ by Ager (1993, p. 27), but this comment was presumably based upon that author’s observations in the Mediterranean region. In the Caribbean, perhaps only in the Paleocene are fossil echinoids less well documented than the Miocene-Pliocene, with the notable exception of the Miocene of Anguilla (Poddubiuk and Rose, 1985; Poddubiuk, 1987). Otherwise, echinoids are not a particularly well-known component of the Miocene fauna of the Antilles (see comments in Donovan *et al*., 2005). There are historical difficulties of correlating Miocene (or Oligocene?) echinoids from Cuba with confidence: “Many of the [purported Oligocene] species may be Miocene. In the last 20 years some workers … have placed most of what was thought to be the Cuban Oligocene into the Miocene. Unfortunately, Sánchez Roig usually did not state from what formation his echinoids were collected” (Kier, 1984, p. 6). The Lower Miocene echinoids of Jamaica are best preserved in allochthonous blocks of coralliferous reef limestone, and are mainly fragmentary and/or overgrown by calcite (Donovan, 1993, 2004; Donovan and Portell, 2000; Donovan *et al*., 2005). The Dutch ABC islands, Aruba, Bonaire and Curaçao, had a small fauna of echinoids described from the Miocene-Pliocene Seroe Domi Formation (de Busonje, 1974) which has recently been doubled in an unpublished M.Sc. thesis (Schelfhorst, 2013). The echinoids of the Middle Miocene Grand Bay Formation of Carriacou, the Grenadines (Donovan, 2012) and the Miocene-Pliocene August Town Formation of Jamaica (Donovan, research in progress) similarly await adequate publication. Scattered occurrences of Miocene echinoids are known from other islands, for example, Barbados (Donovan and Veale, 1996, table 1).

2. GEOLOGICAL SETTING

The Cayman Islands are the only sub-aerially exposed parts of the Cayman Ridge, which lies parallel to the Oriente Transform Fault that defines the north boundary of the Cayman Trough (see Jones, 1994, fig. 5.1, for map). This tectonic system was most probably part of the Late Cretaceous to

Paleogene magmatic arc (Case *et al.*, 1984, pp. 16-17, sheet 1). Bedrock exposed on each of the Cayman Islands is comprised of the Bluff Group, which includes the unconformity bounded Brac Formation (Lower Oligocene), Cayman Formation (Middle Miocene) and the Pedro Castle Formation (Pliocene), that is unconformably overlain by Pleistocene strata that belong to the Ironshore Formation (Fig. 1; Jones *et al.*, 1994a, b). The Ironshore Formation is divided, from oldest to youngest, into Units A to F (Vézina *et al.*, 1999; Coyne *et al.*, 2007). Fossil echinoids are herein recognized for the first time from the Cayman Formation (Locality 1) and Ironshore Formation (Locality 2) on Grand Cayman (Fig. 1A).

2.1. Locality 1: Miocene

The Cayman Formation is composed largely of finely crystalline dolostones that are commonly fossiliferous with corals, gastropods, red algae, foraminifers and rhodolites being locally numerous (Jones and Hunter, 1989; Jones, 1994, p. 89). Any fossils that originally had aragonitic skeletons are now represented by moulds. The echinoids described herein (*Arbacia*? sp., *Schizaster* sp. cf. *S. americanus* (Clark) and *Brissus* sp. cf. *B. oblongus* Wright) were collected from the upper part of the Cayman Formation that is exposed in High Rock Quarry, which is located in the east-central part of Grand Cayman (Fig. 1). All of these specimens came from the eastern side of the quarry, which is now weathered and largely covered with grass on the quarry floor, and bushes and trees along the quarry walls. Although the age of the Cayman Formation is open to some debate, it is generally regarded as being Middle Miocene.

Poorly preserved echinoids have been noted by B.J. in the Cayman Formation at two other localities on Grand Cayman. In Pedro Castle Quarry (Fig. 1A), where the type sections of the Cayman Formation and Pedro Castle Formation are located (Jones and Hunter, 1989, fig. 2), one poorly preserved echinoid, probably *Brissus* (not collected) was seen in the in large boulder from the Cayman Formation that had been blasted from the quarry wall. In a disused quarry just north of Spotts (Fig. 1A), an external mould of the apical surface of *Clypeaster* sp. in a large boulder of dolostone from the Cayman Formation was noted in the early 1980s (see below). This quarry is now overgrown and inaccessible.

2.2. Localities 2A and B: Pleistocene

Exposures of the Ironshore Formation along the western shoreline of North Sound (Fig. 1A) are formed of Unit D that is unconformably overlain by Unit F (Coyne *et al.*, 2007). Coral-rich patch reefs, well-preserved bivalves and gastropods (Coyne *et al.*, 2007), and oolitic grainstones that are characterized by numerous burrows (Pemberton and Jones, 1988) characterize Unit D in this area. This unit, which is 123-147 ka old, formed during the Marine Isotope Stage (MIS) 5e highstand (Coyne *et al.*, 2007). Unit F is formed largely of cross-bedded oolitic grainstones that contain few fossils. Although dating of this unit is problematic because of the scarcity of well-preserved fossils, one Th/U date from Unit F suggests it formed 87 ± 3 ka in association with the MIS 5a highstand (Coyne *et al.*, 2007).

Despite extensive searching, no echinoids have ever been found in Unit D, which is widely exposed on Grand Cayman and Cayman Brac. At two localities, located to the south of Morgan's Harbour on the west coast of North Sound (2 in Fig. 1), fragments of a mellitid sand dollar, *Leodia sexiesperforata* (Leske), were found in the lower part of the cross-bedded ooid grainstones of unit F. The only other fossils found in this unit are rare bivalves, conch shells and very rare corals.

3. MATERIALS AND METHODS

The Miocene echinoids of the Cayman Islands in the present collection are preserved as natural moulds, mainly internal moulds. These were painted with black food colouring to give a uniform body tone and coated with ammonium chloride for photography. Pleistocene specimens are rarer and more fragmentary, but preserve tests. These were similarly coloured and coated with ammonium chloride for photography. Measurements were taken using electronic callipers.

Descriptive terminology used herein follows Melville and Durham (1966), Durham and Wagner (1966) and Smith (1984). The classification follows Kroh and Smith (2010) and Smith and Kroh (2011). The use of open nomenclature follows the protocol recommended by Bengtson (1988). Fossils specimens are deposited in the Department of Earth and Atmospheric Sciences, University of Alberta, Edmonton, Canada (UA) and, in the example of one Eocene specimen from Jamaica, the Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts (MCZ). Recent echinoids used in the present study have been presented to the Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM).

The Miocene material of *Brissus* from the Cayman Islands is moderately well preserved and nearly 30 specimens were available for measurement; however, only some 20 presented useful data. Only two of the 20 specimens yielded a complete measurement set, yet a further 10 of the specimens were included in the multivariate analysis, their missing values for some variates being interpolated by iterative imputation. The dataset thus included 12 specimens of *Brissus* from the Cayman Islands comprising a near complete data matrix, plus 46 specimens of *Brissus* from the Recent of Jamaica (National Museum of Natural History, Smithsonian Institution) and one specimen from the Eocene, the latter probably representing a new species, albeit only known from one specimen (MCZ 3469; see Donovan and Veale, 1996). The multivariate (Principal Components) shape analysis interrogated a correlation matrix of eleven variates (see Donovan and Harper, 2000) measured on all 59 specimens: test length (TL); test width (TW); test height (TH); height at apical system, measured from apical system to labrum or equivalent height (Tha); distance from apical system to anterior (AA); length of petal V (Lv); length of petal IV (Liv); number of pore pairs in outer half ambulacrum of petal V (PPv); number of pore pairs in anterior half ambulacrum of petal IV (PPiv); periproct height (PH); and periproct width (PW). The multivariate analyses were implemented on the software program PAST (Hammer *et al.*, 2001; Hammer and Harper, 2006). For ‘Results of PCA’, see *Brissus* sp. cf. *B. oblongus*, below.

4. SYSTEMATIC PALAEONTOLOGY

Class ECHINOIDEA Leske, 1778

Subclass EUECHINOIDEA Bronn, 1860

Order ARBACIOIDA Gregory, 1900

Family ARBACIIDAE Gray, 1855

Genus *Arbacia* Gray, 1835

Type species. *Cidaris pustulosa* Leske, 1778, p. 150 [=*Echinus lixula* Linné, 1758, p. 664], by subsequent designation of Agassiz and Clark (1908, p. 67; Smith and Kroh, 2011).

Diagnosis. See Smith and Kroh (2011).

Remarks. The sole internal mould of a regular echinoid (Fig. 2) from this site provides less diagnostic data than for either of the spatangoids.

Range. Miocene to Recent, Europe, North Africa, North and South America; Recent, Atlantic, Caribbean, West Pacific (Smith and Kroh, 2011).

Arbacia? sp.

Figure 2

Material. A single test, UA P1669, preserved as an internal mould.

Locality and horizon. Middle Miocene Cayman Formation, Grand Cayman (Locality 1).

Description. Internal mould of regular echinoid. Circular outline, low domed profile, ambitus below mid-height of test. Apical system rounded pentagonal in outline. Three lozenge-like genital plates apparent, but circlet imperfectly preserved.

Ambulacra narrower than interambulacra. Details of ambulacral plating not apparent, ambulacral plates moderately high. Ambulacra preserved as paired, diverging ridges on the apical surface, but it impossible to determine confidently if it these are pore pairs in columns or columns of tubercles immediately adjacent to ambulacra as in *Arbacia*. Pore pairs not distinguishable. Interambulacral plates larger (both higher and wider) than ambulacral plates, with a small central tubercle. Peristome obscured by rock.

Remarks. The gross morphology of this specimen, which preserves too few fine details, is nonetheless essential for determining its probable systematic position. It is certainly neither a cidaroid nor a diadematoid, both of which have bun-like tests with the ambitus at about mid-height. It is not close to the more elliptical test of *Echinodermetra* Gray. Rather, it is more like to be an arbacioid or a toxopneustid. Assuming the specimen to be an adult, the test diameter (<20 mm) is more in the range of modern Antillean *Arbacia punctulata* (Lamarck) or *Lytechinus williamsi* Chesher (albeit with a more pentagonal test) than other toxopneustids (Hendler *et al*., 1995, pp. 214-222, fig. 134A-G). Assuming it to be fully grown, it is tentatively classified as an *Arbacia*? sp. because this is an Antillean Neogene genus that is at least close in gross morphology to the test, although it is more inflated than, for example, Pliocene *Arbacia improcera* (Conrad) (Lewis and Donovan, 1991).

Cohort IRREGULARIA Latreille, 1825

Order SPATANGOIDA L. Agassiz, 1840

Suborder PALEOPNEUSTINA Markov and Solovjev, 2001

Family SCHIZASTERIDAE Lambert, 1905

Genus SCHIZASTER L. Agassiz, 1835

Type species. *Schizaster studeri* L. Agassiz, 1835, p. 185, by the subsequent designation of the International Commission on Zoological Nomenclature (1954, p. 388) (Fischer, 1966, p. U569).

Diagnosis. (After Smith and Kroh, 2011.) Test ovate with deep anterior sulcus; slightly pointed to rear. Apical disc ethmolytic, with four gonopores. Anterior ambulacrum deeply sunken; pore-pairs in adapical portion large and specialized. Other ambulacra also deeply sunken, anterior petals longer and more flexed than posterior petals. Periproct small and marginal, on near-vertical truncate face. Bound by interambulacral plates 5a/b on oral side. Peristome opening facing anterior; kidney-shaped. Labral plate short and wide; not extending beyond half-way along the first ambulacral plate; in broad contact with sternal plates. Sternal plates large and symmetric; sternal-episternal suture at rear of ambulacral plate 5. Aboral tuberculation fine, uniform and dense. Oral tubercles also dense and uniform. Well-developed peripetalous and lateral fascioles. Peripetalous fasciole indented by three plates behind anterior petals; crosses ambulacrum III at plate 7 or 8. Latero-anal fasciole branches off about one-third up from the ends of the anterior petals on plates 1.b.5 and 4.a.5

Remarks. *Schizaster* is a common echinoid taxon in the Antillean region from the Eocene to Recent (Kier and Grant 1965; Kier 1984; Donovan, 1993), particularly the former.

Range. Eocene to Recent (Fischer, 1966, p. U569).

Schizaster sp. cf. *S. americanus* (Clark *in* Clark and Twitchell, 1915)

Figure 3

Material. A single test, UA P1670, preserved as an internal mould.

Locality and horizon. Middle Miocene Cayman Formation, Grand Cayman (Locality 1).

Description. Preserved as an internal mould in dolostone. Test globular, about 27.2 mm long, 27.5 mm wide and 22.5 mm high; highest posterior of centre, widest about centre. Four genital pores, but apical system poorly preserved otherwise. Peristome anterior, but concealed by dolostone; periproct rounded (elliptical?) on concave posterior surface and elevated, in upper half of test. Oral surface with central keel. Anterior ambulacrum (III) not petaloid, depressed, moderately broad and forming a shallow, albeit distinct anterior sulcus. Short, sunken petals developed apically. Anterior ambulacra (II, IV) with about 10-12 pore pairs per petal, petal length *c*. 8.1 mm. Posterior petals (I, V) shorter with about 7 pore pairs per ambulacral column, length *c*. 3.8 mm. Ambitus low with largest interambulacral plates in 1 and 4. Plastron moderately broad and shield-like. External features of test unknown.

Remarks. The Cayman Islands Miocene *Schizaster* is considered closest to the Oligocene *Schizaster americanus* (Clark) from the south-east USA, described and illustrated by Clark and Twitchell (1915, p. 176, pl. 82, figs 3A-D), Cooke (1959, p. 72, pl. 30, figs 5-8) and Oyen and Portell (2002, pl. 2, figs G, H). The Cayman specimen, apart from being younger, is relatively more inflated and highest at the apical system, whereas the holotype of *S. americanus* is highest posterior to the apical system. The apical system of the holotype is within a keel in the posterior interambulacrum (5), although this may be an artefact produced by the test being slightly crushed laterally (see, in particular, Cooke, 1959, pl. 30, fig. 6). Certainly, the geometry of the ambulacral petals, positions of periproct and peristome, and posterior concavity of the test is similar between *S. americanus* and UA P1670.

Miocene *Schizaster* species from Cuba are less similar to UA P1670. *Schizaster egozcue* Lambert has a wedge-shaped gross morphology, and petals II and IV are distinctly closer to ambulacrum III; *Schizaster fernandezi* Sánchez Roig, like *S. egozcue*, has a more posterior apical system, and also longer petals II and IV in a relatively narrower test (Kier, 1984, pl. 18). Similar aspects of gross morphology also differentiate Mio-Oligocene *S. rojasi* Sánchez Roig and *S. sanctamariae* Sánchez Roig from UA P1670 (Kier, 1984, pl. 25). *Schizaster* sp. from the Upper Pliocene of Jamaica is too poorly preserved for worthwhile comparison (Donovan and Portell, 1998).

Poddubiuk and Rose (1985, table 3) recognized two species of *Schizaster* from the Lower Miocene Anguilla Formation of Anguilla, namely *S. clevei* Cotteau, 1875, and *S. loveni* Cotteau, 1875.

Schizaster clevei is strongly heart-shaped, unlike the rounded UA P1670; compare Fig. 3 herein with Cotteau (1875, pl. 5, figs 7, 8). *Schizaster loveni* is a little more rounded than *S. clevei* (Cotteau, 1875, pl. 5, figs 9-13), with a posterior keel behind the apical system and, in larger specimens, moderately long anterior petals curving towards ambulacrum III.

Suborder BRISSIDINA Stockley *et al*., 2005

Family BRISSIDAE Gray, 1855

Genus BRISSUS Gray, 1825

Type species. *Spatangus brissus unicolor* Leske, 1778, p. 248, by the subsequent designation of International Commission on Zoological Nomenclature (1954, p. 387) (Fischer, 1966, p. U582).

Diagnosis. (After Donovan and Veale, 1996, p. 635; based on Mortensen, 1951, p. 506-508; Fischer, 1966, p. U582-U583; Kier, 1984, p. 81.) Test elongate ovoid in outline, moderate to large as adult. Test more or less highly arched aborally; posterior interambulacrum may be raised as a keel. Oral surface flattened to greatly convex. Anterior sinus not developed, posterior truncate. Apical system anterior ethmolytic (Smith, 1984, fig. 3.22), with four genital pores (genital 5 absent); posterior pores larger than anterior. Anterior ambulacrum narrow, not petaloid. Paired ambulacral petals sunken; anterior petals approximately transverse, posterior petals not widely divergent. First plate of interambulacrum 1 followed by single plate. Plastron large, ultramphisternous. Peripetalous and subanal fascioles developed; subanal fasciole broad with lateral lobes. Periproct lenticular in outline, on upper part of truncate posterior margin. Peristome near anterior, semilunate, with broad, but not prominent, labrum; conspicuous phyllodes developed. Tuberculation dense. Pedicellariae usually of five types; globiferous, tridentate, rostrate, ophicephalous and triphyllous.

Remarks. Since the `Modern' echinoid fauna of the Caribbean region first emerged in the Eocene-Oligocene, certain genera have shown a propensity for extreme plasticity in overall form (most notably *Clypeaster* spp.), while others have shown near-stasis in gross morphological features (such as the holectypoid *Echinoneus cyclostomus* group and the spatangoid *Brissus unicolor* group). The influence of environment, dispersion and ecophenotypic variation on these evolutionary patterns is unknown.

Range. Eocene to Recent (Fischer, 1966, p. U583).

Brissus sp. cf. *B. oblongus* Wright, 1855

Figure 4

Material. Twenty seven specimens, UA P1671-P1695 (complete or incomplete internal moulds), UA P1696, P1697 (partial external moulds).

Locality and horizon. Middle Miocene Cayman Formation, Grand Cayman (Locality 1).

Description. Inflated, elliptical *Brissus*, rounded anteriorly, but more broadly in larger tests (Fig. 4A, D, G, K); widest about centre to posterior of centre; flattened posteriorly; oral surface convex; no anterior sulcus. Anterior of test wedge-shaped, steeply sloping (Fig. 4E, F, H, I, O); test highest about two-thirds to three-quarters of test length from anterior. Posterior interambulacrum (5) raised as a keel with a rounded ridge between the posterior petals (Fig. 4B, C, L, M). Ambitus low, rounded and sloping forwards (Fig. 4E, H, O).

Apical system poorly preserved, but anterior of centre. Four genital pores apparent.

Peristome on anterior oral surface, close to anterior margin, kidney-shaped (Fig. 4D, P), moderately broad, sunken and with a raised posterior margin; that is, the peristome is directed anteriorly. Periproct on flattened posterior margin at about mid-height, lensoid and higher than wide (best seen in Fig. 4C).

Four ambulacral petals on apical surface; anterior ambulacrum (III) not petaloid (Fig. 4A, G, K). Petals sunken, short, not extending to ambitus. Anterior paired petals (II and IV) short, extending in a near-straight line laterally on either side of the apical system, petals straight to slightly curved. Posterior paired petals (I and V) longer, narrowly diverging, straight or curving away from interambulacrum 5. Ambulacral pores of petals rounded, arranged in two closely-spaced columns of pore pairs. Anterior ambulacrum (III) narrow, flush with test surface, narrower than petals. Interambulacra broader than ambulacra, but details not preserved.

Ambulacra converge to peristome on oral surface; single pored adjacent to peristome. Plastron (interambulacrum 5) with closely packed, asymmetrical tubercles (Fig. 4N), flanked by curved ambulacra I and V.

Given the mouldic preservation, fine details of the test surface, particularly tuberculation and distribution of fascioles, are not apparent except on the two partial external moulds and specimen UA P1675 which preserves the plastron. These show densely packed primary tubercles, but no fascioles are discernible. They were considered too friable for casting.

Results of PCA. The specimens were plotted against the first and second principal components or eigenvectors (Fig. 6). Whereas the first discriminated the specimens with respect to size, the specimen from the Eocene of Jamaica being by far the largest, the second represents variation in shape. Four variates have marked contributions to the second eigenvectors, PPV, PIV, PH and PV (see Materials and Methods, above). Specimens with positive scores of the second eigenvector have relatively larger values for the first two variates and smaller for values for the second two. Thus, the cluster of specimens from the Cayman islands (BS prefix), including the Eocene specimen (EOC), that have negative scores on the second eigenvector, are characterized by relative large values for PH and PV (the size of the periproct) and smaller values for the numbers of PPV and PIV, the pore pairs in the ambulacral region of petals V and VI.

Remarks. Species of *Brissus* show considerable similarity in time and space. For example, Chesher (1972) compared *Brissus* spp. from either side of the Isthmus of Panama. Biometric analysis showed that specimens from the Bay of Panamá (*Brissus obesus* Verrill) and the tropical Western Atlantic (*Brissus unicolor* (Leske)) differed in the number of plates between the mouth and posterior petals, and the position of the lateral portion of the peripetalous fasciole. Specimens from the Gulf of California, however, were unexpectedly within the range of morphology of *B. unicolor* and not *B. obesus*.

The features used by Chesher (1972) cannot be determined for many fossil specimens, which may preserve details of the test surface only poorly or, as in the case of the Cayman specimens, almost not at all. Donovan and Veale (1996) used a range of biometric criteria to compare Recent (Fig. 5A, B) and fossil *Brissus* from the Antillean region, demonstrating that gross test morphology has remained similar at least since the Middle Eocene. The statistical analysis used herein (Fig. 6) is built on that of Donovan and Harper (2000), who described a Lower Miocene(?) *Brissus* from Jamaica.

Comparison of the Cayman taxon with the extant species from the shallow waters of the Caribbean, *Brissus unicolor* (Leske) (Fig. 5A, B), shows a number of dissimilarities. These include the relatively longer petals of *B. unicolor*, its more divergent posterior petals, more sinuous anterior petals, less rounded sides and more inflated test. A closer comparison with the Miocene species from Malta, *Brissus oblongus* Forbes MSS *in* Wright, 1855, suggests that it may be closely related to the Cayman species. The holotype is certainly similar in gross test outline to the smaller Cayman specimens (compare Figs. 5C, D, with 4G, K). The Maltese taxon has longer anterior petals and relatively more divergent posterior petals, but, overall, is closer to the Cayman specimens than *B. unicolor* and other Antillean *Brissus* spp. Other nominal *Brissus* spp. from the Miocene of Malta (Rose, 1975) are either synonymous with or markedly different in morphology from *B. oblongus*.

The closest *Brissus* from the Miocene of the Antilles to the Cayman species is *Brissus exiguus* Cotteau, 1875 (pp. 35-36, pl. 6, figs 16-18), but the illustrated specimens are more teardrop-shaped in plan view than any specimen in Fig. 4. Kier (1984) discussed five species of *Brissus* from the Cenozoic of Cuba, most of which are broad, inflated and blunt anteriorly. Closest to the Cayman species is *Brissus caobaense* Sánchez Roig, 1953 (Kier, 1984, pp. 83-84, fig. 31, pl. 44, figs 1-4), which has a broadly similar profile, although not as markedly high in the posterior interambulacrum on the apical surface, is blunter anteriorly and posteriorly, has a particularly large periproct and a more hexagonal outline in apical view. The blunt anterior is a feature also seen in the lateral views of three extant species of *Brissus*, including *B. unicolor*, illustrated by Schultz (2005, fig. 722); all have a relatively higher and more steeply sloping anterior than the Cayman species. It may be, of course, that the Cayman tests represent a new species. Given the overall similarity of all *Brissus* spp., it is considered best not to erect a new nominal taxon based on internal moulds.

Superorder MICROSTOMATA Smith, 1984

Order CLYPEASTEROIDA L. Agassiz, 1835

Suborder SCUTELLINA Haeckel, 1896

Family MELLITIDAE Stefanini, 1912

Genus LEODIA Gray, 1851

Type species. *Leodia richardsoni* Gray, 1851, p. 36 (= *Echinodiscus sexiesperforatus* Leske, 1778, p. 199) by original designation (Durham, 1966, p. U485; Mooi, 1989, p. 41; Smith and Kroh, 2011).

Diagnosis. See Smith and Kroh (2011).

Remarks. This genus was monotypic until the description of *Leodia divinata* Mooi and Peterson, 2000, from the Lower Pliocene of Venezuela.

Range. Pliocene to Recent, Cape Hatteras, North Carolina, to Florida Keys, Central and South America, and the Antilles (Mooi, 1989, p. 41; Hendler *et al*., 1995, pp. 234-235).

Leodia sexiesperforata (Leske, 1778)

Figure 7

Material. UA P1698-P1700, Locality 2A; UA P1701-P1704, Locality 2B. All specimens fragmentary.

Locality and horizon. Unit F, Pleistocene Ironshore Formation, Grand Cayman (Localities 2A and B).

Description. See Hendler *et al*. (1995, pp. 234-235 and references therein).

Remarks. Comparison with other Late Pleistocene sites in the Antilles strongly indicates that these fragments, undoubtedly a mellitid, are derived from an extant taxon. At the present day, the mellitids of the Gulf of Mexico and Antilles include only four species, all shallow water (Serafy, 1979; Hendler *et al*., 1995). There are two species of *Encope* L. Agassiz, 1840, have ambulacral notches, not lunules, and these can be easily disregarded. *Mellita isometra* Harold and Telford, 1990, has four long, slender ambulacral lunules, but prefers siliceous sediment substrates (Mooi, 1989, p. 41; Hendler *et al*., 1995, p. 236, fig. 126). Only *Leodia sexiesperforata* has five long, slender ambulacral lunules and a similar anal lunule, and is restricted to carbonate substrates (Mooi, 1989, p. 41). Extant *L. sexiesperforata* occurs in 0-60 m water depth and only on carbonate substrates (Serafy, 1979, table 2; Mooi, 1989, p. 41).

Suborder CLYPEASTERINA L. Agassiz, 1835

Family CLYPEASTERIDAE L. Agassiz, 1835

Genus CLYPEASTER Lamarck, 1801

Type species. *Echinus rosaceus* Linné, 1758, p. 665, by the subsequent designation of Desmoulins (1835, p. 183) (Durham, 1966, p. U462).

Diagnosis. See Smith and Kroh (2011).

Remarks. *Clypeaster* is the commonest and most easily recognizable echinoid genus in the Oligocene and Neogene of the Antilles, in part because of the test which is particularly robust. Fragments are easily identified to genus and, in some instances, species (see, for example, Dixon and

Donovan, 1998).

Range. Late Eocene to Recent, widespread in tropical to temperate regions (Smith and Kroh, 2011); first appeared in the Antillean region in the Late(?) Oligocene (Poddubiuk, 1985).

Clypeaster sp.

Figure 8

Material. External mould of the apical surface of one test, not collected (Fig. 8).

Locality and horizon. Spotts Bay Quarry, Grand Cayman. Middle Miocene Cayman Formation, Grand Cayman, now overgrown.

Remarks. Poddubiuk (1985) rationalized the 60+ nominal species of *Clypeaster* described from the Upper Oligocene-Lower Miocene strata of the Antilles to just seven names. The specimen from Grand Cayman is close to *Clypeaster concavus* Cotteau, 1875 (Cotteau, 1875, p. 16, pl. 2, figs 4-8; Jackson, 1922, pp. 34-36, pl. 2, figs 10-12) and descriptions of *Clypeaster cubensis* Cotteau, 1875, although good illustrations of the latter species are unavailable (but note the comment of Jackson, 1922, p. 37, that it "… has very large petals"). However, an identification to genus based on an image of a partial external mould is considered adequate in this instance.

5. DISCUSSION

Until now, fossil echinoids have not been described from the Cayman Islands, an anomaly if compared to the wealth of nominal taxa known from, for example, nearby Cuba and Jamaica. Although specimens described herein are either mouldic (Miocene) or fragmentary (Pleistocene), three of the five species have been confidently assigned to genus and a fourth identified to species.

Most taxa are Miocene. Apart from the Lower Miocene Anguilla Formation of Anguilla, echinoids from the other Antillean islands have either been recognized as Oligocene or Miocene, requiring stratigraphic revision (such as Cuba; Kier, 1984), or are Miocene-Pliocene, such as the Seroe Domi Formation of Aruba, Bonaire and Curaçao (Jackson and Robinson, 1994), and August Town Formation of Jamaica (Robinson, 1994) (see comments in Donovan *et al*., 2005, pp. 91-92).

Comparison with other mid-Cenozoic echinoid-bearing sites and horizons from Malta and the Antilles is revealing (Table 1). Most of these records are based on multiple sites collected by echinoderm specialists over many years, with the exception of the Lower Miocene of Jamaica (Table 1, site 5). Even the latter essentially samples more than one location; well-preserved echinoids mainly come from allochthonous blocks (shallow water), with different taxa occurring as fragments in the enclosing chalks (deep water). But four species from two localities (Locality 1, Spotts Bay Quarry) is certainly comparable with six from the Lower Miocene of Jamaica. Indeed, S.K.D.'s experience of collecting echinoids from the Upper Oligocene of Jamaica (Table 1, Site 1) and Antigua (Site 2) suggests that four to six taxa from any one site is good.

Multiple taphonomic and collector biases lie behind the data compiled in Table 1. The Miocene of Grand Cayman has only yielded moulds and fragmentary remains are unknown. The mid-Cenozoic echinoids of Antigua, Anguilla and Malta are, in contrast, well-preserved, locally common and moderately easy to collect, and have been the subject of numerous research programmes since at least the mid-19th Century (for example, Wright, 1855, was working on Maltese specimens 160 years ago). The Jamaican Oligocene echinoids occur in well-indurated limestones and were largely ignored until the work of the late Hal Dixon of the University of the West Indies, Mona, in the 1990s (Dixon and Donovan, 1998). Similarly, the Lower Miocene of the same island was collected and prepared by Roger Portell and colleagues of the Florida Museum of Natural History, University of Florida, Gainesville, including fragments and tests in crystal apple preservation (that is, each plate is overgrown by a single calcite crystal; see Donovan and Portell, 2000, for explanation; Donovan *et al*., 2005). That is, the better preserved localities have been collected and described for at least 160 years, whereas the less well-preserved faunas, such as that of the Cayman Formation, have only been examined for about the 25 years we have looked for new localities and new ways to study fossil echinoids.

None of the other Sites (1-5) in Table 1 includes an *Arbacia*, so the tentative assignment of UA P1669 to this genus remains uncertain, although the (dissimilar) arbacioid *Coelopleurus* is known from Malta and Pliocene *Arbacia* is well-known from the Antilles (Lewis and Donovan, 1991; Donovan and Paul, 1998). In contrast, the irregular echinoids identified from Grand Cayman are widely distributed, particularly *Clypeaster*. Again, a taphonomic bias is easily determined, as *Clypeaster* undoubtedly has the most robust test of any echinoid genus; there is no wonder that it is known from all six sites (Table 1). More surprisingly, relatively more delicate taxa, *Schizaster* and *Brissus*, have been found at most sites and, where they are unknown, they may unknowingly be represented by indeterminate spatangoid remains (such as Donovan *et al*., 2005, p. 108, pl. 8).

The Pleistocene record of the Antilles is enriched by the identification of *L. sexiesperforata* from the Ironshore Formation. Sand dollars are poorly known from the Pleistocene of the Antilles (Jackson, 1922, p. 52; Donovan and Embden, 1996, p. 490; Donovan, 2001, p. 184), yet are common in coeval deposits in Florida (Donovan, 2003, table 1). *Leodia sexiesperforata* was previously unknown from the Pleistocene of the Caribbean islands and other genera, namely *Encope* and *Mellita*, included only taxa left in open nomenclature. As Donovan (2003, p. 5) noted, clypeasteroids are a common component of many Eocene to Pliocene successions of the Antilles and include taxa with tests that are especially robust (Smith, 1984, p. 23; Nebelsick, 1994, 1995, 1999; Nebelsick and Kroh, 2002).

It may be that Pleistocene clypeasteroids were living further offshore than the carbonate successions that are currently available for study. For example, the only horizons that are rich in sand dollars from the Jamaican Pliocene-Pleistocene are demonstrably allochthonous (storm) deposits (Donovan *et al*., 1994a, b). The presence of *L. sexiesperforata* only in the cross-bedded unit F of the Ironshore Formation (see above) may similarly demonstrate at least some local transport. It is unlikely to have been derived from a siliciclastic environment (and thus be *M. isometra*) in the carbonate platform setting of the Cayman Islands.

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REFERENCES

Agassiz, A., Clark, H.L. 1908. Hawaiian and other Pacific Echinii. The Salenidae, Arbaciadae, Aspidodiadematidae, and Diadematidae. *Memoirs of the Museum of Comparative Zoology, Harvard College* **34**, 43-132.

Agassiz, L. 1835. Prodrome d'une Monographie des Radiares ou Echinodermes. *Mémoires de la Société des Sciences Naturelles de Neufchâtel* **1**, 168-199.

Agassiz, L. 1840. *Catalogus systematicus Ectyporum Echinodermatum fossilium Musei Neocomiensis, secundum ordinem zoologicum dispositus; adjectis synonymis recentioribus, nec non stratis et locis in quibus reperiuntur. Sequuntur characters diagnostici generum novorum vel minus* *cognitorum*. Petitpierre: Neuchâtel; 20 pp.

Ager, D.V. 1993. *The Nature of the Stratigraphical Record*. Third edition. Wiley: Chichester; xiv+151 pp.

Bengtson, P. 1988. Open nomenclature. *Palaeontology* **31**, 223-227.

Bronn, H.G. 1860. *Die Klassen und Ordnungen des Thier-Reichs, wissenschaftlich dargestellt in Wort und Bilt. Zweiter Band. Actinozoen*. C.F. Winter'sche Verlagshandlung: Leipzig and Heidelberg; 434 pp.

Buisonjé, P.H. de. 1974. Neogene and Quaternary geology of Aruba, Curaçao and Bonaire (Netherlands Antilles). *Uitgaven Natuurwetenschappelijke Studiekring voor Suriname en de Nederlandse Antillen* **78**, 1-291.

Case, J.E., Holcombe, T.L., Martin, R.G. 1984. Map of geologic provinces in the Caribbean region. In: *The Caribbean-South American Plate Boundary and Regional Tectonics*, Bonini, W.E., Hargraves, R.B., Shagam, R. (eds). Geological Society of America Memoir **162**, 1-30.

Chesher, R.H. 1972. The status of knowledge of Panamanian echinoids, 1971, with comments on other echinoderms. In: *The Panamic Biota: Some Observations Prior to a Sea-Level Canal*, Jones, M.L. (ed.). Bulletin of the Biological Society of Washington **2**, 139-158.

Clark, W.B., Twitchell, M.W. 1915. The Mesozoic and Cenozoic Echinodermata of the United States. *Monographs of the U.S. Geological Survey* **4**, 1-341.

Cooke, C.W. 1959. Cenozoic echinoids of eastern United States. *U.S. Geological Survey Professional Paper* **321**, 1-106.

Cotteau, G.H. 1875. Description des echinides Tertiaires des îles St. Barthélemy et Anguilla. *Kongliga Svenska Vetenskaps-Akademiens Handlingar* **13** (6), 1-47.

Coyne, M.K., Jones, B., Ford, D. 2007. Highstands during Marine Isotope Stage 5: evidence from the Ironshore Formation of Grand Cayman, British West Indies. *Quaternary Science Reviews* **26**, 536-559.

Desmoulins, C. 1835. Premier mémoire sur les Échinides. Prodrome dúne nouvelle classification des ces animaux. *Actes de la Société Linnéenne de Bordeux* **7**, 167-245.

Dixon, H.L., Donovan, S.K. 1998. Oligocene echinoids of Jamaica. *Tertiary Research* **18**, 95-124.

Donovan, S.K. 1993. Jamaican Cenozoic Echinoidea. In: *Biostratigraphy of Jamaica*, Wright, R.M., Robinson, E. (eds). Geological Society of America Memoir **182**, 371-412.

Donovan, S.K. 2001. Evolution of Caribbean echinoderms during the Cenozoic: moving towards a complete picture using all of the fossils. *Palaeogeography, Palaeoclimatology, Palaeoecology* **166**, 177-192.

Donovan, S.K. 2003. Completeness of a fossil record: the Pleistocene echinoids of the Antilles. *Lethaia* **36**, 1-7.

Donovan, S.K. 2004. Echinoderms of the mid-Cainozoic White Limestone Group of Jamaica. In: *The Mid-Cainozoic White Limestone Group of Jamaica*, Donovan, S.K. (ed.). Cainozoic Research **3** (for 2003), 143-156.

Donovan, S.K. 2012. Taphonomic criteria for recognizing downslope transport of echinoderms: Neogene of the Antilles. *Geological Society of America Abstracts with Programs* **44** (7), 529.

Donovan, S.K., Embden, B.J. 1996. Early Pleistocene echinoids of the Manchioneal Formation, Jamaica. *Journal of Paleontology* **70**, 485-493.

Donovan, S.K., Harper, D.A.T. 2000. The irregular echinoid *Brissus* Gray from the Tertiary of Jamaica. *Caribbean Journal of Science* **36**, 332-335.

Donovan, S.K., Paul, C.R.C. 1998. Echinoderms of the Pliocene Bowden shell bed, southeast Jamaica. In: *The Pliocene Bowden shell bed, southeast Jamaica*, Donovan, S.K. (ed.). Contributions to Tertiary and Quaternary Geology, **35**: 129-146.

Donovan, S.K., Portell, R.W. 1998. A spatangoid echinoid from the Upper Pliocene of southeast Jamaica. *Caribbean Journal of Science* **34**, 320-322.

Donovan, S.K., Portell, R.W. 2000. Incipient 'crystal apples' from the Miocene of Jamaica. *Caribbean Journal of Science* **36**, 168-170.

Donovan, S.K., Veale, C. 1996. The irregular echinoids *Echinoneus* Leske and *Brissus* Gray in the

Cenozoic of the Antillean region. *Journal of Paleontology* **70**, 632-640.

Donovan, S.K., Dixon, H.L., Littlewood, D.T.J., Milsom, C.V., Norman, Y.J.C. 1994a. The clypeasteroid echinoid *Encope homala* Arnold and Clark, 1934, in the Cenozoic of Jamaica. *Caribbean Journal of Science* **30**, 171-180.

Donovan, S.K., Dixon, H.L., Pickerill, R.K., Doyle, E.N. 1994b. Pleistocene echinoid (Echinodermata) fauna from southeast Jamaica. *Journal of Paleontology* **68**, 351-358.

Donovan, S.K., Portell, R.W., Veltkamp, C.J. 2005. Lower Miocene echinoderms of Jamaica, West Indies. *Scripta Geologica* **129**, 91-135.

Durham, J.W. 1966. Clypeasteroids. In: *Treatise on Invertebrate Paleontology, Part U, Echinodermata 3 (2)*, Moore, R.C. (ed.). Geological Society of America and University of Kansas Press: New York and Lawrence; U450-U491.

Durham, J.W., Wagner, C.D. 1966. Glossary of morphological terms applied to echinoids. In: *Treatise on Invertebrate Paleontology, Part U, Echinodermata 3 (1)*, Moore, R.C. (ed.). Geological Society of America and University of Kansas Press: New York and Lawrence; U251, U253-U256.

Fischer, A.G. 1966. Spatangoids. In: *Treatise on Invertebrate Paleontology, Part U, Echinodermata 3(2)*, Moore, R.C. (ed.). Geological Society of America and University of Kansas Press: New York and Lawrence; U543-U628.

Gray, J.E. 1825. An attempt to divide the Echinida or sea eggs, into natural families. *Annals of Philosophy* (series 2) **10**, 423-431.

Gray, J.E. 1835. On the genera distinguishable in Echinus. *Proceedings of the Zoological Society of London* **3**, 57-60.

Gray, J.E. 1851. Description of two new genera and some new species of Scutellidae and Echinolampidae in the collection of the British Museum. *Proceedings of the Zoological Society of London* **19**, 34-38.

Gray, J.E. 1855. An arrangement of the families of Echinida, with descriptions of some new genera and species. *Proceedings of the Zoological Society, London* **23**, 35-39.

Gregory, J.W. 1900. The Echinoidea. In: *A Treatise on Zoology. Part III. The Echinodermata*, Lankester, E.R. (ed.). A. and C. Black: London; 282-332.

Haeckel, E. 1896. *Systematische Phylogenie der wirbellosen Thiere (Invertebrata). Vol. 2*. George Reimer Verlag: Berlin; xviii + 720 pp.

Hammer, Ø., Harper, D.A.T. 2006. *Palaeontological Data Analysis*. Blackwell, Oxford, 351 pp.

Hammer, Ø., Harper, D.A.T., Ryan, P.D. 2001. PAST – palaeontological statistics software: package for education and data analysis. *Palaeontologia Electronica* **4**, 9 pp.

Harold, A.S., Telford, M. 1990. Systematics, phylogeny and biogeography of the genus *Mellita* (Echinoidea: Clypeasteroida). *Journal of Natural History* **24**, 987-1026.

Hendler, G., Miller, J.E., Pawson, D.L., Kier, P.M. 1995. *Sea Stars, Sea Urchins, and Allies: Echinoderms of Florida and the Caribbean*. Smithsonian Institution Press: Washington, D.C.; xi+390 pp.

International Commission on Zoological Nomenclature. 1954. Opinion 209. Validation of, and designation of type species for, "*Brissus*" Gray, 1825, "*Echinocardium*" Gray, 1825, and "*Spatangus*" Gray, 1825 (Class Echinoidea) under the plenary powers, and designation, under those powers, of a type species for "*Schizaster*" Agassiz (L.), 1836, and in so far as necessary, for "*Moira*" Agassiz (A.), 1872. *Opinions and Declarations Rendered by the International Commission on Zoological Nomenclature* **3**(28), 367-392.

Jackson, R.T. 1922. Fossil Echini of the West Indies. *Carnegie Institution of Washington, Publication* **306**, iv+122.

Jackson, T.A., Robinson, E. 1994. The Netherlands and Venezuelan Antilles. In: *Caribbean Geology: An Introduction*, Donovan, S.K., Jackson, T.A. (eds). University of the West Indies Publishers' Association: Kingston; 249-263.

Jones, B. 1994. The Cayman Islands. In: *Caribbean Geology: An Introduction*, Donovan, S.K., Jackson, T.A. (eds). University of the West Indies Publishers' Association: Kingston; 87-109.

Jones, B., Hunter, I.G. 1989. The Oligocene-Miocene Bluff Formation on Grand Cayman. *Caribbean Journal of Science* **25**, 71-85.

Jones, B., Hunter, I.G., Kyser, K. 1994a. Stratigraphy of the Bluff Formation (Miocene-Pliocene) and the newly defined Brac Formation (Oligocene), Cayman Brac, British West Indies. *Caribbean Journal of Science* **30**, 30-51.

Jones, B., Hunter, I.G., Kyser, K. 1994b. Revised stratigraphic nomenclature for Tertiary strata of the Cayman Islands, British West Indies. *Caribbean Journal of Science* **30**, 53-68.

Kier, P.M. 1984. Fossil spatangoid echinoids of Cuba. *Smithsonian Contributions to Paleobiology* **55**, 336 pp.

Kier, P.M., Grant, R.E. 1965. Echinoid distribution and habits, Key Largo Coral Reef Preserve, Florida. *Smithsonian Miscellaneous Collections* **149** (6), 1-68.

Kroh, A., Smith, A.B. 2010. The phylogeny and classification of post-Palaeozoic echinoids. *Journal of Systematic Palaeontology* **8**, 147–212.

Lamarck, J.B.P.M. de. 1801. *Système des animaux sans vertèbres, ou Tableau général des classes, des ordres et des genres des ces animaux.* Deterville: Paris; 432 pp.

Lambert, J.M. 1905. Échinides du sud de la Tunise environs de Tatahouine. *Bulletin de la Société Géologique de France* (série 4) **5**, 569-577.

Latreille, P.A. 1825. *Famille naturelles de Régne Animal, exposées succinctement et dans un ordre analytique avec l'indication des leurs genres*. Paris; 570 pp.

Leske, N.G. 1778. *Iacobi Theodori Klein Naturalis disposito Echinodermatum, Edita et aucta a N.G. Leske*. Lipsiae; 278 pp.

Lewis, D.N., Donovan, S.K. 1991. The Pliocene Echinoidea of Tobago, West Indies. *Tertiary Research* **12**, 139-146.

Linné, C. 1758. *Systema Naturae per Regna tria Naturae, secundum Classes, Ordines, Genera, Species, cum Characteribus Differentis, Synonymis, Locis*. Holmiae.

Markov, A.V., Solovjev, A.N. 2001. Echinoids of the family Paleopneustidae (Echinoidea, Spatangoida): morphology, taxonomy, phylogeny. *Geos* **2001**, 1-109.

Melville, R.V., Durham, J.W. 1966. Skeletal morphology. In: *Treatise on Invertebrate Paleontology, Part U, Echinodermata 3 (1)*, Moore, R.C. (ed.). Geological Society of America and University of Kansas Press: New York and Lawrence; U220-U251.

Mooi, R. 1989. Living and fossil genera of the Clypeasteroida (Echinoidea: Echinodermata): an illustrated key and annotated checklist. *Smithsonian Contributions to Zoology* **488**, iii+51 pp.

Mooi, R., Peterson, D. 2000. A new species of *Leodia* (Clypeasteroida: Echinoidea) from the Neogene of Venezuela and its importance in the phylogeny of mellitid sand dollars. *Journal of Paleontology* **74**, 1083-1092.

Mortensen, T. 1951. *A Monograph of the Echinoidea. V. 2. Spatangoida. II. Amphisternata. II. Spatangidae, Loveniidae, Pericosmidae, Schizasteridae, Brissidae. Text and atlas*. C.A. Reitzel: Copenhagen; 593 pp.

Nebelsick, J.H. 1994. Taphonomy of *Clypeaster humulis* and *Echinodiscus auritus* (Echinoidea, Clypeasteroida) from the Red Sea. In: *Echinoderms through Time: Proceedings of the 8th International Echinoderm Conference, Dijon, 6-10 September, 1993*, David, B., Guille, A., Feral, J.-P., Roux, M. (eds). Rotterdam: A.A. Balkema; 803-808.

Nebelsick, J.H. 1995. Comparative taphonomy of clypeasteroids. *Eclogae Geologicae Helvetiae* **88**, 685-693.

Nebelsick, J.H. 1999. Taphonomy of Clypeaster fragments: preservation and taphofacies. *Lethaia* **32**, 241-252.

Nebelsick, J.H., Kroh, A. 2002. The stormy path from life to death assemblages: the formation and preservation of mass accumulations of fossil sand dollars. *Palaios* **17**, 378-393.

Oyen, C.W., Portell, R.W. 2002. Oligocene and Miocene echinoids. *Florida Fossil Invertebrates* **2**, 1-22.

Pemberton, S.G., Jones, B. 1988. Ichnology of the Pleistocene Ironshore Formation, Grand Cayman, British West Indies. *Journal of Paleontology*, **62**, 495-505.

Poddubiuk, R.H. 1985. Evolution and adaptation in some Caribbean Oligo-Miocene *Clypeasters*. In: *Echinodermata: Proceedings of the Fifth International Echinoderm Conference, Galway, 24-29 September,* 1984, Keegan, B.F., O'Connor, B.D.S. (eds). Rotterdam: A.A. Balkema; 19-24.

Poddubiuk, R.H. 1987. *Sedimentology, echinoid palaeoecology and palaeobiogeography of Oligo-Miocene eastern Caribbean limestone (in 2 volumes)*. Unpublished Ph.D. thesis, Royal Holloway and Bedford College, University of London, 419 + 148 pp.

Poddubiuk, R.H., Rose, E.P.F. 1985. Relationships between mid-Tertiary echinoid faunas from the central Mediterranean and eastern Caribbean and their palaeobiogeographic significance. *Annales Géologiques des Pays Hélleniques* **32** (for 1984), 115-127.

Robinson, E. 1994. Jamaica. In: *Caribbean Geology: An Introduction*, Donovan, S.K., Jackson, T.A. (eds). University of the West Indies Publishers' Association: Kingston; 111-127.

Rose, E.P.F. 1975. Oligo-Miocene echinoids of the Maltese islands. *VIth Congress Regional Committee on Mediterranean Neogene Stratigraphy, Bratislava*, 75-79.

Sánchez Roig, M. 1953. Neuvos equinodos fosiles de Cuba. *Anales de la Academis de Ciencias Medicas, Fisicas y Naturales de la Habana* **91**, 135-176.

Schelfhorst, R. 2013. *The Echinodermata of the Pliocene of Curaçao*. Unpublished M.Sc. thesis, University of Leiden.

Schultz, H. 2005. *Sea Urchins: A Guide to Worldwide Shallow Water Species*. Heinke and Peter Schultz Partner: Hemdingen, Germany; xii+484 pp.

Serafy, D.K. 1979. Echinoids (Echinodermata: Echinoidea). *Memoirs of the Hourglass Cruises* **5** (3), 1-120.

Smith, A.B. 1984. *Echinoid Palaeobiology*. George Allen and Unwin: London; 191 pp.

Smith, A.B., Kroh, A. (eds) 2011. *The Echinoid Directory.* World Wide Web electronic publication. http://www.nhm.ac.uk/research-curation/projects/echinoid-directory [accessed 21 August

2014].

Stefanini, G. 1912. Osservazioni sulla distribuzione geografica, sulla origini e sulla filogenesi degli Scutellidae. *Bolletino della Societe Geologica Italiana* **30** (for 1911): 739-754.

Stockley, B., Smith, A.B., Littlewood, D.T.J., Lessios, H.A., MacKenzie-Dodds, J.A. 2005. Phylogenetic relationships of spatangoid sea urchins (Echinoidea), taxon sampling density and congruence between morphological and molecular estimates. *Zoologica Scripta* **34**, 447-468.

Vézina, J.L., Jones, B., Ford, D.C. 1999. Sea-level highstands over the last 500,000 years: evidence from the Ironshore Formation on Grand Cayman, British West Indies**.** *Journal of Sedimentary Research* **69,** 317-327.

Wright, T. 1855. On fossil echinoderms from the island of Malta; with notes on the stratigraphical distribution of the fossil organisms of the Maltese beds. *Annals and Magazine of Natural History* (series 2) **15**, 101-127, 175-196, 262-277.

Table 1. A comparison of some mid-Cenozoic echinoid occurrences in carbonate sequences from the Antilles and Malta. Key: 1 = Upper Oligocene of central north Jamaica (Dixon and Donovan, 1998; Donovan, 2004); 2 = Upper Oligocene of Antigua (Poddubiuk and Rose, 1985, table 1); 3 = Oligocene-Miocene of Malta (Rose, 1975, table 12); 4 = Lower Miocene of Anguilla (Poddubiuk and Rose, 1985, table 3); 5 = Lower Miocene of central north Jamaica (Donovan *et al*., 2005); 6 = Middle Miocene of Grand Cayman (herein); + = present; ? = presence uncertain.

Table 1.

	1: U. Oligo. Jamaica	2: U. Oligo. Antigua	3: Oligo-Miocene Malta	4: L. Miocene Anguilla	5: L. Miocene Jamaica	6: Miocene Cayman
CIDAROIDA						
Histocidaris					+	
Phyllacanthus		+	+			
Prionocidaris	+	+	+	+	+	
Stylocidaris?			+			
Tretocidaris				+		
ARBACIOIDA						
Arbacia?						+
Coelopleurus			+			
CAMARODONTA						
Arbacina			+			
ECHINOIDA						
Echinometra		+		+	+	
Psammechinus			+	+		
Schizechinus			+			
Tripneustes				+		
regular echinoids indet.	+					
ECHINONEIOIDA						
Echinoneus	+		+	+	+	
CLYPEASTEROIDA						
Clypeaster	+	+	+	+	?	+
Echinocyamus			+			
Scutella			+			
Sismondia		+		+		
CASSIDULOIDA						
Apatopygus			+			
Echinolampas	+	+	+	+		
Pliolampas			+			
Studeria			+			
SPATANGOIDA						
Agassizia	+			+		
Antillaster		+				
Brissopsis			+	+		
Brissus			+	+		+
Eupatagus	+	+	+	+		
Hemiaster			+			
Heterobrissus			+			
Lovenia		+	+	+		
Meoma		+	+	+		
Pericosmus			+	+		
Schizaster		+	+	+		+
Spatangus			+			
Trachypatagus			+			
spatangoid indet.	+				+	
TOTALS	**8**	**11**	**26**	**17**	**6**	**4**

FIGURE CAPTIONS

Figure 1. (**A**) Geological map of Grand Cayman (modified after Jones *et al.*, 1994b, fig. 1). Key: * = numbered fossil locality. Note that Localities 2A and 2B are close together; greater detail can be gleaned from Coyne *et al*. (2007, fig. 3). (**B**) Schematic stratigraphic succession of the Cayman Islands, showing stratigraphic units, dominant lithologies, fossil biota and nature of fossil preservation (after Jones *et al.*, 1994b, fig. 2). Key: VC = very common; C = common; LC = locally common; R = rare.

Figure 2. *Arbacia*? sp., UA P1669, Middle Miocene, Cayman Formation, Grand Cayman. Internal mould of regular echinoid. (**A**) Lateral view. (**B**) Apical view. (**C**) Oral view. Scale bar represents 10 mm. Specimen whitened with ammonium chloride.

Figure 3. *Schizaster* sp. cf. *S. americanus* (Clark *in* Clark and Twitchell, 1915), UA P1670, Middle Miocene, Cayman Formation, Grand Cayman. Internal mould of irregular echinoid. (**A**) Anterior view. (**B**) Apical view. (**C**) Right lateral view, anterior to right. (**D**) Oral view. (**E**) Posterior view. Scale bar represents 10 mm. Specimen whitened with ammonium chloride.

Figure 4. *Brissus* sp. cf. *B. oblongus* Wright, 1855, Middle Miocene, Cayman Formation, Grand Cayman. Internal moulds of irregular echinoids. (**A-E**) UA P1671, apical, anterior, posterior, oral and right lateral views. (**F, K**) UA P1672, right lateral and apical views. (**G-I, L, M, P**) UA P1678, apical, left lateral, right lateral, posterior, anterior and oral views. (**J, O**) UA P1673, oral and left lateral views. (**N**) UA P1675, oral view, preserving part of test; note tuberculation of plastron. Scale bar represents 10 mm. Specimen whitened with ammonium chloride.

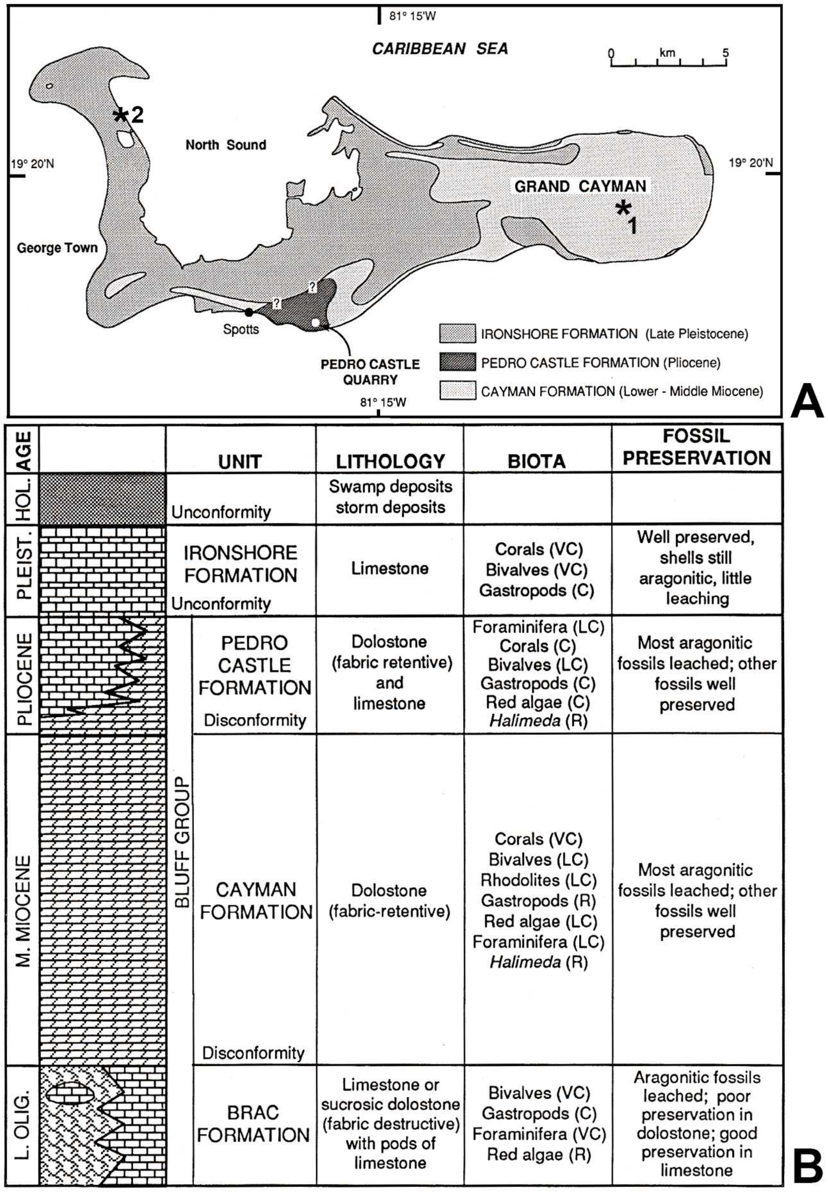
Figure 5. (**A, B**) *Brissus unicolor* (Leske, 1778), USNM E44054 (two specimens), Recent, the

Palisadoes, parish of St Andrew, Jamaica (after Donovan and Veale, 1996, figs 4.1, 4.2). Scale bar represents 10 mm. Specimens painted with dark food colouring and whitened with ammonium chloride. (**A**) Apical surface of test #1. (**B**) Oral surface of test #2. (**C, D**) *Brissus oblongus* Wright, 1855, holotype (after Wright, 1855, pl. 5, figs 2a, b, respectively). (**C**) Apical surface. (**D**) Oral surface. Presumed x 1.

Figure 6. The multivariate (Principal Components) shape analysis, interrogated a correlation matrix of eleven variates (see Donovan and Harper, 2000) measured on 59 specimens. The specimens were plotted against the first and second principal components (eigenvectors). The following fields are discriminated: Recent *Brissus unicolor* (Leske, 1778) from Jamaica, *Brissus* sp. cf. *B. oblongus* Wright, 1855, and a single test, *Brissus* sp. nov.(?), from the Eocene of Jamaica (Donovan and Veale, 1996, pp. 635-638, figs 2.5, 2.6; MCZ 3469).

Figure 7. *Leodia sexiesperforata* (Leske, 1778), UA P1704, Pleistocene Ironshore Formation, oral surface of incomplete test, orientation uncertain. Both ambulacral lunules are of similar size and shape, but that at 10 o'clock is partly occluded by limestone. Scale bar represents 10 mm. Specimen whitened with ammonium chloride.

Figure 8. *Clypeaster* sp., photograph taken in the field of an external mould of the apical surface. Spotts Bay Quarry, Grand Cayman. Middle Miocene Cayman Formation, Grand Cayman. Lens cap for scale.



AGE			UNIT	LITHOLOGY	BIOTA	FOSSIL PRESERVATION
HOL.			Unconformity	Swamp deposits storm deposits		
PLEIST.			IRONSHORE FORMATION Unconformity	Limestone	Corals (VC) Bivalves (VC) Gastropods (C)	Well preserved, shells still aragonitic, little leaching
PLIOCENE		BLUFF GROUP	PEDRO CASTLE FORMATION Disconformity	Dolostone (fabric retentive) and limestone	Foraminifera (LC) Corals (C) Bivalves (LC) Gastropods (C) Red algae (C) *Halimeda* (R)	Most aragonitic fossils leached; other fossils well preserved
M. MIOCENE			CAYMAN FORMATION Disconformity	Dolostone (fabric-retentive)	Corals (VC) Bivalves (LC) Rhodolites (LC) Gastropods (R) Red algae (LC) Foraminifera (LC) *Halimeda* (R)	Most aragonitic fossils leached; other fossils well preserved
L. OLIG.			BRAC FORMATION	Limestone or sucrosic dolostone (fabric destructive) with pods of limestone	Bivalves (VC) Gastropods (C) Foraminifera (VC) Red algae (R)	Aragonitic fossils leached; poor preservation in dolostone; good preservation in limestone

Figure 1. (A) Geological map of Grand Cayman (modified after Jones et al., 1994b, fig. 1). Key: * = numbered fossil locality. Note that Localities 2A and 2B are close together; greater detail can be gleaned from Coyne et al. (2007, fig. 3). (B) Schematic stratigraphic succession of the Cayman Islands, showing stratigraphic units, dominant lithologies, fossil biota and nature of fossil preservation (after Jones et al., 1994b, fig. 2). Key: VC = very common; C = common; LC = locally common; R = rare.
150x213mm (300 x 300 DPI)

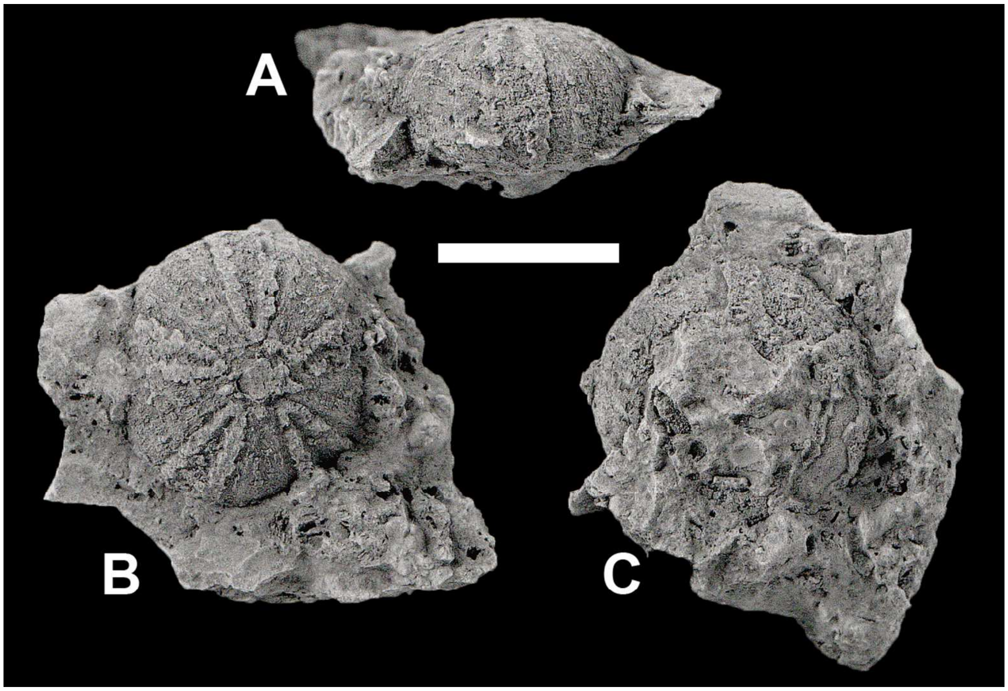


Figure 2. Arbacia? sp., UA P1669, Middle Miocene, Cayman Formation, Grand Cayman. Internal mould of regular echinoid. (A) Lateral view. (B) Apical view. (C) Oral view. Scale bar represents 10 mm. Specimen whitened with ammonium chloride.
110x75mm (300 x 300 DPI)

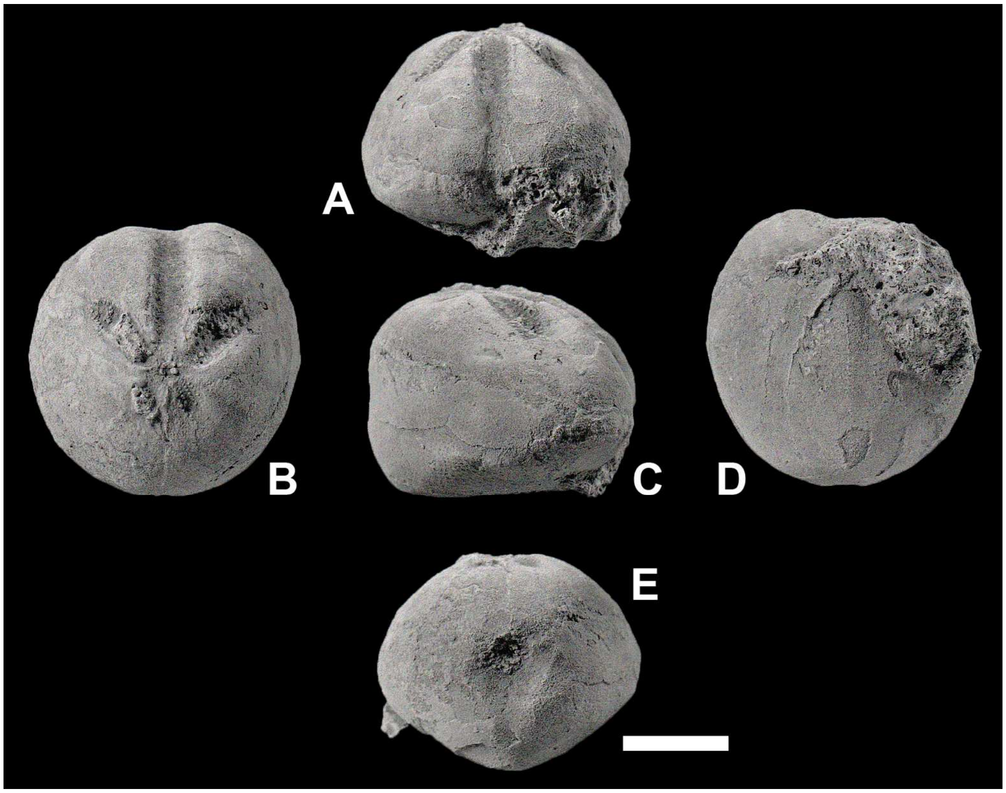


Figure 3. Schizaster sp. cf. S. americanus (Clark in Clark and Twitchell, 1915), UA P1670, Middle Miocene, Cayman Formation, Grand Cayman. Internal mould of irregular echinoid. (A) Anterior view. (B) Apical view. (C) Right lateral view, anterior to right. (D) Oral view. (E) Posterior view. Scale bar represents 10 mm. Specimen whitened with ammonium chloride.
142x111mm (300 x 300 DPI)

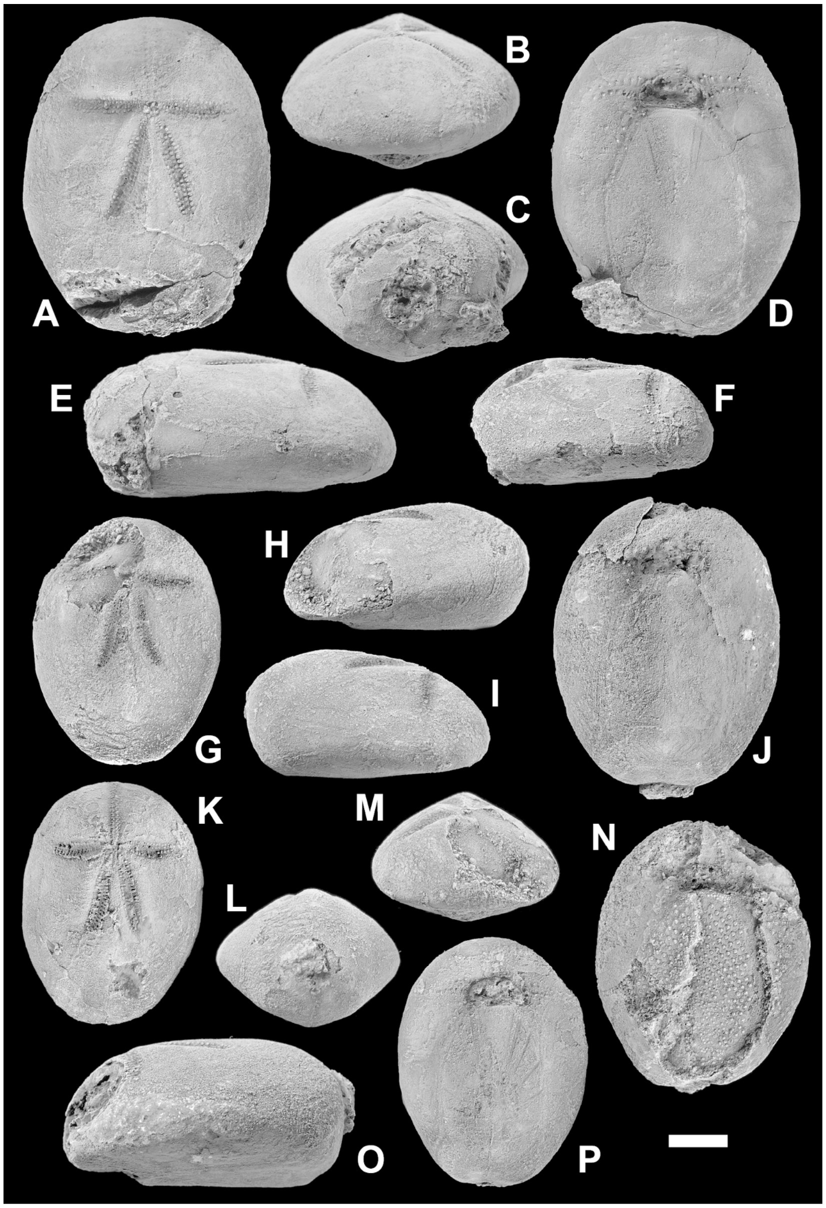


Figure 4. Brissus sp. cf. B. oblongus Wright, 1855, Middle Miocene, Cayman Formation, Grand Cayman. Internal moulds of irregular echinoids. (A-E) UA P1671, apical, anterior, posterior, oral and right lateral views. (F, K) UA P1672, right lateral and apical views. (G-I, L, M, P) UA P1678, apical, left lateral, right lateral, posterior, anterior and oral views. (J, O) UA P1673, oral and left lateral views. (N) UA P1675, oral view, preserving part of test; note tuberculation of plastron. Scale bar represents 10 mm. Specimen whitened with ammonium chloride.
140x204mm (300 x 300 DPI)

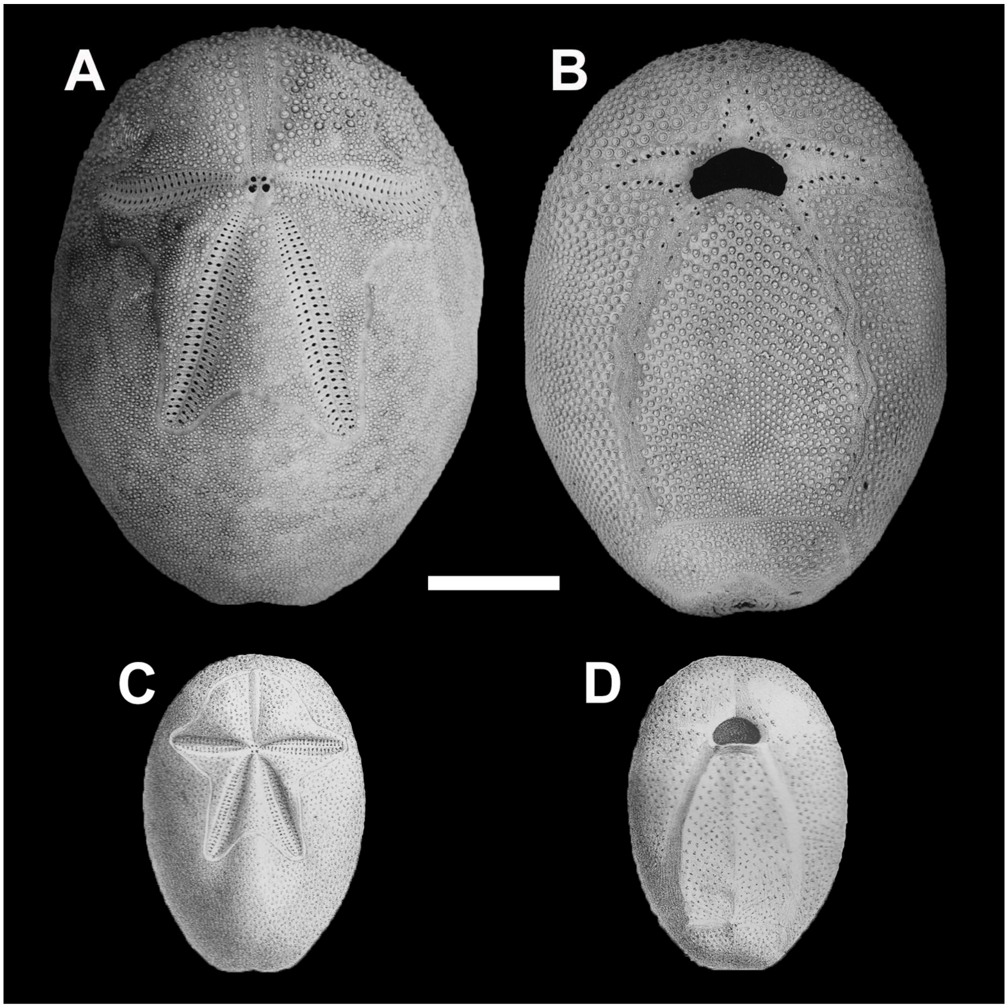


Figure 5. (A, B) Brissus unicolor (Leske, 1778), USNM E44054 (two specimens), Recent, the Palisadoes, parish of St Andrew, Jamaica (after Donovan and Veale, 1996, figs 4.1, 4.2). Scale bar represents 10 mm. Specimens painted with dark food colouring and whitened with ammonium chloride. (A) Apical surface of test #1. (B) Oral surface of test #2. (C, D) Brissus oblongus Wright, 1855, holotype (after Wright, 1855, pl. 5, figs 2a, b, respectively). (C) Apical surface. (D) Oral surface. Presumed x 1.
150x150mm (300 x 300 DPI)

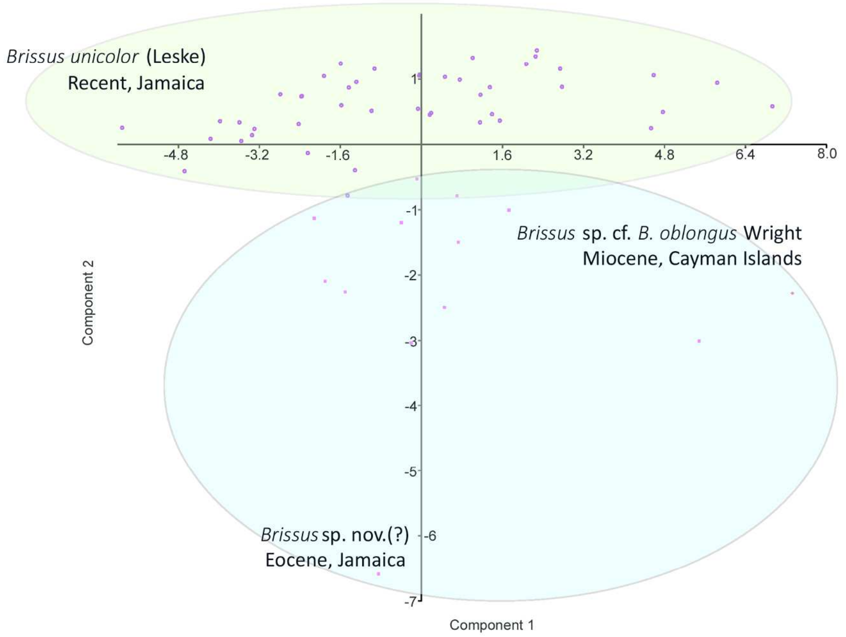


Figure 6. The multivariate (Principal Components) shape analysis, interrogated a correlation matrix of eleven variates (see Donovan and Harper, 2000) measured on 59 specimens. The specimens were plotted against the first and second principal components (eigenvectors). The following fields are discriminated: Recent Brissus unicolor (Leske, 1778) from Jamaica, Brissus sp. cf. B. oblongus Wright, 1855, and a single test, Brissus sp. nov.(?), from the Eocene of Jamaica (Donovan and Veale, 1996, pp. 635-638, figs 2.5, 2.6; MCZ 3469).
198x140mm (300 x 300 DPI)

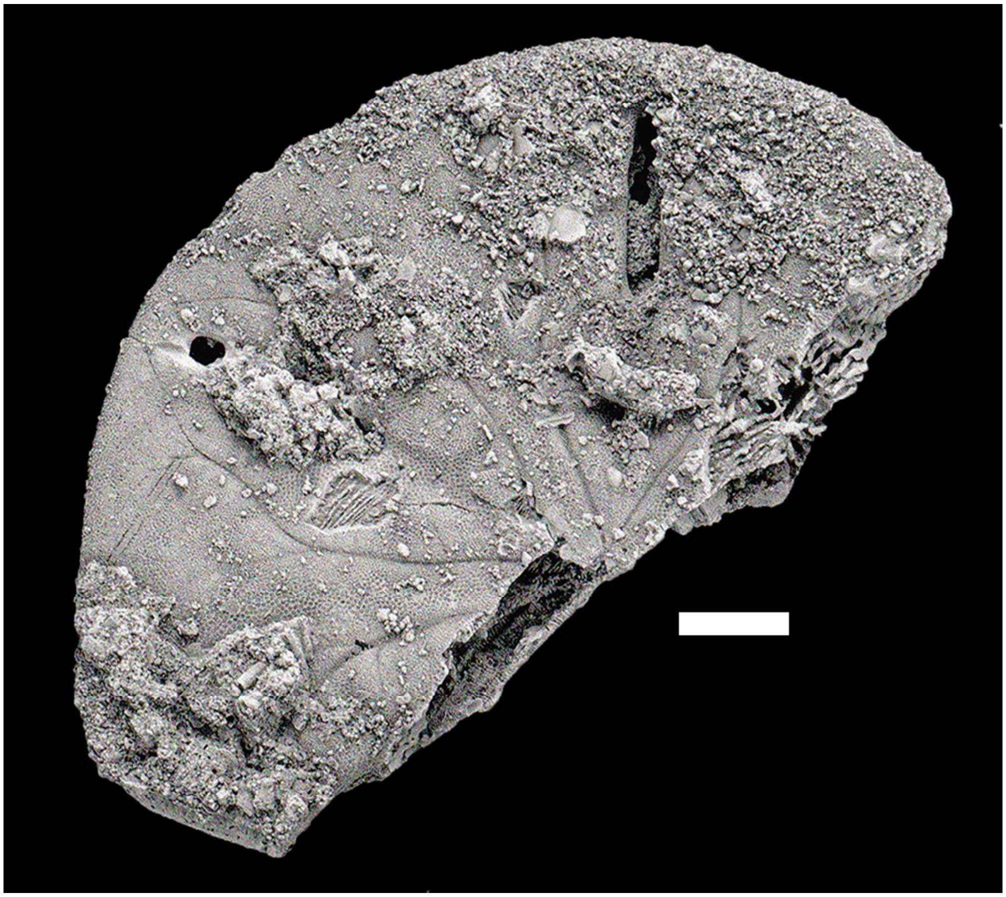


Figure 7. Leodia sexiesperforata (Leske, 1778), UA P1704, Pleistocene Ironshore Formation, oral surface of incomplete test, orientation uncertain. Both ambulacral lunules are of similar size and shape, but that at 10 o’clock is partly occluded by limestone. Scale bar represents 10 mm. Specimen whitened with ammonium chloride.
92x82mm (300 x 300 DPI)

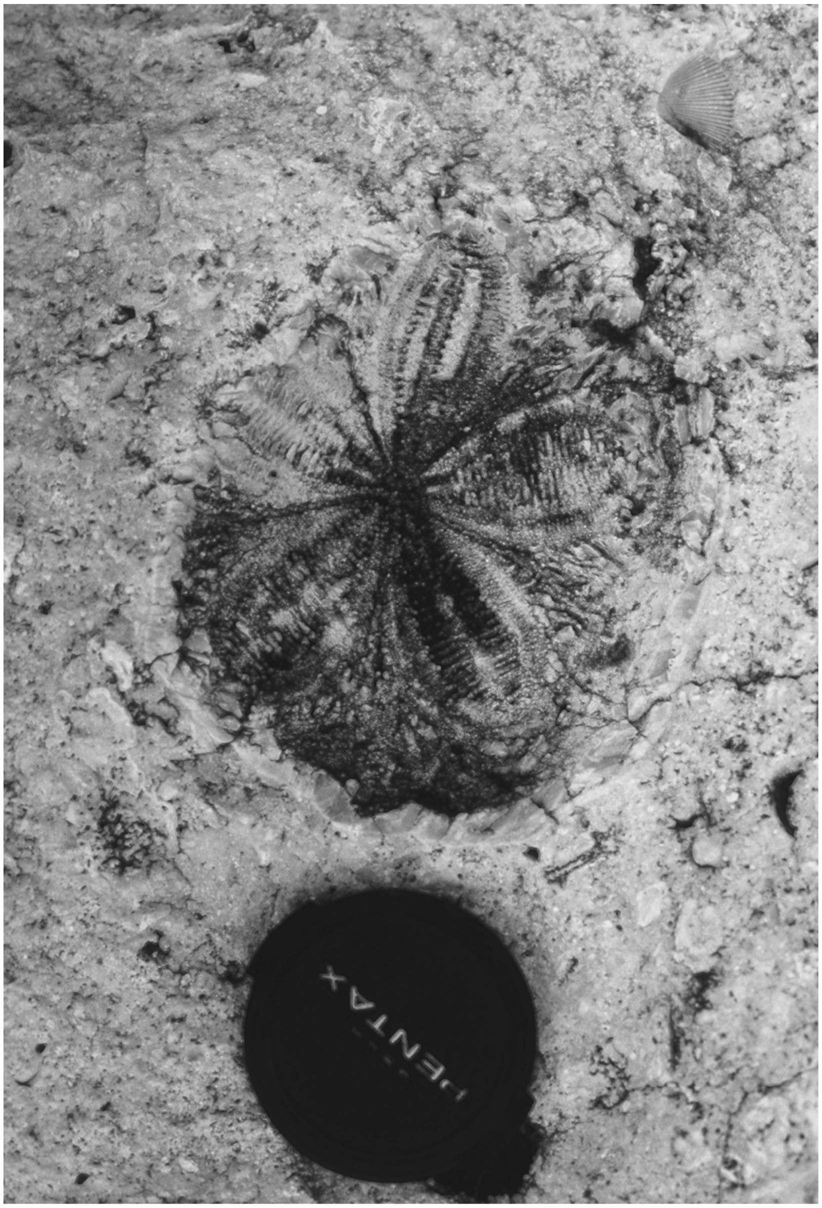


Figure 8. Clypeaster sp., photograph taken in the field of an external mould of the apical surface. Spotts Bay Quarry, Grand Cayman. Middle Miocene Cayman Formation, Grand Cayman. Lens cap for scale.
113x166mm (240 x 240 DPI)