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Urchins on the edge: an echinoid fauna with a mixed environmental signal from the Eocene of Jamaica

Conrad van den Ende[1] · Stephen K. Donovan[2]

Abstract An echinoid fauna from the Early–Middle Eocene of Jamaica has yielded six species of echinoid: the phymosomatoid *Acanthechinus peloria* (Arnold and Clark); the oligopygoid *Oligopygus* sp.; the clypeasteroids *Fibularia jacksoni* Hawkins and *Neolaganum* sp.; and the spatangoids *Eupatagus alatus* Arnold and Clark and *Eupatagus* sp. cf. *E. clevei* (Cotteau). *Eupatagus alatus* has a relatively low test, is broadest posterior of centre, and lacks an anterior sulcus; *Eupatagus* sp. cf. *clevei* is relatively higher and more inflated, more parallel-sided, and blunter anteriorly with an anterior sulcus. The discovery of *F. jacksoni* and *Neolaganum* sp. together with *Oligopygus* sp. is unexpected, as these species commonly have different ecological niches in the Eocene of Jamaica. In previous examples described from the Eocene succession of the island, oligopygoids favoured high-energy shelf edge settings, whereas *Fibularia* and neolaganids prefered low-energy lagoonal settings. The assemblage as a whole likely represents an Early–Mid Eocene echinoid fauna inhabiting a shallow island shelf sea, in a transition between shelf edge and lagoonal setting.

Keywords Yellow Limestone Group · Guys Hill Formation · Systematics · Palaeoecology

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Introduction

Jamaica boasts a wide variety of fossil echinoids, first described in detail by Hawkins (1923, 1924, 1927, 1930) and Arnold and Clark (1927, 1934). Precise data concerning localities and horizons for most of Arnold and Clark's species are unknown because of the manner of collection, mostly from road or railway construction workers who were asked about what were locally known as 'stone sea eggs' (Arnold and Clark 1927, p. 6). If these labourers were cooperative, Arnold was sold or given some specimens, or collected at the location from where the rocks came. From the associated locality data in Arnold and Clark (1927, 1934), we know that many of the echinoids that they figured and described originated from the Eocene Yellow Limestone Group (Donovan 1988a, 1993).

More recently, the Jamaican Cenozoic echinoid fauna has been found to be particularly diverse, but stratigraphically unevenly known, with an inordinate number of taxa coming from the Eocene (Donovan 1993). During the mid-Early and mid-Middle Eocene, echinoid diversity in the Caribbean was at its height, declining towards the Late Eocene (McKinney et al. 1992; Dixon and Donovan 1994). Subsequent studies of Jamaican fossil echinoids have filled some of these gaps by concentrating on the post-Eocene record (for example, Oligocene—Dixon and Donovan 1998a; Miocene—Donovan et al. 2005; Pliocene—Donovan and Portell 2014; Pleistocene—Donovan 2003).

An undescribed collection of fossil echinoids from the Eocene Guys Hill Formation, Yellow Limestone Group, in Jamaica has yielded species that are otherwise limited to contrasting shallow water palaeoenvironments. Herein, we document this unusual association for the first time and relate it to modern reconstructions of Jamaica's Eocene palaeogeography.

The terminology of the echinoid endoskeleton used herein follows Melville and Durham (1966), Durham and Wagner (1966), Smith (1984) and Smith and Kroh (2011). The higher classification of echinoids follows Kroh and Smith (2010), apart from the retention of the family Neolaganidae Durham. Our philosophy of open nomenclature follows (1988).

Locality and horizon

The specimens discussed below were collected in 1996–1997 from the east side of a minor road rising to the north above Thornton after the initial hairpin bend, parish of St. Elizabeth, west central Jamaica (Fig. 1). Ms Tricia Andrew, then an undergraduate in the Department of Geography and Geology, University of the West Indies (UWI), Mona, considered the grid reference of this site to be [NGR 3016 4708] on the old 1:50,000 sheet D, "Mandeville–Black River". This approximates to [NGR 744 714] on Jamaica 1:50,000 (metric edition) sheet #6, "The Cockpit Country" and 77°42′53″W 18°11′33″N.

These rocks form part of the Yellow Limestone Group (mid-Lower to mid-Middle Eocene; Robinson 1994). These oyster-rich beds most probably correspond to "…the higher part of the Guys Hill Formation at the western end of the Central inlier [see Robinson 1994], [where is exposed] an irregularly developed limestone, several metres

thick [which] carries an ostreid-rich molluscan fauna and a larger foraminiferal fauna…indicative of the lower part of Zone 2A of Robinson [see Robinson and Wright 1993]…[it] is here referred to the Dump Member" (Robinson and Mitchell 1999, p. 6; see also Robinson 1988, p. 60, fig. 13).

This locality includes an oyster bed up to 200 mm thick with shells not preserved in any consistent orientation. Specimens of echinoids were collected from this site by S.K.D. with the help of UWI students Andrew and Deslandes (see Andrew 1997, p. 21; Deslandes 1997, pp. 12–13), Dr. S. F. Mitchell and others.

Systematic palaeontology

Remark The specimens discussed below are deposited in the geological collections of the Naturalis Biodiversity Center, Leiden, the Netherlands (prefix RGM).

Class Echinoidea Leske, 1778
Order Phymosomatoida Mortensen, 1904
Family Phymosomatidae Pomel, 1883
Genus *Acanthechinus* Duncan and Sladen, 1882

Type species Acanthechinus nodulosus Duncan and Sladen, 1882, p. 34 [=*Cyphosoma abnormale* Duncan and Sladen, 1882, p. 34], uppermost Paleocene to Lower Eocene of Pakistan (Smith and Kroh, 2011).

Fig. 1 Outline map of the Maggotty–Accompong–Thornton–Windsor area of the parish of St. Elizabeth, west central Jamaica (redrawn and highly simplified after Jamaica 1:50,000 (metric edition) sheets #6 "The Cockpit Country" and #10 "Black River"). Key: *Asterik* Thornton Eocene echinoid locality. Inset map of Jamaica shows the position of the main map (*black square filled box*) and parish boundaries; coastline stippled; *K* Kingston
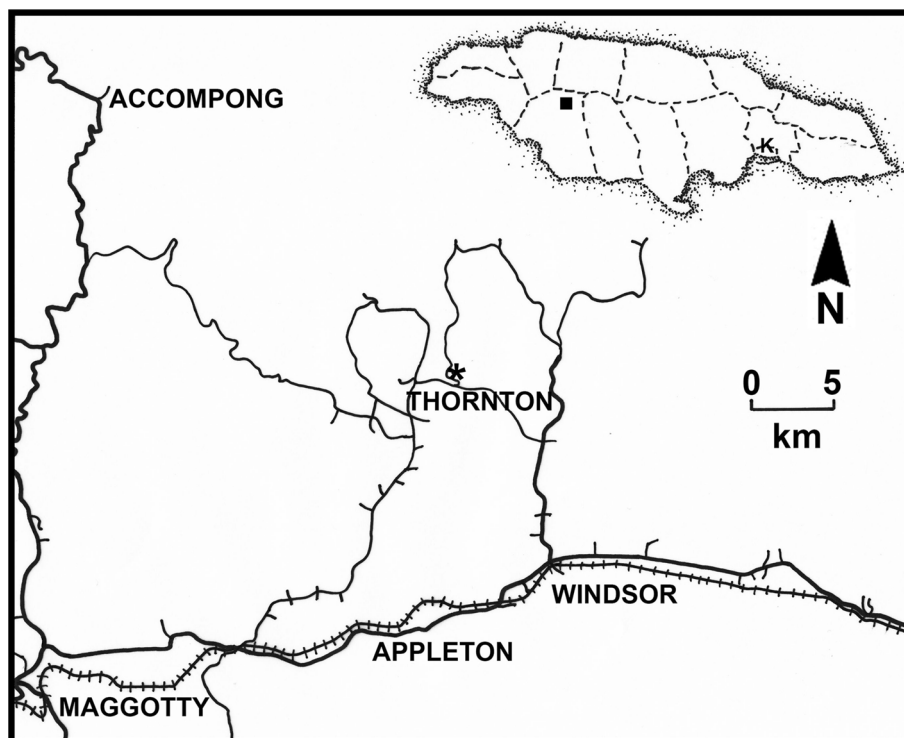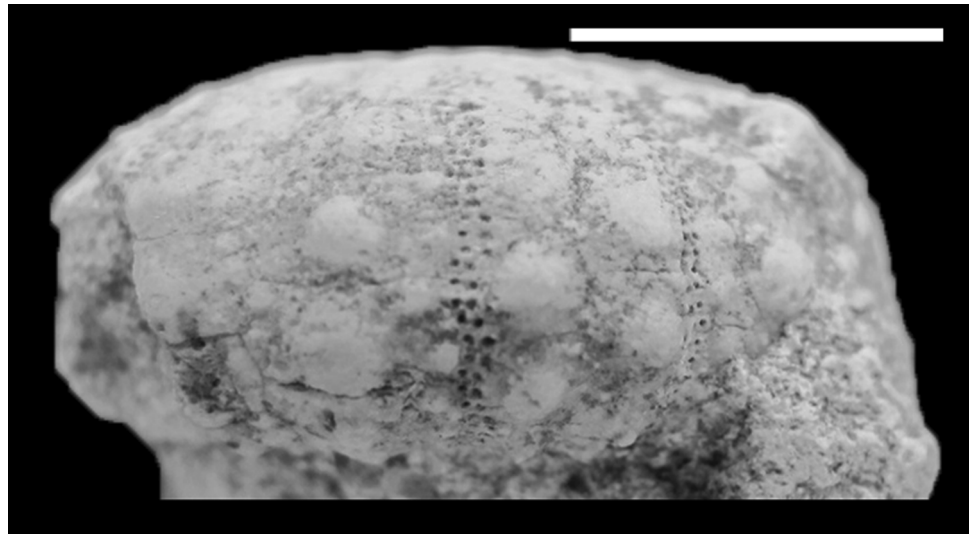
Fig. 2 *Acanthechinus peloria* (Arnold and Clark), RGM 791 235, from the Guys Hill Formation of Jamaica. Lateral view. Specimen uncoated. *Scale bar* represents 10 mm

Acanthechinus peloria (Arnold and Clark, 1927) (Fig. 2)
1923 *Phymosoma peloria* sp. nov., Arnold and Clark, pp. 18–20, pl. 2, figs. 1–3
1988a *Phymosoma peloria* Arnold and Clark; Donovan, table 1
1988b *Phymosoma peloria* Arnold and Clark; Donovan, p. 37
1992 *Phymosoma*; McKinney et al., p. 358, fig. 17.6
1993 *Phymosoma peloria* Arnold and Clark; Donovan, pp. 379–380, fig. 4.6, 4.11

Material One specimen, RGM 791 235, poorly preserved and moderately weathered; its peristome is covered by matrix, the periproct is visible, interambulcra and ambulacra partially visible and the tubercles are moderately intact.

Description See Arnold and Clark (1927, p. 18–20, pl. 2, figs. 1–3) and Donovan (1993, p. 379–380, fig. 4.6, 4.11).

Remarks There are certain points along the ambitus where the specimen is partly entombed or partially missing plating, making a correct assessment of the outline difficult. The most likely shape is circular. There are two moderately well-preserved interambulacral plates visible, both of which house a large tubercle centrally. There are also some smaller tubercles visible, positioned at the outer end of the plates, with the smallest tubercles towards the lower margin of the plate. Figure 2 shows the pattern of ambulacral plating with diadematoid compounding (Donovan, 1993, p. 379; compare with Smith, 1984, fig. 3.6).

The most probable identity for this specimen is *Acanthechinus peloria* (Arnold and Clark, 1927). The pore pairs and straight ambulacra are similar, as are the periproct's size, the low height of the ambitus and the similar ratios of height to diameter. However, RGM 791 235 is smaller than previously described specimens of *A. peloria* and may be a

juvenile; unfortunately, its apical system is not preserved. Another morphologically close species is Upper Eocene *Acanthechinus dixie* (Cooke, 1941), but Cooke's species has a more rounded outline, the ambitus is positioned higher on the test and this younger species has not previously been identified from Jamaica.

Cohort Irregularia Latreille, 1825
Order Clypeasteroida L. Agassiz, 1835
Family Oligopygidae Duncan, 1889
Genus *Oligopygus* de Loriol, 1888

Type species Oligopygus wetherbyi de Loriol, 1888, p. 396, pl. 17, Figs. 7–7d, 8, by original designation (Wagner and Durham 1966, p. U448; Kier 1967, p. 54), from the upper Upper Eocene of the south-east USA (Zachos and Shaak 1978, text-fig. 1; McKinney and Jones 1983).

Oligopygus sp. (Fig. 3)

Material Moderately well-preserved tests include RGM 791 239 (Fig. 3a, b) and 791 241 (Fig. 3c, d), with 46 other specimens, RGM 791 236-791 238, 791 240, 791 242-791 263, 791 264 (20 tests) (Fig. 3e–h). Eighteen specimens with a complete test were used for measurements, to compare with the ratios in Kier (1967), RGM 791 236-791 242, 791 245, 791 248-791 250, 791 253-791 255, 791 258, 791 259, 791 261 and 791 262.

Description. Test elongate/rounded to subpentagonal in larger specimens. Greatest height apically; adoral surface slightly concave with peristome located at the centre of a transverse trough. Apical surface low domed apically, smoothly sloping downwards towards ambitus at about 25 % test height. Apical system central to slightly posterior of centre. Four gonopores set between madreporite and interambulacra (excluding interambulacrum 5), can be either large or small (due to either sexual dimorphism or
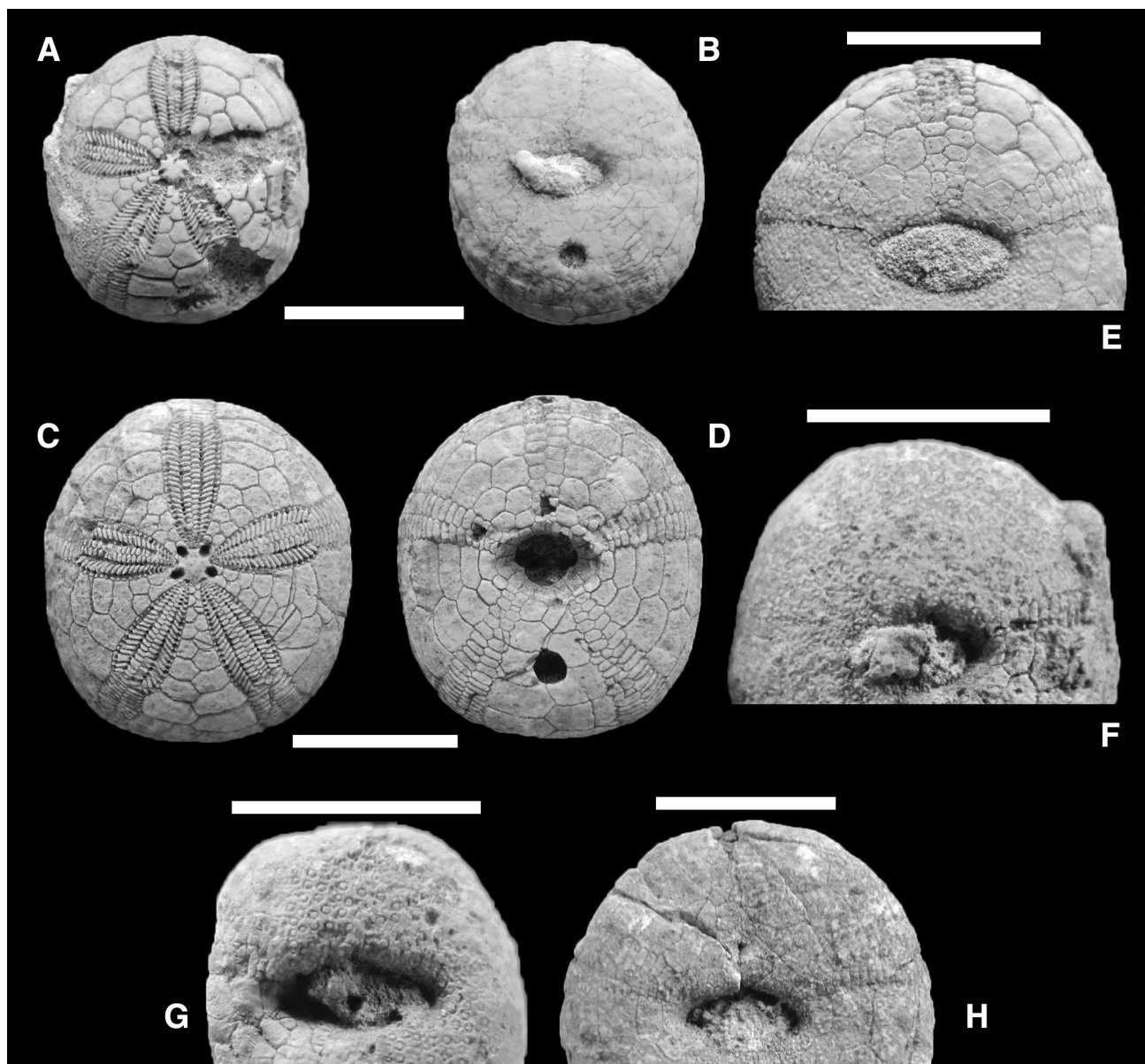
Fig. 3 *Oligopygus* sp. from the Guys Hill Formation of Jamaica. RGM 791 239. Note how the tuberculation is largely lost in most specimens. **a** Apical view, some ambulacra damaged. **b** Oral view, peristome partly occluded by limestone. RGM 791 241. **c** Apical view. **d** Oral view. Peristome outlines (e–h). **e** RGM 791 238. **f** RGM 791 242. **g** RGM 791 246. **h** RGM 791 251. Specimens uncoated. *Scale bars* represent 10 mm

dissolution of calcite; Kier, 1967, p. 17), with the anterior pair situated closer together than the posterior pair.

Ambulacral petals well developed on apical surface only. Five petals consisting of two columns of pore pairs; outer pores slightly oblique, inner pores circular, petals open. Ambulacra expand adorally to petals, then narrow towards peristome; single pored on oral surface. Anterior petal longest; anterior lateral petals shortest. The interambulacra are widest ambitally, plate sutures smooth. Peristome lensoid, wider than high, anterior steeply slopes inwards and is rounded, posterior is pointed and less sloped. Periproct small, circular and situated midway between peristome and posterior margin; in smaller specimens it is located more posteriorly.

Remarks The master reference for differentiating between the species of oligopygoids is Kier (1967). The lensoid peristome (Fig. 3b, d–h) is characteristic of *Oligopygus*. There is an overlap in gross morphology among some species within *Oligopygus* (as well as the closely related *Haimea*; see Rowe, 2004), most relevantly between *Oligopygus curavasica* Molengraaff, 1929, *O. haldemani*

Conrad, 1850, *O. jamaicensis* Arnold and Clark, 1927, and *O. wetherbyi* de Loriol, 1888. The main differences between these species are the relative positions and shapes of the periproct. It is situated most posteriorly in *O. haldemani*, almost against the ambitus. In *O. wetherbyi* the periproct is located halfway between the posterior ambitus and the peristome, whereas in *O. curavasica* it falls between these two with the periproct situated 60–70 % of the distance from the peristome to the ambitus. In *O. jamaicensis* the peristome is central, but shaped as a narrow slit. The similarities in gross morphology of *O. curavasica* to *O. wetherbyi* fossils raise the question whether or not they are actually different species, ecophenotypes or synonyms. *Oligopygus curavasica* has not been recorded from the type area, the Eocene in Curaçao, since it was described by Molengraaff (1929), although this may merely be a reflection of the lack of more recent research on the Eocene of the Netherlands Antilles.

Most specimens in the present collection are weathered quite severely, making it difficult to distinguish any tuberculation, but emphasizing the patterns of test plating (Fig. 3a–d). All of the measured specimens have ratios that closely match those of Kier (1967) for *O. wetherbyi*, with an average width to length percentage of 89 % and an average height to length percentage of 47 %, but the type species is a somewhat younger taxon than that considered herein. In Jamaica, *O. wetherbyi* has only been reported, most probably erroneously, from the upper-Middle Eocene Swanswick Formation, White Limestone Group (Donovan 1993, p. 384; 1994, table 1). Because of the inferior preservation of the Thornton material, we leave it in open nomenclature; it may be closest to *O. jamaicensis* Arnold and Clark, 1927, which has broadly similar gross test dimensions to *O. wetherbyi*, but is more rounded. However, because of the poor preservation of these specimens, the outline of the peristome is poorly seen (Fig. 3b, d, e–h) and some appear closer to *Haimea* than *Oligopygus* (Fig. 3d). Herein, we consider this difference taphonomic—test plates of oligopygoids are thick and surface corrosion common (Fig. 3), altering the outline of the peristome—rather than systematic.

Family Fibulariidae Gray, 1855
Genus *Fibularia* Lamarck, 1816

Type species Fibularia ovulum Lamarck, 1816, p. 16, by the subsequent designation of the International Commission on Zoological Nomenclature (1954, p. 350) (Durham, 1966, p. U469; Smith and Kroh, 2011), from the Recent of the East Indies.

Fibularia jacksoni Hawkins, 1927 (Fig. 4a, b)

Material Complete, but weathered, specimens, RGM 791 265-791 281, 791 282 (eight tests), 791 283-791 285, 791

286 (two tests), 791 287 (two tests) (32 specimens). RGM 791 285 and 791 287 also bear tests of *Neolaganum durhami* (see below). Specimens with a complete test were used for measurements and for comparison with the original description in Hawkins (1927).

Description See Hawkins (1927, p. 76–77, pl. 22, figs. 1–3) and Donovan (1993, p. 388–389, fig. 11).
Measurements Length 5.3–8.2 mm (mean 7.1 mm); height 3.4–7.2 mm (mean 5.4 mm); height to length ratio 0.6–0.8 (mean 0.75); distance between peristome and periproct 0.9–1.2 mm (mean 1.0 mm); ratio peristome-periproct distance to length 0.14–0.17 (mean 0.15). No complete petals available for measurement.

Remarks Although a moderately large collection of *Fibularia jacksoni* Hawkins, 1927, was available, none of the specimens are complete (Fig. 4a, b). Commonly, either the oral or apical surface is damaged or the specimen is partially entombed in limestone, preventing measurements. None of the specimens exhibited easily distinguishable apical systems and only one or two petals are partially visible, preventing measurements of petal length and plating. Genital pores were similarly difficult to distinguish. Five specimens with an intact oral surface allowed measurements of the distance between the peristome and periproct.

The 11 specimens measured by Arnold and Clark (1927, p. 28) and Hawkins (1927, p. 76) have similar dimensions to specimens in the present collection. The specimens measured by Arnold and Clark are slightly larger on the whole than the present sample, varying from 8.5 to 10.0 mm in length (mean 9.5 mm) and a height of 5.75–7.0 mm (mean 6.25 mm), giving a ratio of 0.6–0.7 height to length.

Family Neolaganidae Durham, 1954
Genus *Neolaganum* Durham, 1954

Type species Laganum archerensis Twitchell *in* Clark and Twitchell, 1915, pp. 161–162, pl. 75, figs. 1a–d, by original designation (Durham, 1954, p. 680, 1966, p. U475) from the Upper Eocene of the south-east USA (Smith and Kroh 2011).

Neolaganum sp. (Fig. 4c–e)

Material This description is based on one complete, but severely weathered specimen, RGM 791 288, part of a collection of 11 specimens, RGM 791 285 (with *F. jacksoni*), 791 287 (with *F. jacksoni*), 791 289-791 296.

Description Test ovate to subpentagonal in shape and very low. Size small to medium, length varying from 6.3 to 15.3 mm (mean 10.1 mm) and width 5.8 to 13.3 mm (mean 8.7 mm), giving a width to length ratio of 0.74–0.9 (mean 0.85). The height varies from 1.5 to 2.2 mm (mean 1.5 mm) giving a height to length ratio between 0.14 and 0.24 (mean 0.16).
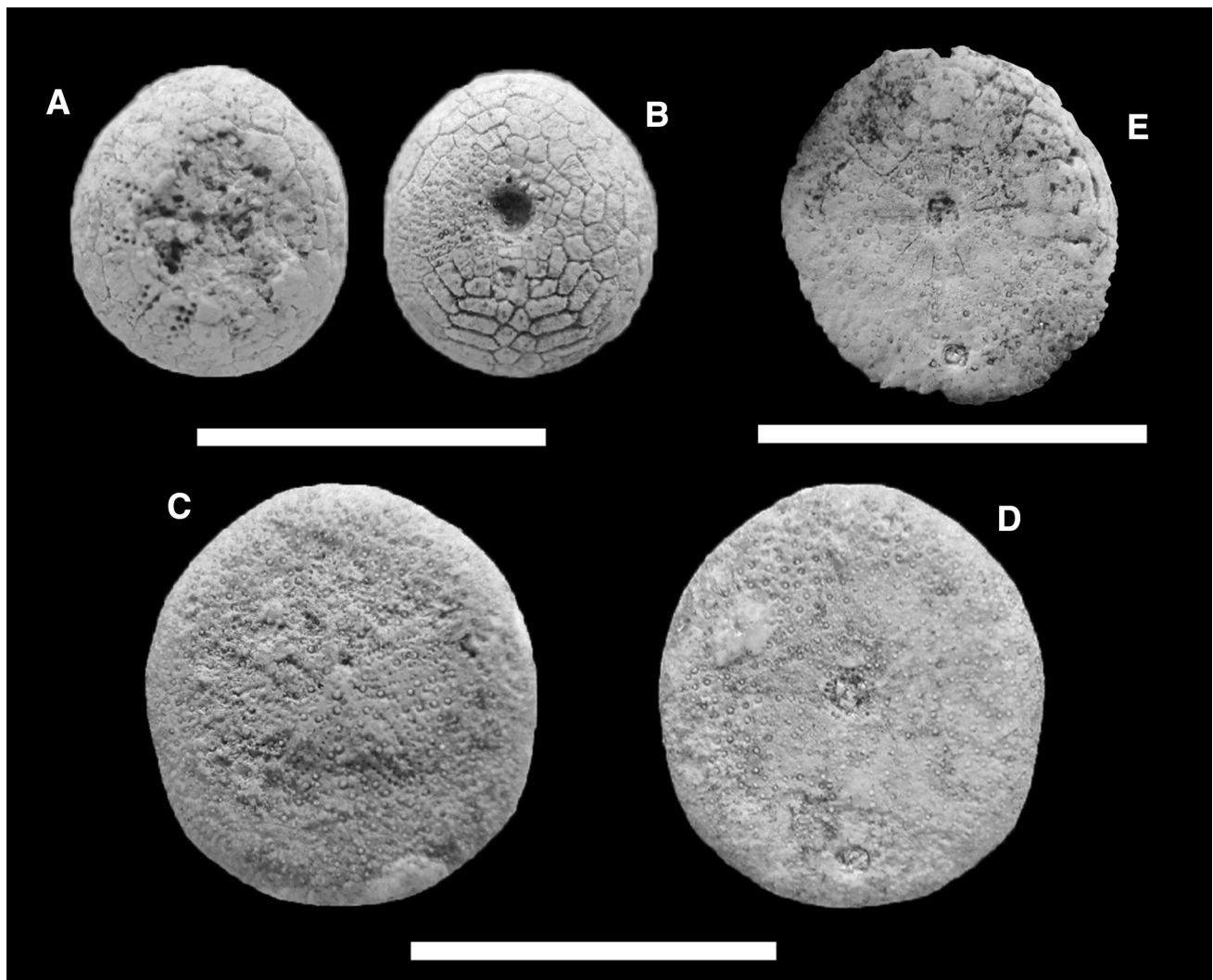
Fig. 4 Clypeasteroids from the Guys Hill Formation of Jamaica. RGM 791 278, *Fibularia jacksoni* Hawkins. **a** Damaged apical surface. **b** Oral surface. *Neolaganum* sp. RGM 791 288, apical (**c**) and oral views (**d**). **e** RGM 791 292, oral surface showing details of plating. Specimens uncoated. *Scale bars* represent 10 mm

Apical system slightly anterior to centre, raised, petals flush with surface; madreporite and genital pores not visible on any specimens. Upper surface of test slightly depressed into margin at end of petals. Petals closed, petal pore pairs not conjugate; petals extend halfway to ambitus from the centre of apical system.

Adoral surface flattened. Peristome slightly anterior, periproct small, rounded, located very close to posterior ambitus.

Remarks Of the 11 specimens, 3 are free of the limestone. Other specimens are partially entombed, with only the adoral surface visible. All specimens are severely weathered, but general outlines can be made out including the positions of the peristome and periproct. One specimen, RGM 791 288 (Fig. 4c, d), has partially visible petals,

allowing the non-conjugate pore pairs and closed petals to be distinguished. The subpentagonal outline of all the specimens is characteristic of neolaganids. The plating of the oral surfaces of RGM 791 285 and 791 292 are directly comparable to that of the type species (Durham 1954, fig. 2b; Fig. 4e herein).

The specimens from the Guys Hill Formation most closely resemble Upper Eocene *Neolaganum durhami* Cooke, 1959, from the south-east USA. The open petals and depressed apical surface with a slightly inflated margin are features typical of neolaganids. The specimens are also comparable to, but more ovate than, the similar *Cubanaster* Sánchez Roig, 1949. In *Neolaganum*, the slightly inflated margin and a raised apical system, which, in turn, is situated in a shallow depression on the aboral surface, is less eccentric in comparison to

Cubanaster, which has a deeper depression giving the margin a more inflated appearance. Additionally, the specimens described herein have some minor grooves on the oral surface leading to the peristome, a further characteristic of neolaganids (Durham 1955). Dixon and Donovan (1998b) briefly reviewed new records of neolaganids from the Eocene of Jamaica without adding any *Neolaganum* species.

Order Spatangoida L. Agassiz, 1840
Family Brissidae Gray, 1855
Genus *Eupatagus* L. Agassiz, 1847

Type species Eupatagus valenciennesi L. Agassiz, 1847, p. 9, by the subsequent designation of Pomel (1883, p. 28)

(Fischer 1966, p. U586) from the Recent of Australia (Smith and Kroh 2011).

Eupatagus alatus Arnold and Clark, 1927 (Fig. 5)
Synonymy See Kier (1984, p. 95).

Material RGM 791 297 (Fig. 5), 13 further tests all moderately well preserved, RGM 791 298-791 310, and 32 poorly preserved or broken tests, RGM 791 311. Even the best-preserved tests do not retain details of the fascioles.

Description (See also Arnold and Clark 1927, pp. 63, 64, pl. 13, figs. 4–7; Kier 1984, pp. 95–98, text-fig. 34, pl. 54, pl. 55, figs. 1, 2; Donovan 1993, pp. 401, 402, fig. 17.3, 17.4.) *Eupatagus* with a relatively low test; its broadest point posterior of centre; and with petals II and IV
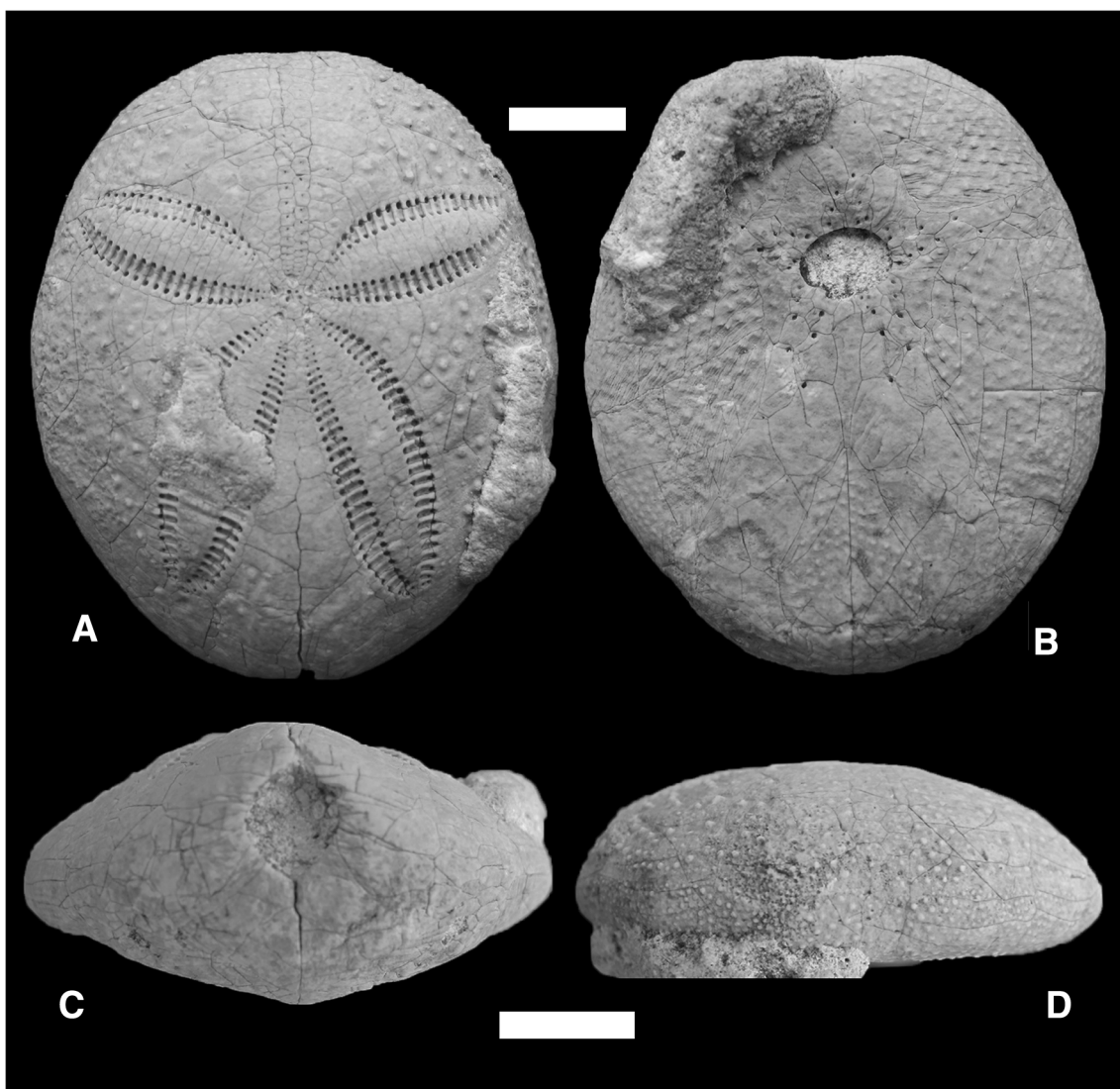

Fig. 5 *Eupatagus alatus* Arnold and Clark, RGM 791 297, from the Guys Hill Formation of Jamaica. **a** Apical view. **b** Oral view. **c** Posterior view. **d** Slightly oblique anterior view. Specimen uncoated. *Scale bar* represents 10 mm

extending towards the anterior ambitus, but terminating before reaching it. Test moderately large, rounded oval in outline, blunt at centre of anterior, length about 44–57 mm (mean 51 mm); width 74–84 % of length (mean 81 %) (Fig. 5a, b). Greatest width slightly posterior to apical system; height 33–37 % of length (mean 35 %); greatest height posteriorly, at anal cone. Apical system anterior; distance from anterior margin to centre of apical system 37–43 % length (mean 41 %); four genital pores, apical system ethmolytic with genital plate 2 separating posterior ocular plates. Anterior ambulacrum III not petaloid, pores small, non-conjugate anisopores, flush with test. Anterior petals (II and IV) moderately long, closing, almost extending to margin, angled towards anterior, petal length 29–38 % of length (mean 34 %). Interporiferous zones wide, tapering towards ends, feather-shaped, poriferous zone narrow. Posterior petals (V and I) long, 36–44 % length (mean 41 %), extending towards anal cone, petals closing distally. RGM 791 297 is 56 mm long, with 62 pore pairs in petal I; RGM 791 301 is 52 mm long, with 58 pore pairs in petal I. Interporiferous zones of petals I, II, IV and V slightly raised; pores strongly conjugate with furrow; inner pore circular, outer pore more oblique.

Peristome anterior of centre, distance from edge of anterior margin to anterior edge of peristome 27–30 % of length (mean 28 %). Periproct situated high on posterior truncation; opening higher than wide, not visible from above. Primary tubercles large apically, slightly smaller orally. RGM 791 297 with largest tubercles 1 mm in diameter, irregularly arranged among interambulacra on aboral surface; this same specimen has a fragment of the peripetalous fasciole visible, next to petal IV. Labrum long, narrow, extending posteriorly, approximately two-thirds past the fourth adjacent ambulacral plate. Plastron composed of four plates, two sternal and two smaller, post-sternal plates.

Remarks Previous reports of *Eupatagus alatus* have described an echinoid similar in size to the Thornton specimens, with a mean test length of 56 mm and a similar width, mean 83 % of length (Kier 1984). However, the broadest point of the test of the Thornton specimens is situated slightly posterior to the centre of the apical system, whereas in *E. alatus* the broadest point is central (Kier 1984). The apical systems resemble each other superficially; however, there are some further differences. The centre of the apical system is located more anteriorly in *E. alatus* with a mean 28 % of length to the anterior margin; in the Thornton specimens this is a mean 41 % of length. The anterior petals, II and IV, have similar dimensions, a mean 34 % of length in *E. alatus* and 32 % of length in the Thornton specimens. However, in *E. alatus* the petals stretch towards the dorsal ambitus at roughly 90° from ambulacrum III; in the Thornton specimens, petals II

and IV are angled more towards the anterior ambitus and terminate before reaching it, making them appear shorter. The main difference between *E. alatus* and specimens from Thornton was found to be the variation of their height to length ratios. *Eupatagus alatus* has a mean height to length ratio of 51 % (Kier 1984), but in the Thornton specimens the mean is 35 %, a large difference. The extension of the labrum differs, too; it extends to the middle of the third adjacent ambulacral plate in *E. alatus*, whereas in Thornton the labrum extends to two-thirds of the fourth adjacent ambulacral plate. However, despite all of these variances, the Thornton specimens are undoubtedly close to *E. alatus*, which has demonstrated a broad range of morphological variations, and are included therein with confidence.

Another similar Antillean taxon to Thornton *E. alatus* is *Eupatagus clevei* Cotteau, 1875, also described in Kier (1984). *Eupatagus clevei*, however, has a high test, albeit similar to that of *E. alatus*, at about 51 % of length. *Eupatagus antillarum* Cotteau, 1875, is similarly not conspecific with the Thornton specimens as its test is too high and its highest point is at the apical system, not posterior at the anal cone.

Eupatagus from the Middle Eocene of the southeastern USA includes *E. carolinensis* Clark *in* Clark and Twitchell, 1915, *E. wilsoni* Kier, 1980, *E. lawsonae* Kier, 1980, and *E. texanus* Zachos *in* Zachos and Molineux, 2003. *Eupatagus carolinensis* has shorter ambulacral petals and a significantly higher test, high and sloping anteriorly (Clark and Twitchell 1915, pp. 153, 154, pl. 71, figs. 3a–d, 4; Kier 1980, pp. 50, 51, fig. 24, pl. 20, figs. 1–6). *Eupatagus wilsoni* is also higher than the Thornton species, rounded in lateral view both anteriorly and posteriorly, and broad at about mid-length (Kier 1980, pp. 51–53, pl. 20, figs. 7–11). *Eupatagus lawsonae* is well rounded proximally, strongly tapered distally, a bun-like profile and relatively narrower ambulacral petals than the Thornton tests (Kier 1980, p. 53, pl. 21, figs. 1–4). *Eupatagus texanus* is diagnosed by Zachos (*in* Zachos and Molineux 2003, p. 504) as being large and fragile with widely divergent anterior petals; it also has long petals which do not close distally and is well rounded anteriorly. None of these is close to *E. alatus* from Thornton.

Similar and congeneric species to the Thornton tests were figured in Smith and Kroh (2011), including *E. rajasthanensis* Srivastava and Singh, 2008, and *E. rostratus* d'Archiac and Haime, 1853. The main difference between *E. rajasthanensis* and Thornton *E. alatus* is the sunken ambulacrum III which forms a shallow groove and its more raised test. *Eupatagus rostratus* has a very similar lateral view (test is low and flat dorsally) and its ambulacrum III is flush with the surface of the test; however, its tuberculation is very different (much larger and less). *Eupatagus rajasthanensis* and *E. rostratus* both come from the Eocene of India (Smith and Kroh 2011).
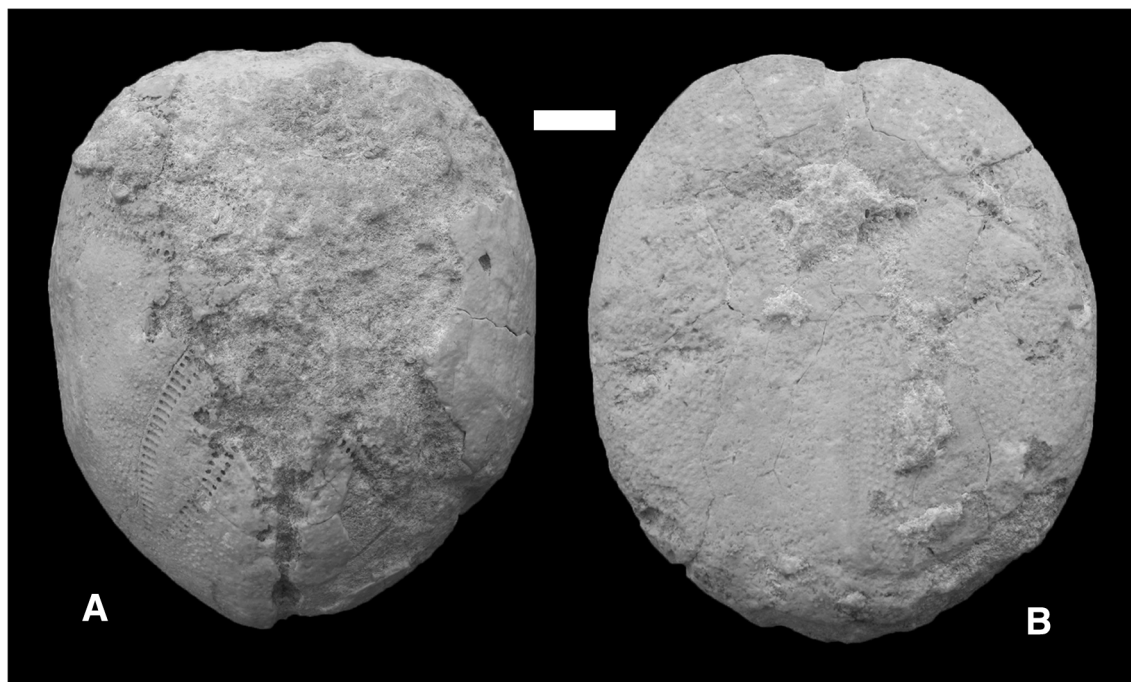
Fig. 6 *Eupatagus* sp. cf. *E. clevei* (Cotteau), RGM 791 312, from the Guys Hill Formation of Jamaica. **a** Damaged apical surface. **b** Oral view. Specimen uncoated. *Scale bar* represents 10 mm

Eupatagus sp. cf. *E. clevei* (Cotteau, 1875) (Fig. 6)

Material An incomplete specimen, RGM 791 312.

Description Test large, oval, broad and rounded, rectangular anteriorly with the anterior ambulacrum slightly infolded at the ambitus; more pointed posteriorly. Length is 95.1 mm; widest centrally, 79.8 mm; height, though incomplete, at periproct, 36.7 mm, which is situated posteriorly forming an anal cone. Ratios: height to length, 0.39; height to width, 0.84. Petals particularly broad. Petals IV and V partially visible; ambulcra III non-petaloid and forms a shallow groove, making the anterior ambitus slightly lobed. Petals IV and V closed, pore pairs conjugate, connected by shallow furrow, both inner and outer pores circular. Periproct posterior, higher than wide, teardrop-shaped, albeit poorly preserved. Peristome positioned anteriorly, wider than high; anterior edge of peristome approximately 21 mm from anterior ambitus. Sub-apical tubercles small, irregularly arranged among interambulacra. No fascioles preserved.

Remarks This test is unusually large for this collection with a gross morphology that distinguishes it from *E. alatus* (compare Figs. 5, 6). It is lacking the complete apical system and much of the surrounding apical surface (Fig. 6a); however, measurements of gross dimensions were made and its oral surface is fairly well preserved. There is also a difference in the height to length ratio, where *E. alatus* has a

mean ratio of 0.35 with a highest ratio of 0.37; RGM 791 312 reaches 0.39, a higher ratio. Furthermore, this *Eupatagus* has a more raised test overall, whereas in *E. alatus* from Thornton the tests are more wedge-shaped, with a very low anterior, making the lateral profile different.

There are some other likely candidates for close relationship with this specimen. The Cuban *Zanolettiaster herrarae* Sánchez Roig, 1952, probably a junior synonym of *Eupatagus clevei* (Cotteau, 1875) (Kier 1984, p. 98), is similar. Both species are approximately 100 mm long, have closed petals, a similar general outline with anterior lobes and a more pointed posterior. Furthermore, they are similar in lateral profile. Both specimens lack complete apical systems, but the partially visible petals do differ, extending to the ambitus in *Z. herrarae*, much further than in this Thornton *E. alatus*. The condition of the tests makes further comparison difficult and an oral view of *Z. herrarae* has not been figured (Sánchez Roig 1952, pl. 8; Kier 1984, pl. 61, figs. 5, 6). *Eupatagus clevei* Cotteau, 1875, is closest in gross morphology, with similar dimensions, to RGM 791 312.

Discussion

The Eocene echinoid fauna of Jamaica is particularly diverse (Donovan 2001). Echinoid diversity declined from the Late Eocene onwards (Fig. 7) and fewer tests are found

Fig. 7 Temporal distribution of fossil echinoids of Jamaica (after Donovan 2001, fig. 2; Donovan et al. 2007, fig. 4). The Eocene record is divided into three uneven parts: lowermost (=turbidites of the Richmond Formation); mid-Lower to mid-Middle (=Yellow Limestone Group); and overlying White Limestone Group
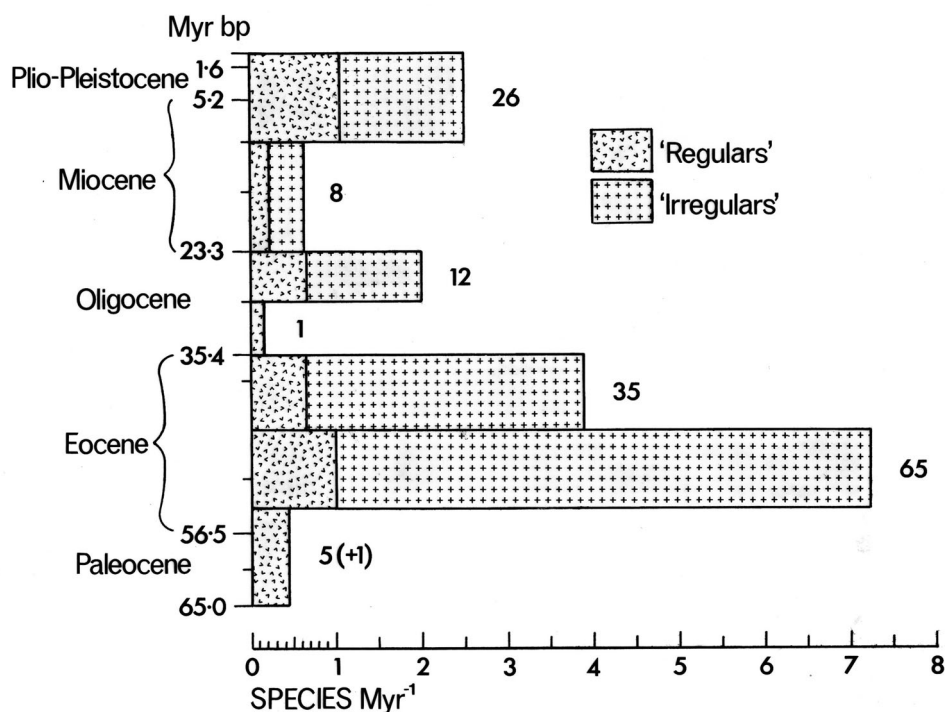
in younger strata. This is most probably a reflection, in part, of a preservation bias in the White Limestone Group (Middle Eocene to Middle Miocene) and related collection failure from these more well-lithified limestones (Donovan 2004).

Throughout the Paleocene and Eocene the climate was warm, with tropical temperatures extending into what is now Canada. The Paleocene/Eocene Thermal Maximum (PETM) has been attributed to various large-scale geological events, including volcanism, continental drift, orbital forcing (Prothero 1994) and, more recently, a Paleocene/Eocene impact event which led to a hypothesized 'Bolide summer', an extended period of warm temperatures (Cramer and Kent 2005). The sustained period of warm climate lasted well into the Eocene, and it was during this time that echinoid diversity in Jamaica and the wider Antilles reached its peak (Donovan 2001; Fig. 7 herein). Although there are various theories as to what caused the Late Eocene extinctions, they are commonly attributed to climatic changes; by the end of the Eocene the first Antarctic ice sheets had formed, lowering sea levels and changing weather patterns and ocean currents (McKinney and Oyen 1989; Prothero 1994; Budd 2000). Because Jamaica is located in the humid tropics, one might not expect large biotic fluctuations in response to variations in climatic conditions, as temperatures do not fluctuate much at this latitude. However, a decline in echinoid diversity by the Oligocene is apparent (Dixon and Donovan 1994, 1998a), likely reflecting changes in currents and primary

production; many echinoid genera and species from the Eocene were extinct by the Oligocene, replaced by taxa analogous to modern faunas by the Pleistocene (Donovan 1993, 2001; Donovan et al. 2007).

In the assemblage of Eocene echinoids from Thornton, the most common taxon is the spatangoid *E. alatus*, with a total of 46 tests and test fragments, followed by *Fibularia jacksoni* (32 tests and fragments) and *Oligopygus* sp. (48 tests and fragments). Other species include *Neolaganum* sp. (eleven tests), a single *Eupatagus* sp. cf. *E. clevei* and one regular echinoid, *Acanthechinus peloria*. The large number of irregular echinoids in this collection likely reflects a bias in preservation potential, due to life mode and morphology (Kier 1977; Smith 1984). The most notable absences are the large spines of cidaroids that form a conspicuous part of many Cenozoic assemblages in Jamaica (Donovan 1993). These are commonly the most prominent evidence of the presence of regular echinoids in an assemblage. We must conclude that they were truly absent from this fauna.

When comparing the present collection to known stratigraphic and palaeogeographic distributions of fossil echinoids from the Eocene of Jamaica, some interesting anomalies are apparent. In Jamaica, an *Oligopygus* close to *Oligopygus wetherbyi* de Loriol, 1888, was previously only known from the White Limestone Group, Swanswick Formation (Donovan 1993 p. 384). The Swanswick Formation was deposited in a high-energy shelf edge environment (Donovan 1993, 2004). *Oligopygus* sp. from the
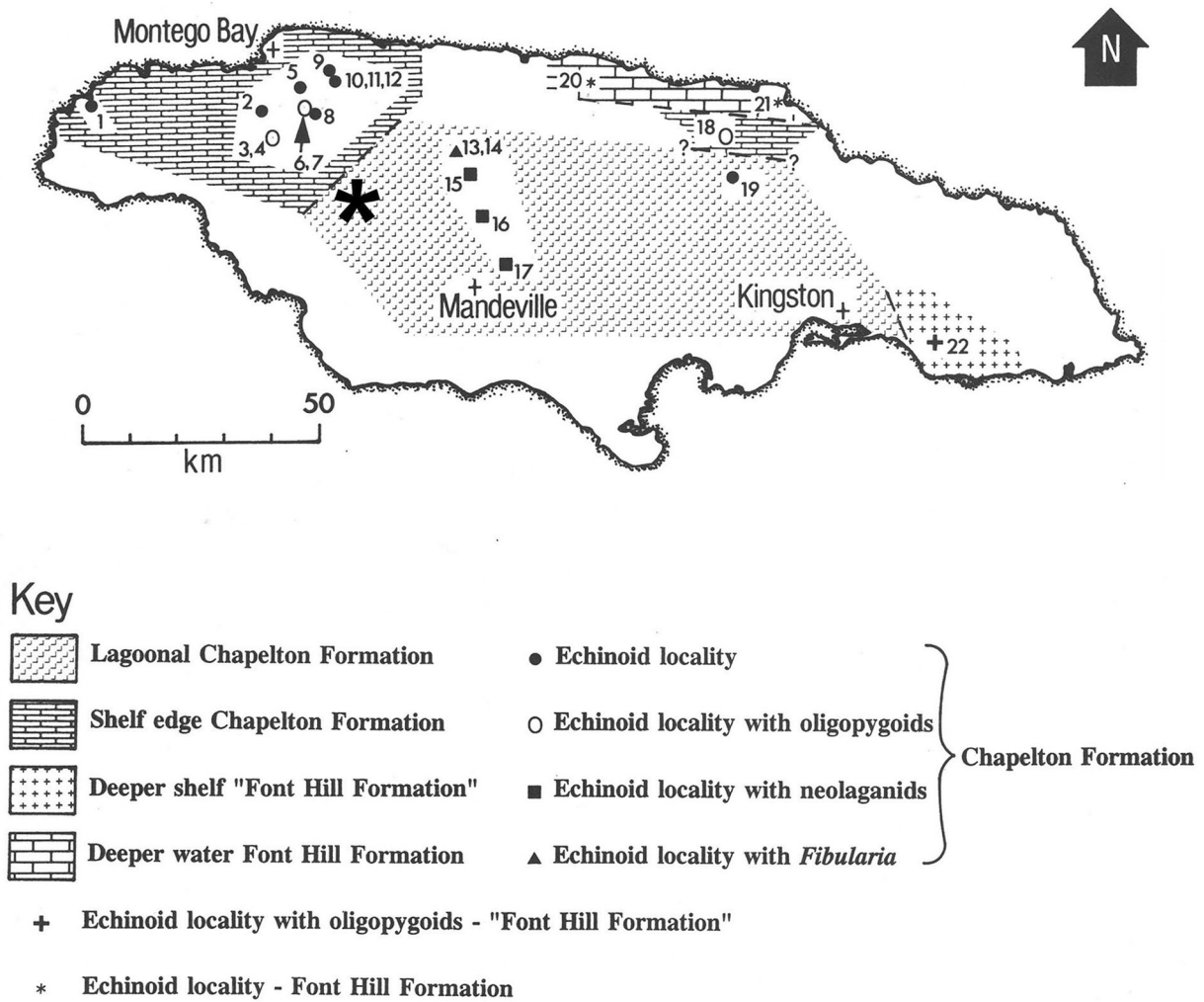
Fig. 8 Geographical distribution of echinoid localities of the Yellow Limestone Group in Jamaica (after Donovan et al. 2007, fig. 5; modified after Miller and Donovan 1996, text-fig. 4, but without the north–south elongation apparent in the original publication), based on time-averaged data sets of unequal sizes that were not necessarily precisely coeval. Key to localities (parishes in parentheses): *asterisk* Thornton, *1* Abingdon (Hanover), *2* Montpelier, *3* Seven Rivers, *4* Cambridge, *5* John's Hall, *6* Spring Mount, *7* Springfield/Welcome Hall, *8* Point, *9* Glasgow, *10* Leyden, *11* Ginger Valley, *12* Somerton (all parish of St. James), *13* Albert Town, *14* Freemans Hall, *15* Wait–a–Bit Cave (all parish of Trelawny), *16* south of Christiana (Manchester), *17* Peace River (Clarendon), *18* Lucky Hill and Gayle (St. Mary), *19* Guy's Hill (St. Catherine), *20* south of Mt. Zion (St. Ann), *21* Ceran Hill (St. Mary), *22* Easington and Yallahs River valley (St. Thomas). For more information on these localities, see Miller and Donovan (1996); for discussion of the formations of the Yellow Limestone Group, see Robinson (1988, 1994) and Robinson and Mitchell (1999)

present collection shows morphological differences to known tests from the Late Eocene of Curaçao. It is possible that these *Oligopygus* tests represent an intermediate step in oligopygoid morphology between *Oligopygus jamaicensis* Arnold and Clark, 1927, and *O. wetherbyi*, as the current specimens exhibit characteristics attributable to both species. Additionally, *Oligopygus jamaicensis* is known from the Early to Middle Eocene, similar to the *Oligopygus* fossils in the present collection.

Fibularia jacksoni and the neolaganids are known from the Troy Formation, deposited in a low-energy lagoon setting and ranging from mid-Middle to Late Eocene strata (Mitchell 2004, fig. 8; Donovan 2004, table 1). *Neolaganum* sp. has not been previously recorded from the Eocene of Jamaica and is otherwise known from the Eocene of southeastern North America. General life modes of neolaganids are similar, thus the palaeoenvironmental signals they present are similar (low-energy

lagoon setting). Oligopygoids do not commonly occur in association with *Fibularia* or neolaganids in Jamaican Eocene strata, although this distinction is not so marked elsewhere. Oligopygoids typically inhabit high-energy shelf edge settings, whereas *Fibularia* and neolaganids inhabit low-energy lagoonal settings. Curiously, in this collection *Fibularia,* neolaganids and oligopygoids occur in association together, possibly suggesting an extended habitat range for oligopygoids during the Early to Middle Eocene or, more probably, this locality represents an intermediate environment in which all three species flourished.

The common occurrence of *E. alatus* and *Oligopygus* sp. at this locality indicate a high-energy shelf edge setting (Donovan 1994); these taxa were locally common occurrence in the mid-Early to mid-Middle Eocene of Jamaica. If the presence of *Fibularia* and neolaganids in this assemblage cannot be attributed to postmortem transportation, perhaps these taxa, too, were more ubiquitous than previously thought.

Miller and Donovan (1996; see also Donovan et al. 2007) examined the palaeoenvironmental distribution of echinoids in the Yellow Limestone group of Jamaica (Fig. 8). Oligopygoids mainly occurred in shelf edge environments (also true in Georgia, but not Florida; B. D. Carter, written communication); clypeasteroids, namely neolaganids and *F. jacksoni,* were commonest in lower energy 'lagoonal' environments; and spatangoids and most cassiduloids were better represented in shelf edge environments. Thornton is the first site in Jamaica from which oligopygoids have been found in association with neolaganids and *F. jacksoni.* Localities with the former association are considered to be shelf edge, while the latter are 'lagoonal'. Interestingly, Thornton plots close to the boundary between these palaeoenvironments (Fig. 8), perhaps suggesting that it represents a transition zone between them.

In conclusion, this assemblage contains six echinoid species. The association of *F. jacksoni* and *Neolaganum* sp. with *Oligopygus* sp. has not been previously recorded from the Jamaican Eocene. This association is interesting because oligopygoids are considered to have preferred high-energy shelf edge settings, in contrast to *Fibularia* and neolaganids, which preferred low-energy lagoonal settings. This suggests a transitional setting for this locality, between shelf edge and lagoon. Of two species of *Eupatagus,* most are assigned to *E. alatus,* a common Eocene taxon in the tropical western Atlantic.

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