

ECHINODERMS OF THE PLIOCENE BOWDEN SHELL BED, SOUTHEAST JAMAICA

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The echinoderm fauna of the late Pliocene Bowden shell bed of southeast Jamaica is more diverse than that of any coeval unit in the Caribbean. The following echinoderm taxa have been identified from the Bowden shell bed: goniasterid or astropectinid asteroid sp. indet., ophiuroid sp. indet., and the echinoids *Eucidaris madrugensis* (Sánchez Roig, 1949), diademid sp. indet., *Arbacia* sp., *Echinometra* sp., *Tripneustes* sp., *Clypeaster* cf. *carrizoensis* Kew, 1914, scutelline sp. indet. and spatangoid sp. indet. Adult echinoids are invariably preserved as fragments; juvenile tests may have survived because of their low volume to surface area ratio, making them less prone to mechanical collapse. At the ordinal level, *Eucidaris* - diademid - *Echinometra* - arbaciid - toxopneustid - *Clypeaster* - scutelline - spatangoid echinoid faunas seem to have been the norm in the Caribbean during the Pliocene. Echinoids across the Pliocene-Pleistocene interval in the Caribbean region may follow a similar pattern of faunal turnover to that of benthic molluscs.

Key words — Bowden shell bed, Pliocene, Echinodermata, Asteroidea, Ophiuroidea, Echinoidea.

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INTRODUCTION

The known echinoid fauna of the Pliocene of Jamaica is sparse (Donovan, 1993). Donovan & Paul (1996) have recently augmented this fauna, otherwise based mainly on reports of more or less complete tests, in a preliminary report of the moderately diverse echinoderms from the late Pliocene Bowden shell bed of southeast Jamaica, the fauna of which is largely disarticulated. The purpose of the present paper is to document fully the fauna of the Bowden shell bed, which is now known to consist of at least one

species of asteroid, an ophiuroid, plus at least eight species of echinoid, making it the most diverse Pliocene echinoderm assemblage known from the Antillean region (Donovan & Paul, 1996).

The echinoids of the Pleistocene deposits of eastern Jamaica have been documented in detail (Donovan *et al.*, 1994b; Donovan & Portell, 1996; Donovan & Embden, 1996) and this analysis is extended into the Pliocene herein. Prior to the account of Donovan & Paul (1996), the only report of a fossil echinoid from Bowden was by Weisbord (1969, p. 309), who noted that, 'In the late Miocene [*Echinometra*] *lucunter* is reported from Bowden, Jamaica.' (The Bowden Formation was previously dated as Miocene; see Donovan, 1998). This specimen(s) has not been located by S.K.D. However, it remains uncertain if it truly came from the Bowden shell bed or even the Bowden Formation. For comparison, Caldwell (1966) recorded a needlefish jaw (subsequently re-identified as the claw of a callianassid crustacean; W.C. Blow *in* Clarke & Fitch, 1979), purportedly from the Bowden Formation, but the description of the

locality shows it to have been collected from an overlying unit, either the Old Pera beds (early Pleistocene) or the Port Morant Formation (late Pleistocene). Prior to Robinson's (1969) definition of the Bowden Formation *sensu stricto*, all of these units were 'lumped together' in a 'Miocene' Bowden Series (E. Robinson, pers. comm.). It should be noted that tests of *Echinometra*, assigned to *E. viridis* A. Agassiz, 1863, and *Echinometra?* sp., occur in the basal conglomerate of the Port Morant Formation (Donovan *et al.*, 1994b). It is considered at least possible, perhaps probable, that this is the horizon which yielded Weisbord's *E. lucunter* (Linné, 1758).

Specimens used in the present study are deposited in the collections of the Natural History Museum, London (BMNH EE 5209-EE 5230, all SEM stubs; and EE 5237-EE 5246) and the Florida Museum of Natural History, Gainesville (UF 67426-67437, 71283). Descriptive terminology of the echinoderm test follows Gale (1987a), Melville & Durham (1966), and Durham & Wagner (1966). The classification of echinoids is that of Smith (1981, 1984) and Smith & Wright (1993). Synonymy lists include reported occurrences in Jamaica only. Plates 1-4 illustrate specimens sputter coated with 60% gold-palladium and examined using a Leica 440 scanning electron microscope (SEM). All BMNH specimens were processed from bulk samples from unit 2 of the Bowden shell bed (*sensu* Pickerill *et al.*, 1998) unless otherwise stated. All specimens are from the Bowden shell bed unless indicated otherwise.

SYSTEMATIC PALAEOLOGY

Class Asteroidea de Blainville, 1830
Subclass Neoasteroidea Gale, 1987b
Family Astropectinidae Gray, 1840 or
Goniasteridae Forbes, 1841

Asteroid sp. indet.
Pl. 1, Fig. 2

1996 Astropectinid or goniasterid. — Donovan & Paul, p. 166, fig. 1G, table 1.

Material, localities and horizons — Thirteen marginal ossicles from the Bowden shell bed: BMNH EE 5213[1-4], EE 5214[1-3] and BMNH EE 5237[1-6]. EE 5213[1] was illustrated by Donovan & Paul (1996). A further ossicle, BMNH EE 5238, was collected from the Bowden Formation at section 5 of Pickerill *et al.* (1998), towards the top of the formation and over 1 m below the prominent micritic limestone horizon.

Remarks — No complete fossil asteroids have been found in the Jamaican rock record, but disarticulated marginal ossicles are locally common. Previous reports have mentioned specimens from the Upper Cretaceous, Eocene and Oligocene (Donovan *et al.*, 1993; Dixon *et al.*, 1994); they are also known from one Miocene locality (S.K.D., unpubl.

data). The first Pliocene asteroids known from the island are from the Bowden shell bed.

The precise taxonomic assignment of this small collection of marginal ossicles is problematic. The specimen figured by Donovan & Paul (1996) appears to be a typical astropectinid superomarginal (compare with specimens figured by Blake, 1973; J.W.M. Jagt, written comm.). With one possible exception, all of these specimens could conceivably have been derived from a single species. The figured specimen shows the typical facet morphology of these ossicles. Externally they are all smooth and unsculptured or, in at least one example (EE 5214[1]), perhaps weakly pitted. The only exception is the biggest specimen in lot EE 5237, which is broad with a weak, pustular external sculpture, the largest pustules being concentrated adjacent to the proximal and distal facets. This may indicate the presence of a second species, but, until more specimens are available, it is considered conservative to include all ossicles in one species under open nomenclature.

Asteroids are unknown from the Jamaican Pleistocene. Two Recent astropectinids known from the island are recorded from sandy bottoms. Notably, *Astropecten duplicatus* Gray, 1840 (1-550 m water depth) favours 'Soft sediment composed of sand or shell hash' (Hendler *et al.*, 1995, p. 73), suggesting a possible substrate preference for the species preserved in the Bowden shell bed.

Class Ophiuroidea Gray, 1840
Incerti ordinis

Ophiuroid sp. indet.
Pl. 1, Fig. 8

1996 Ophiuroid vertebral ossicles. — Donovan & Paul, p. 166, table 1.

Material — A single vertebral ossicle, BMNH EE 5212.
Remarks — Like asteroids, no complete fossil ophiuroids are known from the Jamaican rock record. Disarticulated vertebral ossicles have been recorded from the Oligocene and Pleistocene of the island (Donovan *et al.*, 1993; Dixon *et al.*, 1994); they are also known from the Miocene (R.W. Portell, pers. comm.). The Bowden vertebra differs from those previously described from Jamaica in having a streptospondylous, hourglass-shaped, 'ball-and-socket' articulation (G. Hendler, written comm.; compare with, for example, Mortensen, 1933, fig. 2). Smith *et al.* (1995, p. 236) noted this type of articulation in the Ophiocanopidae, Ophiobysinae, Hemieuryalinae and the euryalid groups. In the extant Caribbean shallower water fauna, these groups are mainly represented by gorgonocephalids and hemieuryalids (Hendler *et al.*, 1995).

Class Echinoidea Leske, 1778

Subclass Cidaroida Claus, 1880
 Order Cidaroida Claus, 1880
 Family Cidaridae Gray, 1825
 Genus *Eucidaris* Pomel, 1883

***Eucidaris madrugensis* (Sánchez Roig, 1949)**
 Pl. 1, Figs 1, 5-7, 9

- 1996 *Eucidaris madrugensis* (Sánchez Roig). — Donovan & Paul, p. 166, fig. 1C, table 1.
 1996 *Eucidaris madrugensis* (Sánchez Roig). — Donovan, p. 35, fig. 1A.
 in pr. *Eucidaris madrugensis* (Sánchez Roig). — Donovan, fig. 6.12B.

Material — 89 spines, UF 67434 (52 spines), BMNH EE 5211[1-4], EE 5229[1], EE 5230[1-4], BMNH EE 5246[1-28]; a genital plate (madreporite), BMNH EE 5218[1]; and 10 test plates/test fragments, BMNH EE 5219[1-3], EE 5245[1-7]. For a more complete synonymy, see Cutress (1980, p. 70).

Remarks — Spines of *Eucidaris* Pomel are locally a common component of Jamaican sedimentary deposits of late middle Eocene age and younger (Donovan *et al.*, 1991; Donovan, 1993). Cutress (1980) identified two nominal species from the fossil record of the Caribbean, *Eucidaris tribuloides* (Lamarck, 1816) and *E. madrugensis*. The former species is common in the Recent (Hendler *et al.*, 1995) and Pleistocene (Donovan & Emden, 1996; Table 1 herein) of the island, but *E. madrugensis* has only been identified in Jamaica from the Bowden shell bed (Donovan & Paul, 1996), where it forms a distinctive and abundant part of the echinoid fauna. Primary spines of this species have a low, ribbed crown with a central, raised boss and longitudinal rows of spinules typical of *Eucidaris*, but are distinctive in having some spinules developed as thorns, often arranged in circlets (Pl. 1, Figs 5-7).

The only Caribbean species with broadly similar spines is the approximately coeval *Prionocidaris cojimarensis* (Lambert & Sánchez Roig in Sánchez Roig, 1926), of Miocene-Pliocene(?) age (Cutress, 1980). However, spines of the latter taxon lack the typical *Eucidaris* crown and show a much broader range of morphologies than is seen in the Bowden shell bed. *Eucidaris madrugensis* is otherwise limited to the Miocene-Pliocene of Cuba and the Dominican Republic (Cutress, 1980; but see comments by Kier, 1992, p. 14).

Subclass Euechinoidea Bronn, 1860
 Order Diadematoida Duncan, 1889
 Family Diadematidae Gray, 1855

Diadematid sp. indet.
 Pl. 2, Figs 1, 6

- 1996 Diadematoid sp. indet. — Donovan & Paul, p. 166,

- fig. 1D, table 1.
 1996 Indeterminate diadematoid. — Donovan, p. 35, fig. 1B.
 in pr. Diadematoid. — Donovan, fig. 6.12D.

Material — 27 spines, UF 67433 (19 spines), BMNH EE 5216[1-7], EE 5229[2]; and one test plate, BMNH EE 5210[1].

Remarks — Diadematoids in the Bowden shell bed are represented by fragments of spines and rare test fragments, but there is little prospect of classifying these further without superior material (C.M. Gordon, 1990). However, the nature of the diadematoid test precludes the possibility that they will be preserved in the turbidite deposits (Pickering *et al.*, 1998) of the Bowden shell bed (Greenstein, 1991; Donovan & Gordon, 1993). Although unknown from articulated specimens in the Jamaican fossil record, the distinctive spines of diadematoids are now known from the early Palaeocene (Donovan & Veltkamp, 1992), late Pliocene, early Pleistocene (Donovan *et al.*, 1994b; Donovan & Emden, 1996) and late Pleistocene of the island (C.M. Gordon, 1990). Two species, *Diadema antillarum* (Philippi, 1845) and *Astropyga magnifica* A.H. Clark, 1934, are common in modern shallow water environments in the Caribbean (Hendler *et al.*, 1995).

Order Arbacioida Gregory, 1900
 Family Arbaciidae Gray, 1855
 Genus *Arbacia* Gray, 1835

***Arbacia* sp.**

Pl. 2, Figs 2, 8; Pl. 3, Figs 1-4, 6

- 1996 *Arbacia* sp. — Donovan & Paul, p. 167, table 1.
 1996 Juvenile regular echinoids incerti ordinis. — Donovan & Paul, p. 167, fig. 1E, F, table 1.
 1996 Toxopneustid fragments (*pars*). — Donovan & Paul, p. 167, table 1.

Material — Three tests, UF 67430, BMNH EE 5215 [1, 2]; and two test fragments, BMNH EE 5226 [1, 2]. For comment on possible *Arbacia* spines, see *Tripneustes* sp. below.

Remarks — UF 67430 is only moderately preserved (unfortunately, it readily absorbed glue in being mounted for SEM) and small in size (= juvenile?). However, it is apparently an *Arbacia*, a genus common in the Neogene of the southeastern USA and Caribbean (Cooke, 1959; de Buissonjé, 1974; Lewis & Donovan, 1991). Other specimens attributed to *Arbacia* herein include certain test fragments from the adoral region (note buccal notches; Pl. 2, Figs 2, 8) and two further, small, juvenile tests (Pl. 3, Figs 2-4, 6). That the latter are, indeed, juveniles is shown by the absence of genital pores (Pl. 3, Figs 3, 4) and the gaps between plate sutures within plate columns (Pl. 3, Fig. 2). The smaller specimen (Pl. 3, Figs 4, 6) appears to have single pores, not pore pairs, in the ambulacral regions. BMNH EE

5215[1, 2] are not dissimilar to some *Lytechinus* species, such as *Lytechinus williamsi* Chesher, 1968, one of four species of extant Western Atlantic *Lytechinus* (for further comment on this genus, see *Tripneustes* sp.). However, there appears to be a weakly developed, granular sculpture present interradially, and on the genital and ocular plates, in the smallest tests (Pl. 3, Figs 2-4, 6); also note what appears to be a similar sculpture on the smaller test fragment (Pl. 2, Fig. 8). This is at least reminiscent of sculpture seen in Pliocene *Arbacia improcera* (Conrad, 1843) and morphologically similar, coeval species (see Lewis & Donovan, 1991).

Assuming that the three juvenile tests were truly derived from the same species, then they represent a growth series from BMNH EE 5215[2] (Pl. 3, Figs 4, 6) through BMNH EE 5215[1] (Pl. 3, Figs 2, 3) to UF 67430 (Pl. 3, Fig. 1). The smallest test is single-pored, but pore pairs have developed in the specimen of intermediate size. Only the largest test has developed typically arbacioid naked zones in the interambulacra.

This is only the third species of arbaciid recognised from the Jamaican fossil record, after the late Cretaceous *Goniopygus supremus* Hawkins, 1924, and an indeterminate species from the early Pleistocene (Donovan & Embden, 1996). Extant *Arbacia punctulata* (Lamarck, 1816) has not been recognised from modern shallow water environments of Jamaica (J.D. Woodley, pers. comm.).

Order Echinoida Claus, 1876
Family Echinometridae Gray, 1825
Genus *Echinometra* Gray, 1825

***Echinometra* sp.**
Pl. 2, Fig. 7

1996 *Echinometra* sp. — Donovan & Paul, p. 167, table 1.

Material — An ambulacral plate with an arc of at least five pore pairs, BMNH EE 5210[2].

Remarks — This single ambulacral plate is the only evidence of the presence of *Echinometra* in the Bowden fauna (compare Pl. 2, Fig. 7 with Gordon & Donovan, 1992, fig. 2A), although some spines may have been derived from this genus (see below). C.M. Gordon (1991) discussed why *Echinometra* has an apparently poor fossil record in the Caribbean, despite having a relatively robust test; however, it is locally common as disarticulated elements (Gordon & Donovan, 1992). As noted above, *Echinometra lucunter*, noted from Bowden by Weisbord (1969), was probably from the basal Port Morant Formation. Fossil *Echinometra* in Jamaica is best known from the Pleistocene, but elsewhere in the region it is also recorded from the Oligocene and Miocene (Sánchez Roig, 1949; W.A. Gordon, 1963; Poddubiuk & Rose, 1985). Extant *E. lucunter* and *E. viridis* are common components of hard substrate, shallow water

faunas throughout the region (Hendler *et al.*, 1995). The Bowden shell bed specimen is (at least superficially) closer to *E. viridis*, which has its pore pairs arranged in arcs of five (Donovan, 1993, p. 382).

Family Toxopneustidae Troschel, 1872
Genus *Tripneustes* L. Agassiz, 1841

***Tripneustes* sp.**
Pl. 2, Fig. 3

1996 Toxopneustid fragments (*pars*). — Donovan & Paul, p. 167, table 1.

Material — 28 ambulacral fragments, BMNH EE 5226[3], BMNH EE 5227[1, 2], BMNH EE 5239[1-25]; and 13 interambulacral fragments, UF 67428, BMNH EE 5240[1-12]. BMNH EE 5209[1] is a rotula probably derived from a toxopneustid (compare Pl. 1, Fig. 3 with C.M. Gordon, 1990, text-fig. 2-26). 115 spines (Pl. 2, Figs 4, 5) may be derived from *Arbacia* sp. and/or *Echinometra* sp. and/or *Tripneustes* sp.; UF 67435 (85 spines), BMNH EE 5218[2], EE 5229[3], EE 5241[1-28]. A keeled tooth, BMNH EE 5209[2], is probably derived from *Tripneustes* sp. or *Echinometra* sp.

Remarks — The following comments by Mortensen (1943, p. 383) were of particular relevance in identifying the toxopneustid fragments of the Bowden shell bed: 'The simplest [toxopneustid] ambulacral type is found in the [genus] ... *Lytechinus* [amongst others] ... the plates being trigeminate, each with a primary tubercle. The pore arcs are more or less oblique ... Trigeminate ambulacral plates are found also in ... *Tripneustes* [amongst others], but here a primary tubercle is found only on every second or third (or fourth) plate (except the adoral plates which have a primary tubercle each). This results in the plates being lower than where each plate carries a primary tubercle, and the pore-arcs being more horizontal, and the pore pairs becoming more separated from each other, so as to form three separate vertical series ... This is carried to an extreme in *Tripneustes*, where even the original trigeminate plates become partly occluded from the midline of the ambulacrum and combine to form pseudo-polyporous plates ...'. Fragments of toxopneustid test from the Bowden shell bed (Pl. 2, Fig. 3) are typical of *Tripneustes*. Indeed, the arrangement of pore pairs is at least close to that seen in the extant Caribbean *Tripneustes ventricosus* (Lamarck, 1816) (compare Pl. 2, Fig. 3 with Mortensen, 1943, figs 239c, 299a).

The only other Pliocene toxopneustids noted from the Caribbean region are *Lytechinus variegatus* (Lamarck, 1816) and *Tripneustes* cf. *ventricosus* (Lamarck) from Venezuela. The former record is based on two fragmentary tests (Cooke, 1961, pl. 4, figs 1, 2), while the latter is based on four fragments of test (Weisbord, 1969, pl. 15, figs

6-13). It is probable that Pliocene members of this family are more widespread within the Antillean region than is recognised, but the generally fragmentary preservation probably discourages identification. The two common toxopneustid genera in the Caribbean at the present day are *Lytechinus* and *Tripneustes* (Hendler *et al.*, 1995).

Cohort Irregularia Latreille, 1825
 Order Clypeasteroidea A. Agassiz, 1872
 Suborder Clypeasterina A. Agassiz, 1872
 Family Clypeasteridae L. Agassiz, 1835
 Genus *Clypeaster* Lamarck, 1801

***Clypeaster cf. carrizoensis* Kew, 1914**

Fig. 1

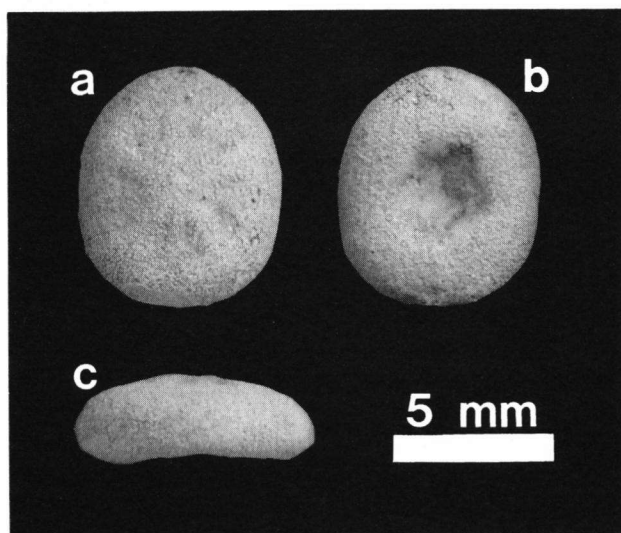


Fig. 1. *Clypeaster cf. carrizoensis* Kew, 1914, UF 71283, a - apical view, b - oral view, c - lateral view (anterior towards left). Specimen whitened with ammonium chloride sublimate.

Material — A single juvenile test, UF 71283. For discussion of clypeasteroid fragments, see scutelline sp. indet., below.

Remarks — The juvenile test from the Bowden shell bed is close in gross morphology to the ‘*cotteau*’ morphotype of Rose & Poddubiuk (1987) (compare Fig. 1 herein with Cooke, 1959, pl. 12, figs 1-3). There are at least ten nominal species of *Clypeaster* known from the Pliocene of the Caribbean region (Donovan & Paul, 1996, table 1). Of these, only *Clypeaster carrizoensis* Kew, illustrated by de Buissonjé (1974, p. 240, pl. 11, figs 5-7) from Curaçao, has the same broadly open petals and gross morphology seen in

the Bowden specimen. This adds yet another nominal *Clypeaster* to the Jamaican fossil fauna (Donovan & Portell, 1996).

Suborder Scutellina Haeckel, 1896
 Incertae familiae

Scutelline sp. indet.
 Pl. 3, Figs 5, 8; Pl. 4, Fig. 2

- 1996 Lunulate scutelline gen. et sp. indet. — Donovan & Paul, p. 167, fig. 1A, B, table 1.
- 1996 Juvenile scutelline clypeasteroid. — Donovan, p. 35, fig. 2.

Material — Two juvenile tests, UF 67429 and 67431; plus fragments of tests; BMNH EE 5217, UF 67432 and 67436. There are very numerous fragments of clypeasteroid, including many that are obviously scutelline, in BMNH EE 5220[1-4], EE 5224[1-4] (Pl. 3, Fig. 7), EE 5225[1-4], EE 5243 (numerous, larger fragments of test, mainly scutelline) and EE 5244 (numerous smaller fragments of test).

Remarks — The Bowden shell bed scutelline clypeasteroid is best recognised from low ambital fragments with rarely preserved parts of lunules (Pl. 4, Fig. 2). Comparison with complete tests of the approximately coeval *Encope homala* Arnold & Clark, 1934, from Jamaica (Donovan *et al.*, 1994a) suggests that they are not conspecific. Rare juvenile clypeasteroids from Bowden, always with a poorly preserved apical region, are low, button-like and are presumed to be conspecific with the fragments in the shell bed, although they are too small to have developed lunules (Pl. 3, Figs 5, 8). Nominal, coeval scutellines from elsewhere in the Caribbean (Donovan & Paul, 1996, table 2) are limited to *Encope* spp.; however, the Bowden scutelline does not appear to belong to this genus.

The majority of test fragments listed above are scutelline in origin, particularly those from the ambital region, although some of the smaller, more nondescript fragments may be derived from *Clypeaster cf. carrizoensis* Kew. It is interesting to note that, despite their high preservation potential (Kier, 1977; Donovan, 1991; Greenstein, 1993), mature clypeasteroid echinoids in the Plio-Pleistocene succession of the Bowden area are invariably preserved as fragments, suggesting long residence time of dead tests in the sea floor rather than catastrophic entombment of live specimens. At least some breakage of specimens is certainly due to post-mortem transport, based on sedimentological evidence, in both the Bowden shell bed (Pickerill *et al.*, 1998) and the overlying Old Pera beds (Donovan *et al.*, 1994b).

Order Spatangoida Claus, 1876
 Incertae familiae

Spatangoid sp. indet.
Pl. 1, Fig. 4; Pl. 4, Figs 1, 3, 4

- 1996 Spatangoid sp. indet. — Donovan & Paul, p. 167, table 1.
in pr. Indeterminate spatangoid. — Donovan, fig. 6.14C.

Material — Numerous test fragments, BMNH EE 5221, EE 5222[1-3], EE 5223[1-3], EE 5228, EE 5242 (numerous specimens), UF 67426 (2 fragments), UF 67427 (2 fragments); and six radioles, BMNH EE 5218[3], UF 67437.

Remarks — That this spatangoid followed a burrowing habit is indicated by common test fragments preserving fascioles (Pl. 4, Fig. 1); ambulacrum III (anterior) with pores indicating the presence of tube feet adapted for constructing a respiratory funnel (Pl. 4, Fig. 3; compare with Smith, 1980); and rare fragments of sunken ambulacral petals (Pl. 4, Fig. 3). The only apical system so far identified includes three genital pores. This arrangement is unknown from any of the nominal Pliocene spatangoids, including various brissids and schizasterids, hitherto identified from the region (Donovan & Paul, 1996, table 2). However, McNamara (in press) has noted intraspecific variation in the number of gonopores in an extant Australian *Schizaster*, suggesting that a genetic relationship may nevertheless be possible between the Jamaican material and coeval specimens from elsewhere in the region.

Although referred to a single species, the range of test thicknesses and variations in tuberculation shown by the Bowden shell bed spatangoid fragments may indicate that more than one taxon is present. Partial tests of spatangoids have been collected from the overlying Bowden Formation, and are awaiting preparation (Donovan & R.W. Portell, research in progress).

DISCUSSION

Two distinct preservational styles are shown by echinoid specimens in the Bowden shell bed. Only juveniles occur as complete tests, begging the question - were live adults not present in the original fauna or were they all destroyed by transport in the turbidity currents? It is already known that tests of small echinoids can survive transport and deposition as part of a turbidite (see, for example, Donovan & Pickerill, 1993), so the occurrence of juveniles (at least three out of the eight species) is perhaps not surprising. Although 'fresh' tests of mature echinoids that were tumbled by Kidwell & Baumiller (1990) showed only slow mechanical breakdown, this would presumably have been greatly accelerated under the more abrasive conditions of turbidite deposition. Therefore, it is at least probable that the fragmentary echinoid debris documented herein is a mixture of remains representing specimens that were both alive and dead at the time of deposition, the former being broken up during transport. Fragments derived from 'live' echinoids may be represented by test fragments broken

across plate boundaries (such as Pl. 2, Figs 2, 8), although some of this breakage certainly represents damage during post-collection preparation, while complete, disarticulated plates were probably derived from long dead specimens (for example, Pl. 2, Fig. 3; Pl. 3, Fig. 7) (Smith, 1984, pp. 17-19). Juvenile tests may have survived because of their low volume to surface area ratio when compared with adults, making them less prone to mechanical collapse; it is perhaps significant that the only test to retain spines (Pl. 3, Figs 4, 6) is also the smallest.

At the level of echinoid order, the fauna of the Bowden shell bed is more diverse than that of any other Pliocene stratigraphic unit in the Caribbean region (Donovan & Paul, 1996, table 2). The paucity of known Pliocene echinoderms noted for Jamaica (Donovan, 1993) seems to extend to the rest of the region. However, as noted by Donovan & Paul (1996), comparison of the Bowden shell bed echinoids with coeval Caribbean faunas does suggest some similarities. Clypeasteroids and spatangoids are the most widespread groups. Nominal clypeasteroids are limited to *Clypeaster* spp. and the scutelline *Encope* spp. Spatangoids include various brissids and schizasterids; the fragments from Bowden suggest that the Jamaican species, too, was a deep burrower. Regular echinoids are poorly known and are mainly *Eucidaris* spp., a taxon that is easily identified from its large, distinctive spines (Cutress, 1980). Venezuelan toxopneustids have been assigned to extant Caribbean species. Only the Bowden shell bed seems to include diadematoids, but other faunas have not been examined for microscopic fragments. *Echinometra* is known from complete tests in Jamaica and Curaçao. At the ordinal level, it therefore seems probable that *Eucidaris* - diadematoid - *Echinometra* - arbaciid - toxopneustid - *Clypeaster* - scutelline - burrowing spatangoid echinoid faunas may have been the norm for the Caribbean during the Pliocene.

Table 1 illustrates the distribution of known echinoid taxa in the Pliocene to Pleistocene interval of Jamaica, in rocks representing a number of depositional environments. At the level of echinoid order/family, the fauna of the Bowden shell bed (although almost certainly including species from a range of palaeoenvironments) shows good agreement with that seen in Jamaican Pleistocene deposits from both shallow and deeper water shelf environments; indeed, a similar association of higher taxonomic groups is seen in the modern shallow-water fauna of the Caribbean (Hendler *et al.*, 1995). Those groups that are noticeable common throughout this range are *Eucidaris*, diadematids, *Echinometra*, *Clypeaster*, scutellines and spatangoids. However, the rare species (*Eucidaris madrugensis*, *Clypeaster* cf. *carrizoensis*) from the Bowden shell bed that are recognisable to the level of species, however tentatively, differ from those of the same genus that are common throughout the Pleistocene. Although the data available from Bowden and elsewhere (Donovan & Paul, 1996, table 2) are far from perfect, there is no reason to doubt that echinoids across the Pliocene-Pleistocene interval in the

Caribbean region may follow a pattern of faunal turnover similar to that shown by the benthic molluscs (Jackson *et al.*, 1993; Allmon *et al.*, 1993).

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	PLIO	P-P	PLEISTOCENE			
			EARLY		LATE	
	BSB	RHB	Man	OPB	PMF	FaF
Order CIDAROIDA						
<i>Stylocidaris affinis</i>	-	-	+	-	-	-
<i>Cidaris (Tretocidaris) bartletti</i>	-	-	+	+	-	-
<i>Eucidaris madrugensis</i>	+	-	-	-	-	-
<i>Eucidaris tribuloides</i>	-	+	+	+	+	+
Order DIADEMATOIDA						
Diadematiid sp. indet.	+	-	+	+	-	+
Order PHYMOSOMATOIDA						
<i>Arbacia</i> sp.	+	-	-	-	-	-
Arbaciid sp. indet.	-	-	+	-	-	-
Order TEMNOPLEUROIDA						
<i>Lytechinus</i> sp. indet.	-	-	-	-	-	?
<i>Tripneustes</i> sp. indet.	+	-	-	-	-	?
Order ECHINOIDA						
<i>Echinometra lucunter</i>	-	-	-	-	-	+
<i>Echinometra viridis</i>	-	+	-	-	+	+
<i>Echinometra</i> sp. indet.	+	-	-	-	+	+
Order HOLECTYPOIDA						
<i>Echinoneus cyclostomus</i>	-	-	+	-	-	-
Order CASSIDULOIDA						
<i>Echinolampas depressa</i>	-	-	+	-	-	-
Order CLYPEASTEROIDA						
<i>Clypeaster</i> cf. <i>carrizoensis</i>	+	-	-	-	-	-
<i>Clypeaster lamprus</i>	-	-	+	-	-	-
<i>Clypeaster rosaceus</i>	-	+	-	+	-	-
<i>Clypeaster subdepressus?</i>	-	-	-	+	-	-
<i>Encope homala</i>	-	+	-	-	-	-
Scutelline sp. indet.	+	-	-	-	+	-
Clypeasteroid sp. indet.	-	-	-	+	-	+
Order SPATANGOIDA						
<i>Meoma ventricosa</i>	-	-	-	+	-	-
<i>Paleopneustes cristatus</i>	-	-	+	-	-	-
<i>Schizaster doederleini</i>	-	-	-	-	+	-
Spatangoids sp. indet.	+	+	+	-	-	+
Incerti ordinis						
Indeterminate regulars	-	-	+	+	-	+

Table 1. Stratigraphic distribution of the Plio-Pleistocene echinoids of Jamaica (expanded after Donovan & Embden, 1996). Key — PLIO = Pliocene; P-P = Plio-Pleistocene; BSB = Bowden shell bed; RHB = Round Hill beds, August Town Formation (nearshore siliciclastics/limestones); Man = Manchioneal Formation (including Navy Island Member) (deeper water limestones); OPB = Old Pera Beds (siliciclastics); PMF = Port Morant Formation (siliciclastics); FaF = Falmouth Formation (raised reef); + = present; - = absent.

PLATE 1

Asteroids, ophiuroids and echinoids of the Pliocene Bowden shell bed, Jamaica.

Figs 1, 5-7, 9. *Eucidaris madrugensis* (Sánchez Roig, 1949), 1 - BMNH EE 5218[1], madreporite, x 25; 5 - primary spine, BMNH EE 5230[1], x 18; 6 - primary spine, BMNH EE 5211[1], x 20; 7 - primary spine, BMNH EE 5230[2], x 18; 9 - interambulacral plate, BMNH EE 5219[1], x 25.

Fig. 2. Astropectinid or goniasterid asteroid sp. indet., BMNH EE 5214[1], profile of marginal ossicle, x 22.

Fig. 3. Toxopneustid? sp., BMNH EE 5209[1], rotula, x 20.

Fig. 4. Spatangoid sp. indet., BMNH EE 5218[3], spine, x 14.

Fig. 8. Ophiuroid sp. indet., BMNH EE 5212, proximal surface, x 24.

PLATE 1

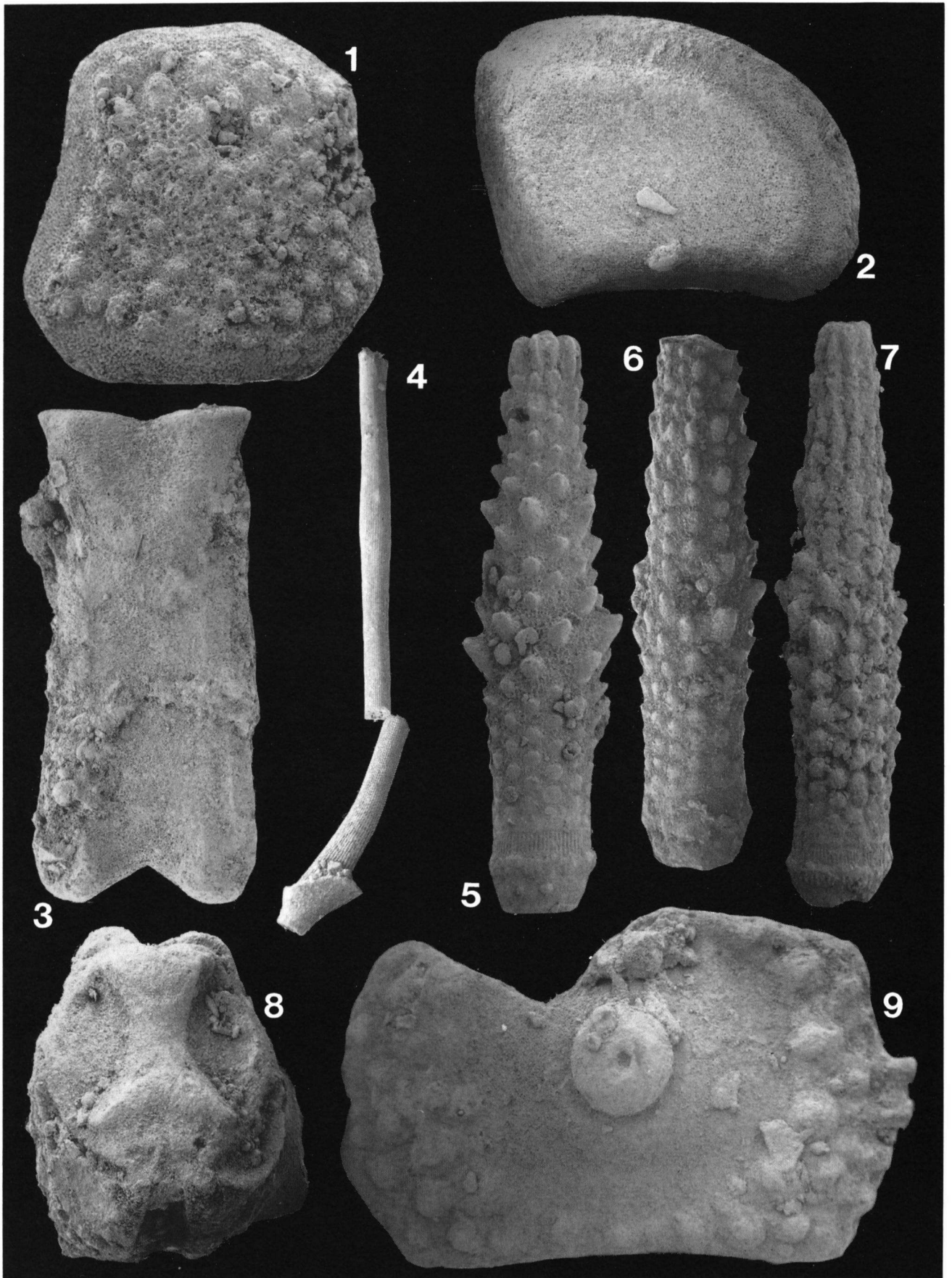


PLATE 2

Echinoids of the Pliocene Bowden shell bed, Jamaica.

- Figs 1,6. Diadematid sp. indet., 1 - BMNH EE 5216[1], spine, x 18; 6 - BMNH EE 5210[1], interambulacral (?) plate, x 18.
Figs 2, 8. *Arbacia* sp., 2 - BMNH EE 5226[1], x 14; 8 - BMNH EE 5226[2], x 30.
Fig. 3. *Tripneustes* sp., BMNH EE 5227[1], fragment of ambulacrum, x 12.
Figs 4,5. Indeterminate regular echinoid spines, 4 - BMNH EE 5229[3], x 7; 5 - BMNH EE 5218[2], x 20.
Fig 7. *Echinometra* sp., BMNH EE 5210[2], ambulacral plate, x 25.

PLATE 2

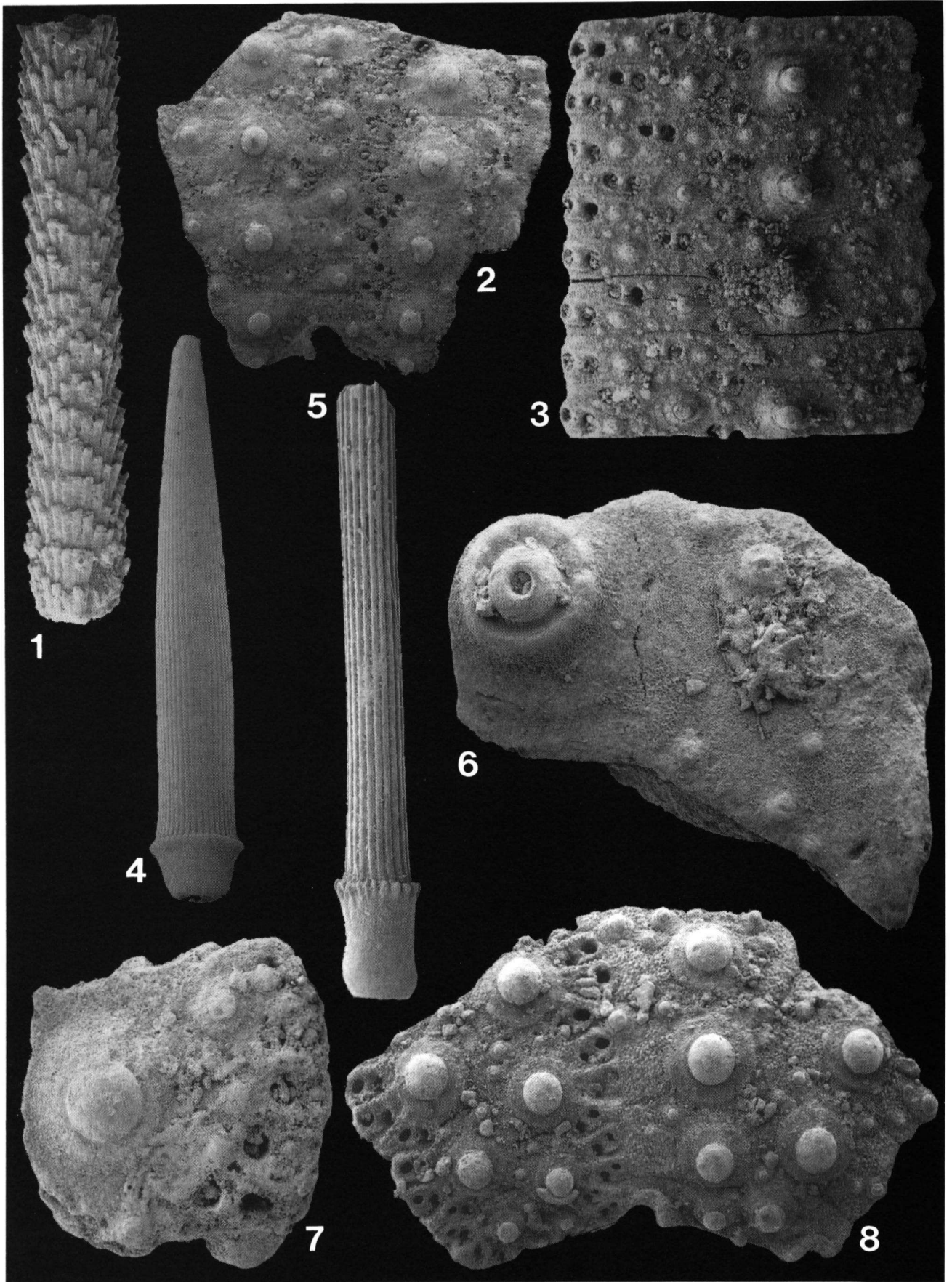


PLATE 3

Echinoids of the Pliocene Bowden shell bed, Jamaica.

Figs 1-4, 6. *Arbacia* sp., 1 - UF 67430, apical view, x 19; 2, 3 - lateral view (interambulacrum 4 centre) and apical view of BMNH EE 5215[1], x 38 and x 30, respectively; 4, 6 - apical view and lateral view (interambulacrum centre; note single ambulacral pores) of BMNH EE 5215[2], x 38 and x 48, respectively.

Figs 5, 8. *Scutellina* sp. indet., juvenile tests, 5 - UF 67429, oral surface, x 25; 8 - UF 67431, apical surface (petaloid region not preserved), x 40.

Fig. 7. *Scutellina* ? sp. indet., BMNH EE 5224[1], test fragment, x 25.

PLATE 3

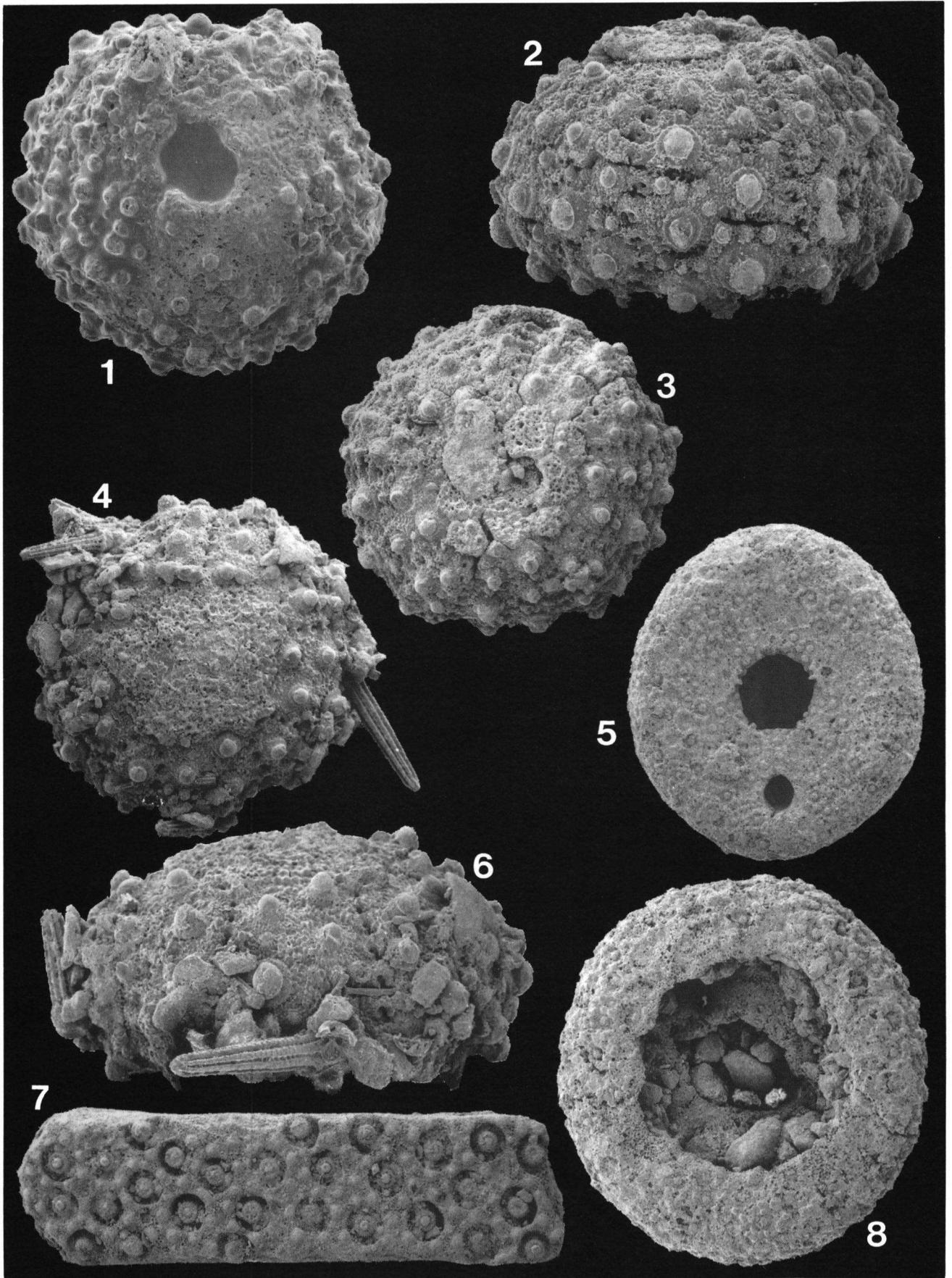


PLATE 4

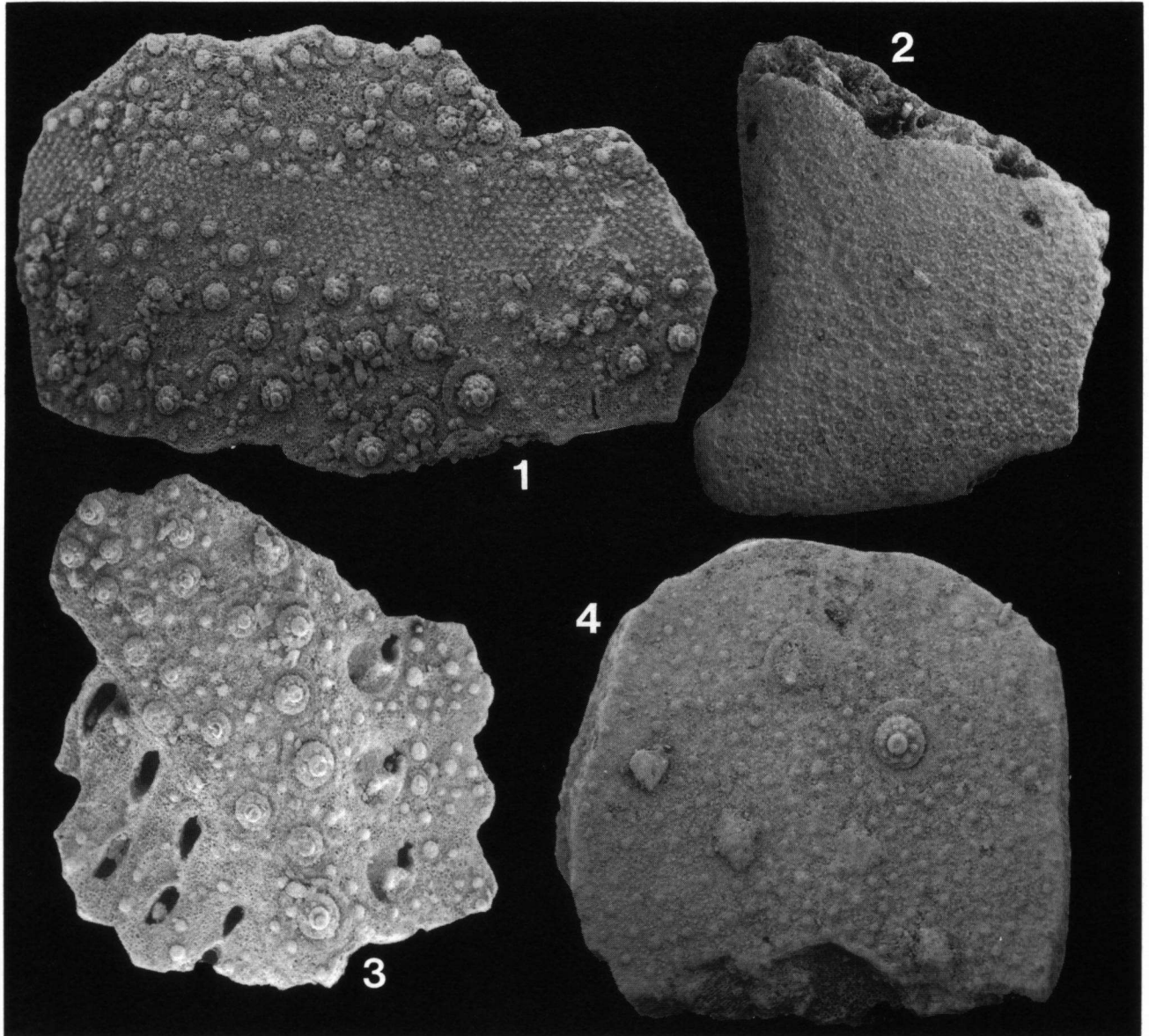


PLATE 4

Echinoids of the Pliocene Bowden shell bed, Jamaica.

Figs 1, 3, 4. *Spatangoid* sp. indet., 1 - BMNH EE 5222[1], test fragment with fasciole, x 20; 3 - BMNH EE 5222[2], fragment from adjacent to apical system (anterior towards top of page), showing ambulacra III (right) and IV, and interambulacrum 3, x 18; 4 - BMNH EE 5221, indeterminate test fragment, x 12.

Fig. 2. *Scutelline* sp. indet., BMNH EE 5217, ambital fragment of test with edge of lunule (left), x 12.