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Pleistocene echinoids from Tobago, West Indies

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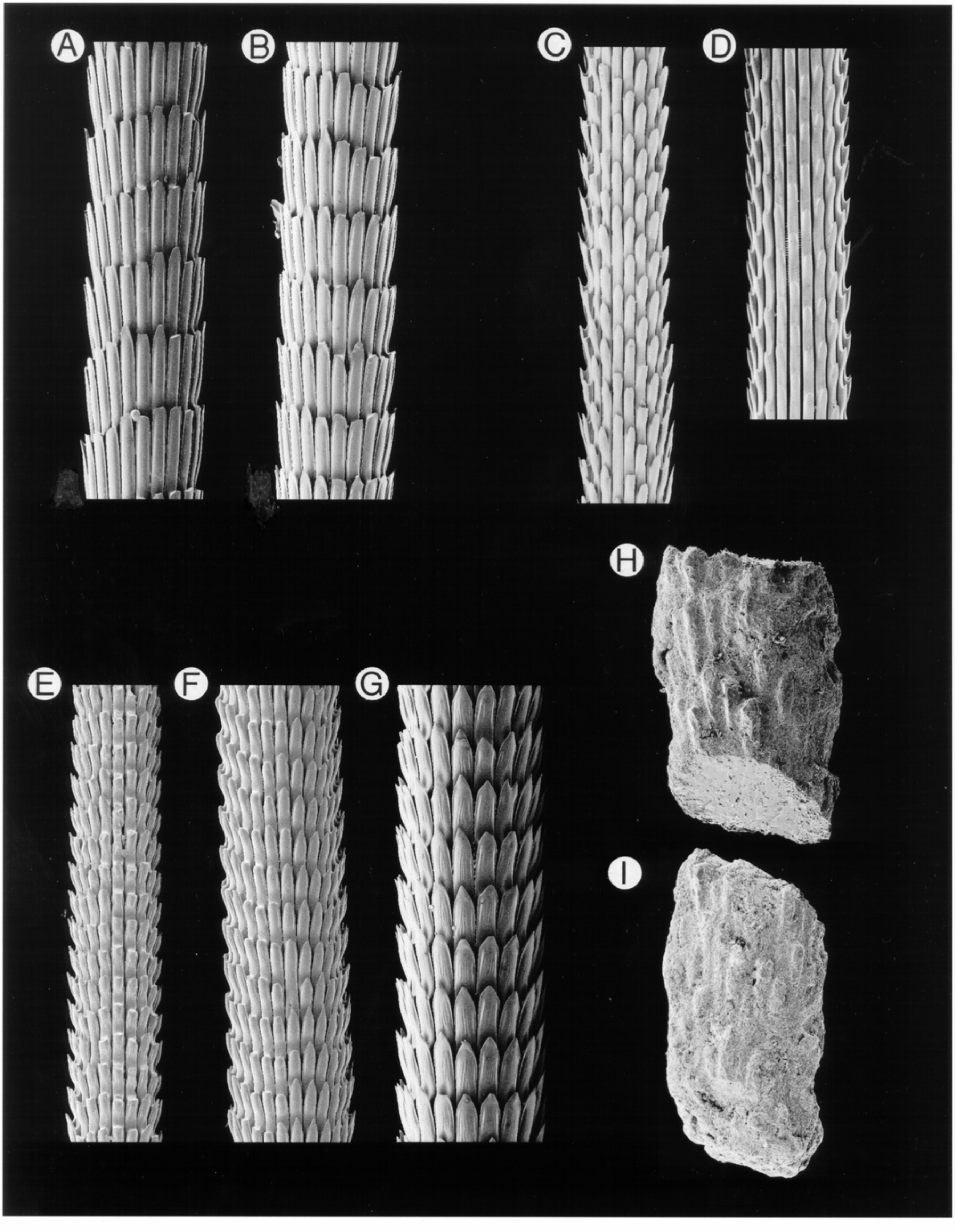
Abstract – The late Pleistocene (Sangamonian) coral limestone of Tobago, West Indies, has yielded three species of regular echinoid, *Eucidaris tribuloides* (Lamarck), *Astropyga magnifica* A. H. Clark and *Lytechinus variegatus* (Lamarck). Of these, only *L. variegatus* is known from tests; all species are still extant and common in Antillean, shallow-water environments. Spines of *E. tribuloides* and diadematids are a common component of late Cenozoic, shallow water assemblages in the Antillean region. External morphology is sufficient to differentiate *E. tribuloides* from the only other member of this genus in the late Cenozoic of the region, *E. madrugensis* (Sánchez Roig). Fossil diadematid fragments have hitherto been left in open nomenclature, but comparison of the Tobago specimen with primary spines from extant Antillean species has shown it to be *A. magnifica*. The fossil tests of *L. variegatus* from Tobago are small, probably a contributory factor in their preservation, although presenting problems for identification when compared with larger, more mature individuals with a more abundant tuberculation. Both tests of this species were encrusted by calcareous algae, which may have further aided in fossilization. This 'assemblage' of echinoids suggests that the late Pleistocene reef limestones of Tobago were deposited in 11-50 m of water.

INTRODUCTION

TOBAGO IS a geologically diverse island in the southeast corner of the Antillean region. It does not form part of the Lesser Antillean chain, but, rather, represents a fragment of the Antillean Cretaceous island arc (Frost and Snoke, 1989; Jackson and Donovan, 1994). The island can be divided into essentially three geological 'provinces', based on the surface outcrop, respectively comprised of sedimentary (in the southwest), igneous and metamorphic rocks (Jackson *et al*., 1988). Rocks of the sedimentary 'province', which unconformably overlie Cretaceous volcanic rocks, include two principal units, the underlying siliciclastic succession of the Pliocene Rockly Bay Formation (Donovan, 1989) and the overlying coral limestone. The latter is a Pleistocene raised reef of probable last interglacial age (Sangamonian) (Trechmann, 1934; Wadge and Hudson, 1986), but a detailed paleoenvironmental analysis of this deposit has yet to be undertaken.

Fossil echinoids are poorly known from the late Cenozoic fossil record of Tobago, although this is true of coeval successions in many parts of the eastern Antillean region. Hitherto, only two taxa have been identified from the island, *Arbacia improcera* (Conrad) from the Rockly Bay Formation, preserved as rare tests, and *Eucidaris tribuloides* (Lamarck), found as spines in both the Rockly Bay Formation and the coral limestone (Lewis and Donovan, 1991). To this meagre total, we add two further taxa, including rare tests of *Lytechinus*, an extant taxon with a wide modern distribution in the tropical western Atlantic, but restricted both geographically and stratigraphically in the fossil record of the region.

Descriptive terminology used herein follows Melville and Durham (1966), and Durham and Wagner (1966). The classification of echinoids is essentially that of Smith (1981, 1984), and Smith and Wright (1989). Synonymy lists for species refer to the fossil record of Tobago only. All fossil specimens are now deposited in the Department of Palaeontology, The Natural History Museum, London (NHM). Recent specimens used for comparative studies are in the collections of the Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D. C. (USNM). A geological locality map for the southeast Tobago appeared in Lewis and Donovan (1991, fig. 1).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SYSTEMATIC PALAEONTOLOGY

Class Echinoidea Leske, 1778

Subclass Cidaroidea Claus, 1880

Order Cidaroida Claus, 1880

Family Cidaridae Gray, 1825

Genus *Eucidaris* Pomel, 1883

Type species. *Cidarites metularia* Lamarck, 1816, by the subsequent designation of H. L. Clark (1909), supported by Bather (1909) (Fell, 1966a, p. U333).

Diagnosis of primary spines. (Based on Mortensen, 1928, p. 384; Fell, 1966a, p. U333, U335; Donovan, 1993, p. 377). Cylindrical, commonly abruptly truncate, otherwise fusiform or clavate (see Fell, 1966a, fig. 250). Base low, smooth and gently tapered, milled ring low and gently convex, neck low. Shaft moderately long, with sculpture of low, domed, separate spinules or ridges arranged in distinct longitudinal series. In life covered by thick coat of anastomosing hair. Shaft truncated by low, castellated crown with central, raised boss.

Discussion. Mortensen (1928, p. 384) considered that, "The main character of the genus [*Eucidaris*], evidently, is that of the primary spines." There are two nominal species within this genus known from the late Cenozoic of the Antillean region, *Eucidaris tribuloides* (Lamarck, 1816) and *Eucidaris madrugensis* (Sánchez Roig, 1949). Primary spines of *E. madrugensis* are easily distinguished from those of *E. tribuloides* in having some spinules in circlets towards the centre of the shaft developed as distinctive thorns (Cutress, 1980; Donovan and Paul, 1998).

Eucidaris tribuloides (Lamarck, 1816)

1991 *Eucidaris tribuloides* (Lamarck); Lewis and Donovan, p. 140.

Material and localities. Sixteen spine fragments, NHM E 82882 (12 specimens) and E 82883 (four specimens). E 82882 is from the bay between Back Bay and Courtland Point, Plymouth, Tobago (60º 46' 39" W 11º 13' 13" N). E 82883 is from Mount Irvine Bay, Tobago (60º 47' 57" W 11º 11' 20" N).

Diagnosis of primary spines. Moderately long, slightly inflated medially. Spinules rounded to elongate domed, separate, arranged in longitudinal rows and separated by a coarse, reticulate stereom surface.

Description. See Cutress (1980, p. 67) and Donovan (1993, p. 377).

Discussion. The primary spines of *E. tribuloides* are a well-known and near-ubiquitous component of Antillean echinoid faunas of Pleistocene age. The Tobagonian specimens are too fragmentary to warrant illustration, but well-preserved primary spines of this species have been illustrated elsewhere (Donovan, 1993, fig. 5). Modern *E. tribuloides* occurs in water depths of 0-800 m (Serafy, 1979, table 2).

Subclass Euechinoidea Bronn, 1860

Order Diadematoida Duncan, 1889

Family Diadematidae Gray, 1855

Genus *Astropyga* Gray, 1825

Type species. *Cidaris radiata* Leske, 1778, by original designation (Fell, 1966b, p. U350).

Diagnosis of spines. (After Mortensen, 1940, p. 182.) "Spines slender, not very long, in large specimens scarcely as much as half the horizontal diameter of the test, or much less (in younger specimens relatively longer). They are densely thorny [see Fig. 1C, D herein], but not distinctly verticillate. The central cavity to a varying degree filled out by an irregular meshwork."

Discussion. Now that they have been widely recognized, preserved as test plates and fragments of spines, diadematids are known to be a common component of late Cenozoic echinoid assemblages in the Antillean region, even though they are unknown as articulated fossil tests (see, for example, Gordon and Donovan, 1992, 1994; Donovan and Paul, 1998). Hitherto, all such specimens have been classified broadly as diadematid or diadematoid sp. indet. (see comments of Mortensen, 1940, p. 255, regarding the identification of diadematid spines even to generic level, but also see discussion below). Mortensen (1940, p. 256) considered the one fossil diadematid species from the Antillean region to be based on test material, *"Diadema" principeana* Weisbord, 1934, to belong outside this family on the basis of its polyporous ambulacral plating.

Figure 1. Scanning electron micrographs of primary spines of diadematid echinoids from the tropical western Atlantic (Recent unless stated otherwise). (A, B) *Centrostephanus longispinus* (Philippi, 1845), USNM E33259, north Atlantic Ocean, Florida, 27º 49' 18" N 79º 57' 36" W, 95-99 m, both x21. (C, D) *Astropyga magnifica* A. H. Clark, 1934, USNM E36651, north Atlantic Ocean, Florida Keys, Key Largo Coral Reef Preserve, both x 21. (E-G) *Diadema antillarum* (Philippi, 1845), USNM 33219, Gulf of Mexico, Florida, Loggerhead Key. (E, F) Both x17. (G) x25. (H, I) *Astropyga magnifica*, NHM EE 6606, late Pleistocene coral limestone, Tobago, spine fragment broken in half, x45. All specimens coated with 60% gold-palladium.

Astropyga magnifica A. H. Clark, 1934

Figure 1H, I

Material and locality. A single, poorly preserved fragment of spine, NHM EE 6606 (Fig. 1H, I). EE 6606 is from Orange Hill Road, Tobago (60º 47' 20" W 11º 10' 35" N). Collected by H.V. and I.M.B.

Diagnosis of primary spines. Elongate, slender, with external sculpture of more (Fig. 1C) or less (Fig. 1D) plate-like spinules, orientated distally, not verticillate, but rather arrayed both in columns and with a distinct spiral appearance. Internal longitudinal cavity of spine occluded in part by irregular stereom meshwork.

Description. Short spine fragment, broken in half (Fig. 1H, I). External sculpture of spinules arrayed in columns and also with an obvious spiral organization. Internal structure not apparent due to infill of calcite spar.

Discussion. This is the first fossil diadematid spine from the Antillean region to be identified below the level of family. Serafy (1979) noted three extant species of diadematid from the Gulf of Mexico and Antillean region: *Diadema antillarum* (Philippi, 1845) (0-400 m); *Astropyga magnifica* A. H. Clark, 1934 (11-88 m); and *Centrostephanus longispinus* (Philippi, 1845) (33-310 m). The spines of *Astropyga* are not hollow, as in the other two species, but are infilled with a secondary stereom meshwork in mature individuals, although not in juveniles (Mortensen, 1940, fig. 96b, c). Unfortunately, the Tobagonian specimen has a diagenetic infill of calcite spar (Fig. 1H) and such internal structures cannot be identified. However, as is demonstrated in Figure 1, the external morphology of these extant species is sufficiently distinct to permit fossil representatives to be identified with confidence.

Both *D. antillarum* and *C. longispinus* have distinctly verticillate spines, perhaps more regularly arranged in the former species (compare Fig. 1A, B with 1E-G). The spinules of *D. antillarum* are also less elongate. However, both of these taxa are in strong contrast with *A. magnifica*, which has spines arranged strongly in columns and with a distinctly spiral arrangement in at least some specimens (Fig. 1C, D). Comparison of EE 6606 with these spines shows that it has a spiral arrangement of spinules that immediately identify it as *A. magnifica*.

The distinctiveness of the external morphology in the extant species of diadematids from the region permits more accurate identification of Antillean fossil diadematid spines that have hitherto been left in open nomenclature (Table 1). Interestingly, although doubts exist in some cases due to indifferent preservation, all other examples are at least close to *Diadema*.

Superorder Echinacea Claus, 1876

Order Temnopleuroida Mortensen, 1943

Family Toxopneustidae Troschel, 1872

Genus *Lytechinus* A. Agassiz, 1863

Type species. *Echinus variegatus* Lamarck, 1816, p. 48, by original designation of A. Agassiz (1863) (Fell and Pawson, 1966, p. U427).

Other species. Mortensen (1943) recognized seven extant species of *Lytechinus*: *L. variegatus* (Lamarck, 1816); *L. anamesus* H.L. Clark, 1912; *L. callipeplus* H.L. Clark, 1912; *L. euerces* H.L. Clark, 1912; *L. panamensis* Mortensen, 1921; *L. pictus* (Verrill, 1867); and *L. semituberculatus* (Valenciennes *in* Agassiz and Desor, 1846, p. 368). The type species has been divided into a number of subspecies (see, for example, Rosenberg and Wain, 1982), one of which, *Lytechinus pallidus* H.L. Clark, 1925, was elevated to the level of species by Serafy (1973). The only other, new extant species recognized since 1943 is *Lytechinus williamsi* Chesher, 1968. Fossil species, in stratigraphic order, include *L. floralanus* (Cooke, 1941) (Eocene of Alabama and Georgia; see Cooke, 1959); *L. baldwini* Linder, Durham and Orr, 1988 (Oligocene of Oregon); *L. crassus* H.L. Clark, 1945 (Pliocene of Fiji); and *Lytechinus* sp. (Pliocene of California; Hertlein

Table 1. Fossil diadematids from the Antilles (figured specimens only). Key: * = identification based at least in part on internal features of spines, not discussed in detail herein (Donovan, research in progress). Provisional generic assignments are provided for pre-Pleistocene taxa.

Age	Location	Unit	Identification	Reference
late Pleistocene	Tobago	coral limestone	*Astropyga magnifica*	herein
late Pleistocene	Jamaica	Falmouth Formation	*Diadema antillarum**	Gordon (1990), Gordon and Donovan (1992)
late Pliocene	Jamaica	Bowden shell bed	Probably *Diadema**	Donovan and Paul (1998)
Neogene	St. Croix, USVI		*Diadema*?	Gordon and Donovan (1994)
early Paleocene	Jamaica	Richmond Formation	*Diadema*?	Donovan and Veltkamp (1992)

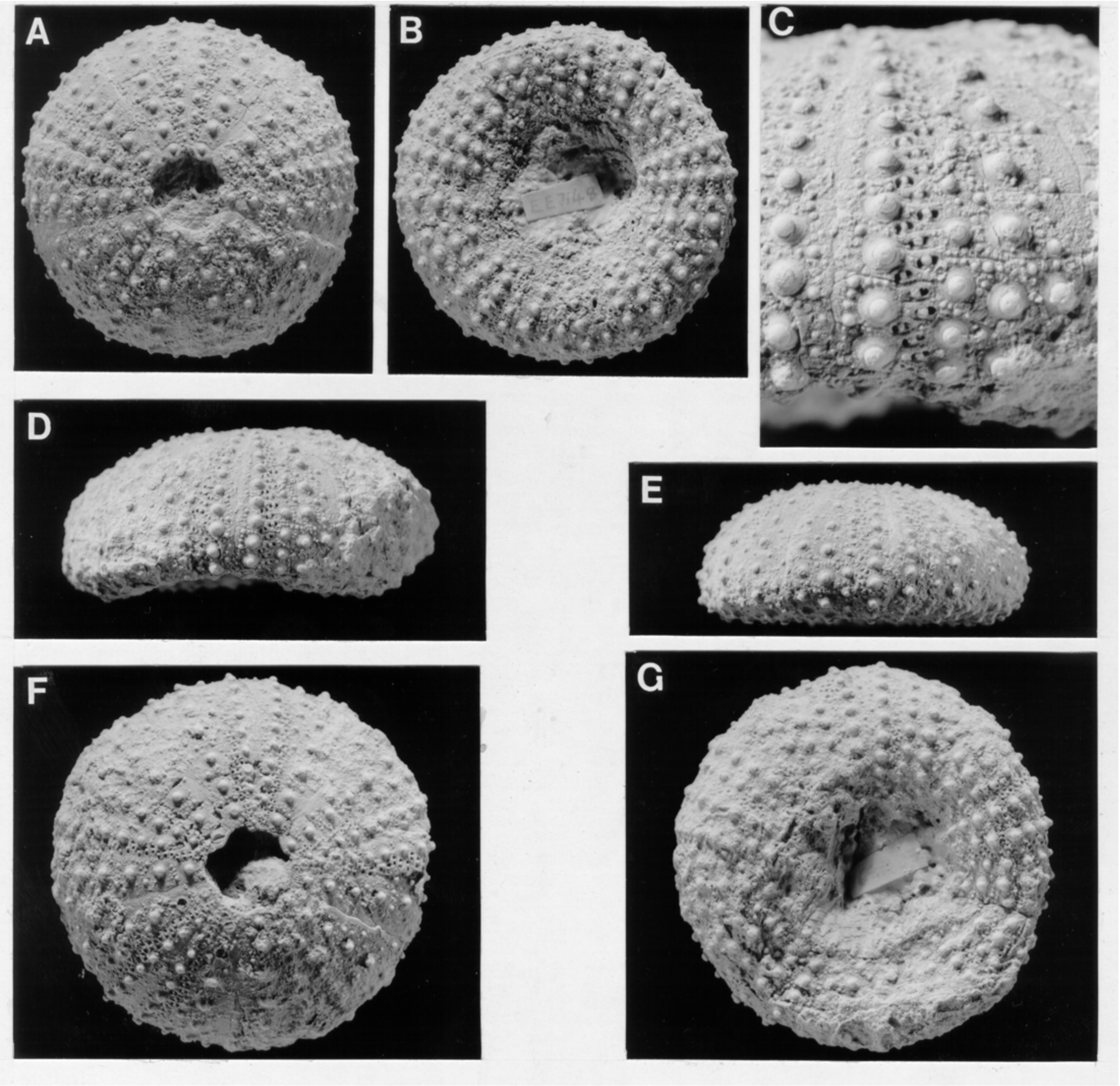

Figure 2. *Lytechinus variegatus* (Lamarck, 1816), from the late Pleistocene coral limestone of Tobago. (A, B, E) NHM EE 7148. (A) Apical view. (B) Oral view. (E) Lateral view. (C, D, F, G) NHM EE 7149. (C) Detail of ambulacral plate compounding and tuberculation (left and centre), and interambulacral tuberculation (right), x 5. (D) Lateral view. (F) Apical view. (G) Oral view. All x 2 unless stated otherwise. Specimens coated with ammonium chloride sublimate.

and Grant, 1960, p. 109, 110). Marcopoulou-Diacantoni (1967, p. 347, 348, pl. 49, fig. 3) identified *L. serialis* (Pomel, 1887) from the Neogene of Greece. However, the available figure of the apical surface shows the secondary tubercles of the ambulacra to be regularly arranged as in *Schizechinus* Pomel, 1869 (see discussion in Mortensen, 1943, pp. 463-465).

Diagnosis. (Based on Mortensen, 1943, p. 434; Fell and Pawson, 1966, p. U427). Test moderate to large in size, low hemispherical in shape. Ambulacral compounding as echinoid triads, each compound plate supporting a single primary tubercle; secondary ambulacral tubercles not in regular series. Commonly conspicuous naked zones adapically in both ambulacra (perradially) and interambulacra (interradially). Buccal notches distinct and moderately deep, buccal membrane bearing numerous plates in addition to the orals. Spines moderately long, slender, not covering test uniformly.

Discussion. *Lytechinus variegatus* (0-250 m water depth) is the commonest member of this genus in Caribbean shallow water environments; *L. williamsi* (5-92 m), *L. callipeplus* (22-350 m) and *L. euerces* (55-777 m) have more limited geographic ranges (Serafy, 1979; Hendler *et al.*, 1995).

Lytechinus variegatus (Lamarck, 1816)

Figures 2, 3

Material examined. Two incomplete tests (Figs 2, 3), NHM EE 7148, EE 7149. EE 7149 is slightly more crushed and distorted than EE 7148. The tests were embedded within a framework of branching coralline algae within a fallen boulder (maximum dimension 2 m) of the late Pleistocene (Sangamonian) coral limestone, on the coast at the western end of Back Bay to the north of Plymouth (approximately 60° 46' 41" W 11° 13' 15" N), Tobago, West Indies, close to a locality that has yielded *E. tribuloides* (see above). In this area, the coral limestone forms a layer 2-4 m thick, unconformably overlying biotite tonalites. Collected by H.V. and I.M.B.

Diagnosis of small (juvenile) individuals. Test of moderate size, circular in outline, low hemispherical, with up to three rows of non-crenulate, imperforate tubercles per interambulacral column from about one third of the way adorally from the apical disc. Oral surface flattened with slightly sunken peristome. Very narrow ambulacral naked zones and broad interambulacral naked zones. Compounding in echinoid triads, with a demiplate the middle component. Pore-pairs in regular arcs. Scrobicular circles contiguous.

Description. Test low hemisphere, with flat oral surface with sunken peristome, outline circular. Apical disc not preserved in either specimen. Peristome large, slightly more than half the diameter of test, sunken, though not deeply, and has moderately deep, rimmed, buccal notches.

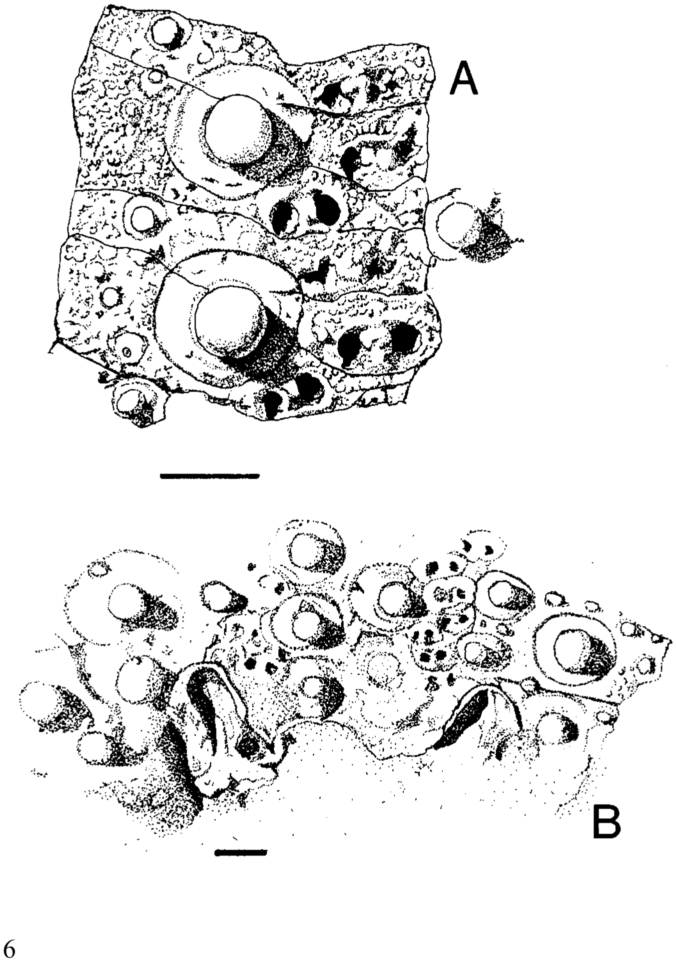

Figure 3. *Lytechinus variegatus* (Lamarck, 1816), NHM EE 7149, from the late Pleistocene coral limestone of Tobago. (A) Two ambulacral plates just adapical to the ambitus, showing plate compounding. (B) Margin of peristome, showing buccal notches. Camera lucida drawings. All scale bars represent 1 mm.

Ambulacra straight, broad, widening rapidly to the ambitus and narrowing to the peristome, where they are about 80% of the width of the interambulacra. Very narrow, rather indistinct naked zone perradially, extending from the disc to the ambitus and just adorally. Ambulacral plates trigeminate, compounding echinoid, with the demiplate being the middle plate and the adoral plate bearing the primary tubercle. Pore pairs oval, almost circular, separated by low protuberance and have a low oval rim adapically. Primary and secondary ambulacral tubercles non-crenulate, imperforate. Primary boss low, circular, with diameter just less than half width of plate, smooth, slightly concave sided, without a platform. Mamelon hemispherical, relatively large, about half diameter of boss, with a short, slightly undercut neck. Diameter of primary tubercles close to apical disc less than half that of primary interambulacral tubercles, but increase to ambitus, where they are almost as large and continue to be so adorally. Scrobicular circles contiguous, incomplete adjacent to the pore-pairs. One tubercle of each plate slightly larger than the rest, situated on the adapical perradial portion of the plate, may be up to one third of size of primary tubercle at the ambitus, slightly less elsewhere. About eight secondary tubercles in scrobicular circle. Structure and proportions are similar to those of primaries.

Interambulacra broad, expanding rapidly from apical disc to ambitus and narrowing gradually towards peristome. At the disc, interambulacra are four times as wide as ambulacra, at the ambitus about 40% wider. Wide naked zone extends from disc to ambitus. Plates as tall as they are long at disc; at ambitus height is 40% of width; on adoral surface about 34% of width. Interambulacral primary tubercles imperforate, non-crenulate, with low, circular boss with slightly concave sides and mamelon which is hemispherical, relatively large, about half diameter of boss, with short, slightly undercut neck and no platform. Position on each plate adorally adradial and form straight columns. Primary tubercles fairly constant in size down the column, except those adjacent to disc, where they are a little over half the diameter of those at ambitus. Adorally, their diameter is about 75% that of ambital tubercles. Interambulacral secondary tubercles of similar structure; miliary tubercles are also present. Largest secondaries situated towards interradius, more or less equidistant from adoral and adapical sutures of the plates. At the ambitus, their diameter is about 75% that of primary tubercles, forming a regular column down each interambulacrum. Other secondary tubercles situated close to adradius, usually one per plate, but sometimes two. Where there is only one, it is located slightly towards the adapical adradial portion of the plate. When there are two, they are located adradial-adapically and adradial–adorally on the plate. Together, primary and secondary tubercles form up to three regular rows per interambulacral column, one initially from the disc, then two others from about a third of the way adorally down each column. Scrobicular circles are contiguous, and include miliary tubercles and granules.

No spines or other appendages are preserved.

For measurements of these specimens, see Table 2.

Table 2. Dimensions of *Lytechinus variegatus* (Lamarck) from the late Pleistocene coral limestone of Tobago. All measurements in mm.

Dimensions of tests	EE 7148	EE 7149
diameter at ambitus	30	34
diameter of peristome	*ca.* 16	*ca. >13*
diameter of apical disc	6	7
height	12	14
width of ambulacra at ambitus	7	8
width of interambulacra at ambitus	13	14
number of primary ambulacral tubercles	a - 17 b - 16	a - 17 b - 16
number of primary interambulacral tubercles	a - 12 b - 11	a - >12 b - >11
ambital width of primary tubercles to plates		
ambulacra	50%	44%
interambulacra	28%	29%

Discussion. The commonest extant taxon of *Lytechinus* in the tropical western Atlantic is the type species. However, the Tobagonian specimens are not immediately comparable with figured specimens of *L. variegatus* (for example, compare Fig. 2 herein with Mortensen, 1943, pls 24, 25, figs 1-9). Mature *L. variegatus* has many more rows of tubercles in each ambulacral and interambulacral column, and the tests are taller and more bun-shaped. Secondary ambulacral tubercles of the Tobagonian species are very much smaller. However, comparison with small tests of Recent *L. variegatus* (Fig. 4) shows that these differences are due to a scale factor. The tests in Figure 4 are of similar size to the Tobagonian specimens, have naked zones of similar proportions and, most importantly, have a similar pattern of ambulacral and interambulacral tuberculation (compare Figs 2 and 4). Both fossil specimens show the effects of post-mortem crushing (particularly EE 7149), suggesting that they were at least slightly more inflated in life. We therefore assign the Tobagonian specimens to *L. variegatus* with confidence. *L. variegatus* is commonest between 0-50 m, although it occurs down to 250 m (Hendler *et al*., 1995, p. 216).

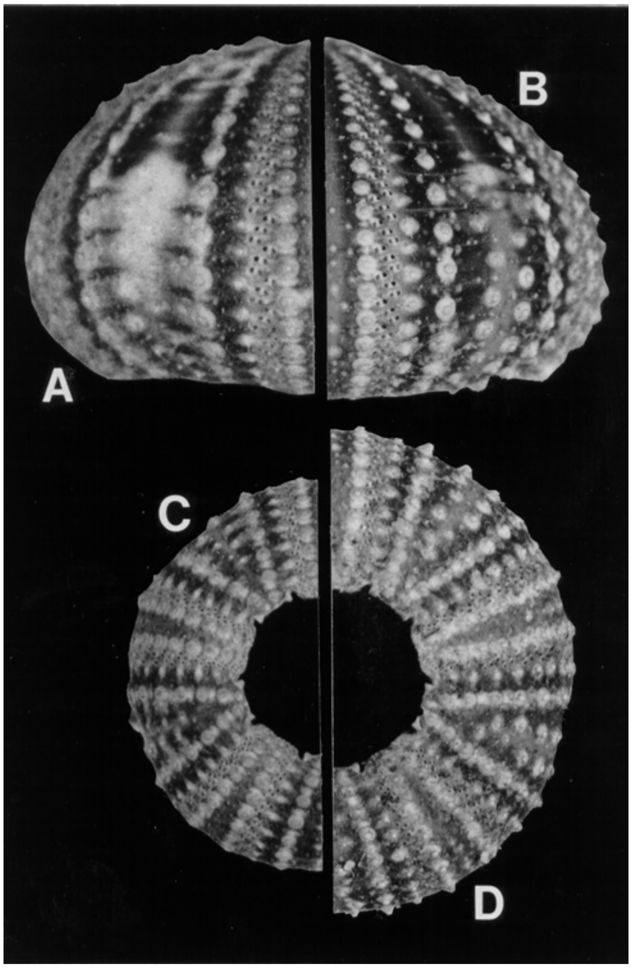

Figure 4. ***Lytechinus variegatus*** **(Lamarck, 1816), USNM E1443, Recent, Kingston, Jamaica. Three specimens (informally called a, b, c herein) out of eight are illustrated; a and b are slightly smaller than the Tobago fossils, and c is slightly larger. Half views presented to permit easier comparison. (A) USNM E1443a, lateral view (a small specimen, printed about the same size as (B) for easy comparison); note interambulacral rubercles sparse below ambitus, x3.3. (B, D) USNM E1443c. (B) Lateral view, note relatively denser sub-ambital tuberculation, x2.5. (D) Oral view, x2.1. (C) USNM E1443b, oral view, printed same magnification as (D) for comparison of sizes; note relative paucity of interambulacral tubercles, x2.1. Specimens uncoated.**

The Tobagonian tests do not closely approach any of the other extant species of *Lytechinus* from the Antillean region. *L. williamsi* has a different arrangement of secondary tubercles on the adapical portion of interambulacral plates, and has a more inflated test with a less flattened oral surface and a higher ambitus (Chesher, 1968). Neither *L. callipeplus* nor *L. euerces* have naked zones in the ambulacra or interambulacra (Serafy, 1973). Comparison with other extant and fossil *Lytechinus* species revealed no closely similar taxa.

It is important to note that tests of *L. variegatus* are rare fossils in the Antillean rock record (Table 3). However, this is a not surprising pattern for an Antillean, shallow water toxopneustid (Greenstein, 1991; Donovan and Gordon, 1993). The rare preservation of juvenile(?) tests of *L. variegatus* in the Pleistocene of Tobago may be due, at least in part, to their small size and their surface encrustation of calcareous algae. Apart from the well-known bias of the echinoid fossil record to complete tests to irregular echinoids (Kier, 1977; Smith, 1984), there also seems to be preferential preservation of smaller tests, larger specimens being more likely to be preserved as, at best, large test fragments. This is presumably due to the greater likelihood with which the vault of a large, unsupported test might be crushed or broken up post-mortem by weight of overburden or transport following rotting of collagenous ligaments.

Tests of modern *L. variegatus* collapse into their component plates soon after death and following rotting of binding ligamentation (Kier, 1977, p. 171). However, Kidwell and Baumiller (1990, p. 264) considered that encrusting organisms might act to strengthen the echinoid corona against post-mortem collapse. Both of the Tobagonian tests of *L. variegatus* were encrusted after death by calcareous algae, which presumably strengthened them by growing over and thus stabilizing plate sutures (note that the Tobagonian specimens were partly cleaned of algae prior to photography, although some encrustation is still apparent in Fig. 2). This is further supported by Pleistocene *Lytechinus* in raised reef deposits in Barbados, which have a similar pattern of algal encrustation (Donovan *et al.*, 2001).

Table 3. Fossil *Lytechinus* in the late Cenozoic of the Antilles and adjacent regions.

TAXON	AGE/UNIT	LOCATION	PRESERVATION	REFERENCE
Lytechinus? sp. or spp.	Sangamonian - Falmouth Formation	Jamaica	rare spines	Gordon and Donovan (1992)
Lytechinus variegatus	Sangamonian - coral limestone	Tobago	encrusted tests	This paper
Lytechinus sp. cf. *L. variegatus*	Middle Pleistocene - Middle Coral Rock	Barbados	encrusted tests	Donovan *et al.* (2001)
Lytechinus variegatus	Early Pleistocene - Waccamaw Formation	North Carolina	complete and fragmentary tests	R.W. Portell (written comm.), DuBar Collection, FlMNH
Lytechinus variegatus	Pleistocene - Pamlico Formation	South Carolina	?	Cooke (1941, 1959)
Lytechinus variegatus	Pliocene - San Gregorio Formation	Venezuela	fragmentary tests	Cooke (1961)
Lytechinus variegatus plurituberculatus	Pliocene - Tamiami Formation; Plio-Pleistocene - Caloosahatchee Formation	Florida	complete tests	Kier (1963)

Table 4. Known depth ranges of echinoid taxa identified from the Pleistocene coral limestone of Tobago. Depth range data from Serafy (1979, table 2) and Hendler *et al.* (1995). Key: * = given as 11-88 m elsewhere, but Hendler *et al.* (1995, p. 209) refer to specimens in 0.6-1.2 m and USNM E33259 (Fig. 1A, B) is from 95-99 m.

TAXON	TOTAL DEPTH RANGE	COMMONEST DEPTH	COMMENTS (after Hendler *et al.*, 1995)
Eucidaris tribuloides	0-800 m	0-50 m	"On coral reef in small crevices ... under rocks and rubble in back reef lagoons" (p. 206).
Astropyga magnifica	0.6-99 m*		"... algal sand, carbonate sand, and crushed shell habitats and limestone outcroppings" (p. 209).
Lytechinus variegatus	0-250 m	0-50 m	"Most common in quiet water ..." (p. 216).

DISCUSSION

Plio-Pleistocene raised reefs are important coastal deposits in many parts of the Antillean region, and it might be expected that their included echinoderm faunas would be both diverse and well-studied. However, the degree of lithification is an important controlling factor when collecting from such deposits. For example, the Sangamonian Falmouth Formation of Jamaica's north coast includes a range of reef biolithofacies, yet it is only at the east Rio Bueno Harbour site that very abundant echinoid debris and rare tests have been easily collected due to the enclosing sediment being very poorly cemented. In contrast, other localities are well-cemented and have yielded their secrets grudgingly, mainly through thin sectioning, a much more laborious task than bulk sampling and sieving (Gordon, 1990; Gordon and Donovan, 1992). The 'rotted' Pleistocene coral limestone of Tobago lies somewhere between these two diagenetic extremes. These limestones have yet to be submitted to a detailed campaign of bulk sampling and the potential exists for the echinoderm fauna to be further enhanced.

An unusual feature of the Pleistocene of Tobago is the absence of irregular echinoids, despite the widely recognized, higher preservation potential of such taxa when compared with regular echinoids (Kier, 1977; Smith, 1984). Additionally, there are no fossil irregular echinoids known from the Pliocene of the island. At least part of the explanation of this must be collecting methods. Two of the known Plio-Pleistocene echinoid taxa from Tobago are known from tests only, while a third has been identified on the basis of large, distinctive spines. Only *A. magnifica* has been identified from a microscopic fragment. Again, it is suggested that more processing of bulk samples, preferably as part of a more systematic study of the late Cenozoic echinoderm fauna than has been attempted hitherto, would yield a greater diversity of echinoderms, not just irregular echinoids, but also further regular echinoids and members of other echinoderm classes (compare with the coeval Falmouth Formation of Jamaica; Gordon, 1990; Gordon and Donovan, 1992; Donovan *et al.*, 1993; Donovan and Collins, 1997).

Although there are few echinoid species identified from the Pleistocene coral limestone of Tobago, taken together they do suggest a broad palaeobathymetric interpretation of this raised reef deposit. Although they have not all been collected from the same locality, all three species are typical of the shallow-water fauna of the modern Antilles (Hendler *et al.*, 1995) and, indeed, all are most common in the 11-50 m depth range (Table 4). Although this interpretation awaits confirmation by analysis of associated scleractinian and benthic molluscan taxa, this determination agrees well with palaeobathymetric determinations of coeval raised reefs within the Antillean region.

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REFERENCES

Agassiz, L. and Desor, P. 1846-1847. Catalogue raisonné des espèces, des genres et des familles d'echinides. *Annales des Sciences Naturelles, Zoologie, Paris*, series 3, **6**, 305-374; **7**, 129-168; **8**, 5-35, 355-380.

Agassiz, A. 1863. List of the echinoderms sent to different institutions in exchange for other specimens, with annotations. *Bulletin of the Museum of Comparative Zoology, Harvard*, **1**, 17-28.

Bather, F. A. 1909. The type of *Cidaris*. *Annals and Magazine of Natural History*, **73**, 88.

Bronn, H. G. 1860. *Klassen und Ordnung des Thier-Reiches. Volume 1.* Amorphozoen. Leipzig and Heidelburg, 434 pp.

Chesher, R. H. 1968. *Lytechinus williamsi*, a new sea urchin from Panama. *Breviora*, **305**, 1-13.

Clark, A. H. 1934. A new sea-urchin from Florida. *Journal of the Washington Academy of Sciences*, **24**, 52-53.

Clark, H. L. 1909. The type of *Cidaris*. *Annals and Magazine of Natural History*, **73**, 88.

Clark, H. L. 1912. Hawaiian and other Pacific echini. The Pedinidae, Phymosomatidae, Stomopneustidae, Echinidae, Temnopleuridae, Strongylocentrotidae, and Echinometridae. *Memoirs of the Museum of Comparative Zoology, Harvard*, **34**(4), 180 pp.

Clark, H. L. 1925. *A Catalogue of the Recent Sea-Urchins (Echinoidea) in the Collection of the British Museum (Natural History).* British Museum (Natural History), London, xxviii+250 pp.

Clark, H. L. 1945. Echinoidea: in **H. S. Ladd and J. E. Hoffmeister** (eds), Geology of Lau, Fiji. *Bulletin of the Bishop Museum, Honolulu*, **181**, 312-328.

Claus, C. F. W. 1876. *Grundzüge der Zoologie* (3rd edition). Marburg and Leipzig, 822 pp.

Claus, C. F. W. 1880. *Grundzüge der Zoologie* (4th edition). Marburg and Leipzig, vii+821 pp.

Cooke, C. W. 1941. Cenozoic regular echinoids of eastern United States. *Journal of Paleontology*, **15**, 1-20.

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

Cooke, C. W. 1961. Cenozoic and Cretaceous echinoids from Trinidad and Venezuela. *Smithsonian Miscellaneous Collections*, **142**(4), 35 pp.

Cutress, B. M. 1980. Cretaceous and Tertiary Cidaroida (Echinodermata: Echinoidea) of the Caribbean area. *Bulletins of American Paleontology*, **77**(309), 221 pp.

Donovan, S. K. 1989. Palaeoecology and significance of barnacles in the mid-Pliocene *Balanus* Bed of Tobago, West Indies. *Geological Journal*, **24**, 239-250.

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

Donovan, S. K. and Collins, J. S. H. 1997. Unique preservation of an *Echinometra* Gray (Echinodermata: Echinoidea) in the Pleistocene of Jamaica. *Caribbean Journal of Science*, **33**, 123-124.

Donovan, S. K. and Gordon, C. M. 1993. Echinoid taphonomy and the fossil record: supporting evidence from the Plio-Pleistocene of the Caribbean. *Palaios*, **8**, 304-306.

Donovan, S. K., Gordon, C. M., Veltkamp, C. J. and Scott, A. D. 1993. Crinoids, asteroids and ophiuroids in the Jamaican fossil record: in **R. M. Wright and E. Robinson** (eds), *Biostratigraphy of Jamaica. Geological Society of America Memoir*, **182**, 125-130.

Donovan, S. K. and Harper, D. A. T., with Blackman, I. M. and Simpson, G. A. 2001 (in press). Pleistocene echinoids from fore reef palaeoenvironments in Barbados and eastern Jamaica: a comparison: in **T. A. Jackson** (ed.), *Transactions of the 15th Caribbean Geological Conference, 29th June - 2nd July, 1998, Kingston, Jamaica*. The Press, University of the West Indies, Mona.

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

Donovan, S. K. and Veltkamp, C. J. 1992. A diadematoid echinoid from the Lower Paleocene of Jamaica. *Caribbean Journal of Science*, **28**, 222-224.

Duncan, P. M. 1889. A revision of the genera and great groups of the Echinoidea. *Zoological Journal of the Linnean Society of London*, **23**, 1-311.

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

Fell, H. B. 1966a. Cidaroids: in **R. C. Moore** (ed.), *Treatise on Invertebrate Paleontology, Part U, Echinodermata* **3**(1), pp. U312-U339. Geological Society of America and University of Kansas Press, New York and Lawrence.

Fell, H. B. 1966b. Diadematacea: in **R. C. Moore** (ed.), *Treatise on Invertebrate Paleontology, Part U, Echinodermata* **3**(1), pp. U340-U366a. Geological Society of America and University of Kansas Press, New York and Lawrence.

Fell, H. B. and Pawson, D. L. 1966. [Echinacea] Systematic descriptions: in **R. C. Moore** (ed.), *Treatise on Invertebrate Paleontology*, *Part U, Echinodermata* **3**(2), pp. U375-U440. Geological Society of America and University of Kansas Press, New York and Lawrence.

Frost, C. D. and Snoke, A. W. 1989. Tobago, West Indies, a fragment of a Mesozoic oceanic island arc: petrochemical evidence. *Journal of the Geological Society, London*, **146**, 953-964.

Gordon, C. M. 1990. *Taxonomy and Palaeoecology of the Echinoids of the Late Pleistocene Falmouth Formation of Jamaica.* Unpublished M.Phil. thesis, University of the West Indies, Mona, xvi+297 pp.

Gordon, C. M. and Donovan, S. K. 1992. Disarticulated echinoid ossicles in paleoecology and taphonomy: the last interglacial Falmouth Formation of Jamaica. *Palaios*, **7**, 157-166.

Gordon, C. M. and Donovan, S. K. 1994. Some fossil echinoids (Echinodermata) from the Neogene of St. Croix, U.S. Virgin Islands. *Caribbean Journal of Science*, **30**, 69-75.

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. 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.

Greenstein, B. J. 1991. An integrated study of echinoid taphonomy: predictions for the fossil record of four echinoid families. *Palaios*, **6**, 519-540.

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

Hertlein, L. G. and Grant, U. S., IV. 1960. The geology and paleontology of the marine Pliocene of San Diego, California. Part 2a, paleontology (Coelenterata, Bryozoa, Brachiopoda, Echinodermata). *Memoirs of the San Diego Society of Natural History*, **2**, 73-133.

Jackson, T. A. and Donovan, S. K. 1994. Tobago: in **S. K. Donovan and T. A. Jackson** (eds), *Caribbean Geology: An Introduction*, pp. 193-207. University of the West Indies Publishers' Association, Kingston.

Jackson, T. A., Duke, M. J. M., Smith, T. E. and Huang, C. H. 1988. The geochemistry of the metavolcanics in the Parlatuvier Formation, Tobago: evidence of an island arc origin: in **L. Barker** (ed.), *Transactions of the 11th Caribbean Geological Conference, Dover Beach, Barbados, July 20th - 26th, 1986*, p. 21.1-21.8.

Kidwell, S. M. and Baumiller, T. 1990. Experimental disintegration of regular echinoids: roles of temperature, oxygen, and decay thresholds. *Paleobiology*, **16**, 247-271.

Kier, P. M. 1963. Tertiary echinoids from the Caloosahatchee and Tamiami Formations of Florida. *Smithsonian Miscellaneous Collections*, **145**(1), 1-63.

Kier, P. M. 1977. The poor fossil record of the regular echinoid. *Paleobiology*, **3**, 168-174.

Lamarck, J. B. P. A. de M. de. 1816. *Histoire naturelle des animaux sans vertèbres, présentant les caractères, généralaux et particuliers de ces animaux, leurs distribution, leurs classes, leurs familles, leurs genres et la citation synonymique des principales espèces qui s'y rapportent.* 1st edition, Volume 3. Paris, 586 pp.

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

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

Linder, R. A., Durham, J. W. and Orr, W. N. 1988. New late Oligocene echinoids from the central Western Cascades of Oregon. *Journal of Paleontology*, **62**, 945-958.

Marcopoulou-Diacantoni, A. 1967. La fauna des Echinides néogenes des Pays helléniques. *Annales Géologiques des Pays Hélleniques*, **18**, 331-406.

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

Mortensen, T. 1921. *Studies of the Development and Larval Forms of Echinoderms.* Gad, Copenhagen, 261 pp.

Mortensen, T. 1928. *A monograph of the Echinoidea. I. Cidaroidea* (in two volumes). Reitzel, Copenhagen, 551 pp. (text) + 24 pp. (atlas).

Mortensen, T. 1940. *A monograph of the Echinoidea. III.1. Aulodonta with additions to vol. II (Lepidocentroida and Stirodonta)* (in two volumes). Reitzel, Copenhagen, 370 pp. (text) + 22 pp. (atlas).

Mortensen, T. 1943. *A monograph of the Echinoidea. III.2. Camarodonta I. Orthopsidae, Glyphocyphidae, Temnopleuridae and Toxopneustidae* (in two volumes). Reitzel, Copenhagen, 553 pp. (text) + 23 pp. (atlas).

Philippi, R. A. 1845. Beschreibung einiger neuer Echinodermen (*Spatangus excavata*, *Sp. cavernosus*, *Sp. australia*, *Sp. placenta*, *Sp. canaliferus*) nebst kritischen Bemerkungen über einige weniger bekannte Arten. *Archiv für Naturgeschite*, **11**, 344-359.

Pomel, A. 1869. *Revue des Échinodermes et Leur Classification pour servir d'Introduction á l'Étude des Fossiles*. Paris, i-lxvii p.

Pomel, A. 1883. *Classification Méthodique et Genera des Échinides Vivants et Fossiles*. Adolphe Jourdan, Alger, 131 p.

Pomel, A. 1887. *Paléontologie ou Description des Animaux Fossiles de l'Algérie: Échinodermes*. Adolphe Jourdan, Alger.

Rosenberg, V. A. and Wain, R. P. 1982. Isozyme variation and genetic differentiation in the decorator sea urchin, *Lytechinus variegatus* (Lamarck, 1816): in **J. M. Lawrence** (ed.), *Echinoderms: Proceedings of the International Conference, Tampa Bay*, pp. 193-197. Balkema, Rotterdam.

Sánchez Roig, M. 1949. Los equinodermos fosiles de Cuba. *Paleontologia Cubana*, **1**, 1-302.

Serafy, D. K. 1973. Variation in the polytypic sea urchin *Lytechinus variegatus* (Lamarck, 1816) in the western Atlantic (Echinodermata; Echinoidea). *Bulletin of Marine Science*, **23**, 525-534.

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

Smith, A. B. 1981. Implications of lantern morphology for the phylogeny of post-Palaeozoic echinoids. *Palaeontology*, **24**, 779-801.

Smith, A. B. 1984. *Echinoid Palaeobiology*. George, Allen and Unwin, London, 190 pp.

Smith, A. B. and Wright, C. W. 1989 (for 1987). British Cretaceous echinoids. Part 1, general introduction and Cidaroida. *Monograph of the Palaeontographical Society, London*, **141**(578), 1-101.

Trechmann, C. T. 1934. Tertiary and Quaternary beds of Tobago, West Indies. *Geological Magazine*, **71**, 481-493.

Troschel, F. H. 1872-1873. Die Familie der Echinocidariden. *Archiv für Naturgeschichte*, **38**, 293-356; **39**, 308-356.

Verrill, A. E. 1867-1871. Notes on the Radiata in the Museum of Yale College, with descriptions of new genera and species. *Transactions of the Connecticut Academy of Arts and Sciences*, **1**, 247-613.

Wadge, G. and Hudson, D. 1986. Neotectonics of southern Tobago: in **K. Rodrigues** (ed.), *Transactions of the 1st Geological Conference of the Geological Society of Trinidad and Tobago, Port-of-Spain, July 10th - 12th, 1985*, pp. 7-20.

Weisbord, N. E. 1934. Some Cretaceous and Tertiary echinoids from Cuba. *Bulletins of American Paleontology*, **20**(70C), 165-270.

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