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by

Harold E. Vokes and Emily H. Vokes

13. The Class Echinoidea (Echinodermata)

by

Porter M. Kier

Paleontological Research Institution
1259 Trumansburg Road
Ithaca, New York, 14850 U.S.A.

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NEOGENE PALEONTOLOGY IN THE NORTHERN DOMINICAN REPUBLIC
12. The Genus *Spondylus* (Bivalvia: Spondylidae)

By

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ABSTRACT

Only three species of *Spondylus* have been collected in the Neogene strata of the northern Dominican Republic. These include: *S. bostrychites* Guppy, which is largely confined to the more shallow facies of the late Miocene–early Pliocene Gurabo Formation; and *S. gumanomocon* Brown and Pilsbry, which is largely confined to the coralline facies of the Gurabo Formation and the Mao Adentro Member of the Mao Formation. The third species is represented by a single specimen of *S. lucasi* Maury from the Gurabo Formation. No specimens are known from the early Miocene Baitoa Formation and only three specimens (one of *S. bostrychites* and two of *S. gumanomocon*) have been collected in the late Miocene Cercado Formation.

RESUMEN

Se han colectada solo tres especies de *Spondylus* en los stratos Neógenos del norte de la República Dominicana. Estas incluyen: *S. bostrychites* Guppy, por la mayor parte restringida a las facies más someras de la Formación Gurabo del Mioceno tardío al Plioceno principio; y *S. gumanomocon* Brown y Pilsbry, por la mayor parte restringida a las facies coralinas de la Formación Gurabo, y del Miembro Mao Adentro de la Formación Mao. La tercera especie está representada por un solo espécimen de *S. lucasi* Maury de la Formación Gurabo. No se encuentran especímenes de *Spondylus* en la Formación Baitoa del Mioceno principio y solamente tres (uno de *S. bostrychites* y dos de *S. gumanomocon*) se han colectado en la Formación Cercado del Mioceno tardío.

INTRODUCTION

This study is a small contribution to the on-going project on the Neogene fossils from exposures in the Cibao Valley, northern Dominican Republic (Text-fig. 1). The geological setting and the history of the Dominican Republic Project have been thoroughly covered by several authors (see Saunders, Jung, and Biju-Duval, 1986; Jung, 1986; E. Vokes, 1989; H. Vokes, 1989).

The material upon which this paper is based was collected by both the the Naturhistorisches Museum Basel team of John Saunders and Peter Jung, and by the authors, as has been documented in the aforementioned papers. For information on localities, stratigraphy, and ages, the reader is referred to the first work in this series: Saunders, Jung, and Biju-Duval (1986).

ACKNOWLEDGMENTS

This study owes an immense debt of gratitude to Peter Jung, of the Naturhistorisches Museum Basel, who photographed and measured all of the type material for the species of *Spondylus* Linnaeus, 1758 that are involved. His labors made the remainder of the work much less time-consuming. In addition, he and John Saunders led the NMB team that collected much of the material utilized herein. We are grateful to Dr. Niles Eldredge, American Museum of Natural History, New York, and Dr. George M. Davis and Ms. Elena Benamy, Academy of Natural Sciences, Philadelphia, for the loan of type material, and to Dr. Thomas R. Waller, U. S. National Museum of Natural History, and Dr. Gary Rosenberg, Academy of Natural Sciences, Philadelphia, for reviewing the manuscript.

BIOSTRATIGRAPHY AND PALEOECOLOGY

As there are but three species of Spondylidae in the Dominican Republic beds, and one of these is represented by a single specimen, not a great deal of information can gleaned from their occurrence. The most abundant species is *S. bostrychites* Guppy, 1867, and from all evidence it followed a life-style unlike the vast majority of living spondylids, which attach to dead corals or other hard substrate. The bulk of the material for *S. bostrychites* comes from beds that, on the basis of other molluscan species present, we think of as "shallow-water Gurabo" (see E. Vokes, 1989, p. 21), with water depths of about 20 to 50 m. From all appearances the specimens of *S. bostrychites* were not attached but lay "floating" in the fine silty sediment.

This quiet environment permitted the growth of long delicate spines (see Text-fig. 2).

The other species for which we have enough material to consider is the more massive *S. gumanomocon* Brown and Pilsbry, 1913, which is found primarily in the coralline facies of the Gurabo Formation and the Mao Adentro Member of the Mao Formation. It evidently lived in the more normal spondylid fashion, attached to dead coral.

Most of the records of these two species are from the Gurabo Formation and the Mao Formation, but the occurrence of both is more dependent on environment than on time, as there is one specimen of *S. bostrychites* and two of *S. gumanomocon* from the Cercado beds. One of the specimens of *S. gumanomocon* is from locality NMB 16853, which is just upstream from the mouth of Arroyo Bellaco, in the Río Cana drainage, where a very large coral reef is located (loc. TU 1422; see Saunders, Jung, and Biju-Duval, 1986, text-fig. 15 [loc. TU 1282 is at the mouth of Arroyo Bellaco and TU 1422 is off the map]).

No specimens of any species of *Spondylus* Linnaeus, 1758 are known from the Baitoa Formation. It is assumed that this is due to the very shallow-water nature of this formation. The facies of the Baitoa is extremely similar to the shallow-water Cercado Formation, where specimens of *Spondylus* are almost non-existent. Throughout the Caribbean, species of *Spondylus* occur in other early Miocene beds that are correlated with the Baitoa Formation.

ABBREVIATIONS OF REPOSITORY INSTITUTIONS

The following abbreviations for repository institutions are used in this paper:

ANSP: Academy of Natural Sciences, Philadelphia, PA, U.S.A.

BMNH: British Museum (Natural History), London, England, U.K.

NMB: Naturhistorisches Museum Basel, Basel, Switzerland.

PRI: Paleontological Research Institution, Ithaca, NY, U.S.A.

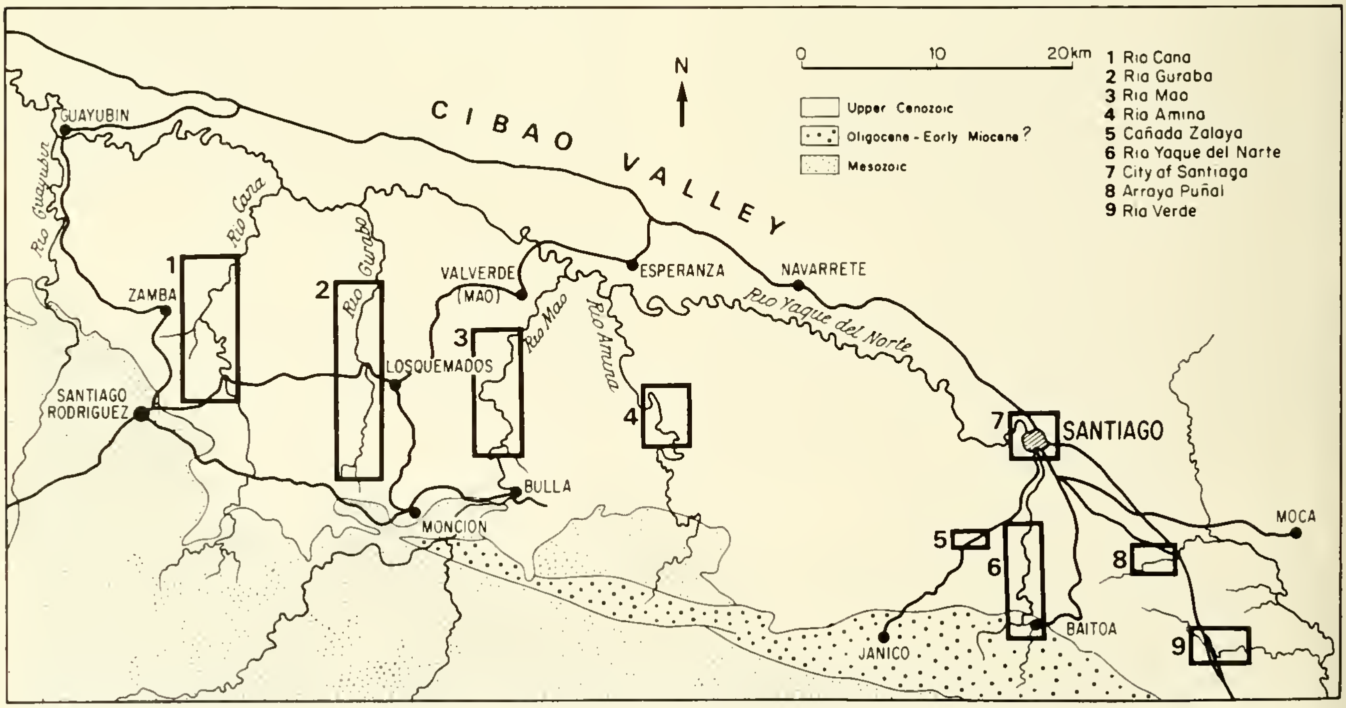
TU: Tulane University, New Orleans, LA, U.S.A.

USNM: United States National Museum of Natural History, Washington, DC, U.S.A.

SYSTEMATIC PALEONTOLOGY

INTRODUCTION

The genus *Spondylus* Linnaeus, 1758 is known from the Jurassic to the Recent (Hertlein and Cox, 1969, p. N378) and today is found in all tropical and subtropical marine waters. The shell is highly variable in shape and ornamentation to the extent that no two specimens of a species are entirely alike. The variation in shape is due to the nature of the surface to which the right valve becomes attached, but the surface ornament is influenced by the environment in which it is growing. The shell spines are produced by extensions of the



Text-figure 1.—Geological sketch map of the Cibao Valley, northern Dominican Republic, showing areas from which samples for this project were collected (after Saunders, Jung, and Biju-Duval, 1986, text-fig. 3).

mantle beyond the shell margin and, as noted by Root (1988, p. 7), the "feathery, fingerlike projections" of the mantle, which produce the spines, are strongly affected by the force of the current; large elongate spines can form in quiet waters, while those in a swift current have to be short because the projection cannot be held out long enough to permit the secretion of a large calcareous spine.

The net result of this great variability has been the assignment of numerous generic and specific names to spondylid species. The problem is also accentuated in Recent species by the tendency to have color variations ranging, for example in the eastern Pacific *Spondylus princeps* Broderip, 1833, from white to pink, orange or coral-red, often with spines that may vary somewhat from the color of the shell itself.

Just to give an idea of the complicated taxonomy of the Recent species of *Spondylus*, in a recent popular work (illustrated by exquisite color photographs), Lamprell (1987) states that 224 specific names have been proposed for species of *Spondylus*. Of this number he considers approximately 75 (even he is uncertain) as valid species, the remainder synonyms.

In the Recent fauna of the western Atlantic there are probably six species, plus another three on the eastern Pacific coast of tropical America (Lamprell, 1989). In the Neogene of the Americas there are possibly 12 valid species, in addition to fossil occurrences of forms described from the Recent fauna.

It is obvious that the determination of the validity of a species on shell morphology alone is impossible. There will have to be some better method of species determination, such as using electrophoresis of amino acids or proteins, before any meaningful synthesis for the living forms can be achieved. This is not going to be a great help with the fossil species. All we can do is try to compare the morphology of spine patterns, numbers and relative sizes of ribs, and overall shell shape. Thus, the determination of which name is correct for any particular fossil is tentative at best. Time may well prove that names used herein are synonyms of some previously described taxon. Likewise, almost certainly, time will prove that there are syynonyms that might have been included in the synonymy of any particular species. We have chosen to take a conservative approach and only include as synonyms those for which we have no doubts.

Measuring these irregular shells is also difficult. In this study the height is measured (as nearly as possible) perpendicular to the hinge, along a line from the umbo to the ventral edge. However, this is easier said than done. For example, the lectotype of *S. gumanomocon*

Text-figure 2.—Right valve of *Spondylus bostrychites* Guppy, 1867, still encased in the outcrop at locality TU 1219, on the Rio Amina, near Potrero.

Brown and Pilsbry, 1913, was stated to be 175 mm in length by the original authors. Palmer (1938, explanation to pl. 16) says "Height 181 mm". If one measures the maximum dimension of this shell it is 181 mm, but if one measures along a line that more or less bisects the valve then it is 175 mm.

The length is here taken as the maximum distance from the anterior to the posterior margins of the shell, along a line as nearly as possible parallel to the hinge and, more importantly, at right angles to the measured height.

Diameter is measured only for paired valves and is the maximum distance between two planes tangent to the outside of the right and left valves, paralleling the valve margins.

SYSTEMATICS

Family **SPONDYLIDAE** Gray, 1826

Genus **SPONDYLUS** Linnaeus, 1758

Spondylus Linnaeus, 1758, p. 690.

Type species.—*Spondylus gaederopus* Linnaeus, 1758 (by subsequent designation, Schmidt, 1818); Recent, "M. Mediterraneo" (Linnaeus, 1758); and "in the eastern Atlantic from Morocco to Senegal, and in the Atlantic islands" (Dodge, 1952, p. 126).

Diagnosis.—Shell pectiniform but usually deformed as a result of fixation of the right valve umbonal area to the substrate; right valve generally larger and more inflated than the left, with a higher triangular cardinal area in which the internal ligament is lodged in a pit located between two stout crural teeth that, in the right valve, are immediately adjacent to the pit but, in the left valve, are outside of the sockets for the reception of those of the right valve; sculpture primarily radial, with ribs of primary, secondary, and tertiary size, the primary almost universally bearing strong pointed spines; smaller spines or pointed nodules often present on the secondary and tertiary radials; right valve may be concentrically foliaceous adjacent to attachment area.

Remarks.—Although *Gaideropa* Deshayes, 1832 is cited as an objective synonym of *Spondylus* Linnaeus, 1758 in the *Treatise on Invertebrate Paleontology* (Hertlein and Cox, 1969, p. N378), when one examines the original reference of Deshayes (1832, p. 163)[1], it is obvious he was merely giving the vernacular name of the species *Spondylus gaederopus* Linnaeus, 1758.

Spondylus bostrychites Guppy

Plate 1, figures 1–3; Plate 2, figure 1; Text-figure 2

Spondylus bifrons Sowerby, 1850, p. 53. (*non S. bifrons* Goldfuss, 1835).

Spondylus bostrychites Guppy, 1867, pp. 164 (list), 176 (*nom. nov. pro Spondylus bifrons* Sowerby *non* Goldfuss) (reprinted Harris, 1921, pp. 191, 203); Gabb, 1873, p. 257; Guppy, 1874, p. 443 (in part); Dall, 1898, p. 758 (in part, not all localities); Maury, 1917, p. 190 (354), pl. 32(58), fig. 4; Vaughan *et al.*, 1921, pp. 129, 145; Pilsbry, 1922, p. 413; Hanna, 1926, p. 477, pl. 24, figs. 3, 4; Palmer, 1938, p. 6(150) (in part, not references to Bowden specimen), pl. 1(16), fig. 2 only; pl. 2(17), figs. 1, 3, 5; pl. 3(18), figs. 1–5; Ramírez, 1956, pp. 13, 15–17; Pflug, 1961, p. 77, pl. 23, figs. 1, 8.

[?] *Spondylus bostrychites* Guppy. Maury, 1920, p. 22.

[?] *Spondylus bostrychites?* Guppy. Hubbard, 1920, p. 97; Vaughan *et al.*, 1921, p. 150.

Spondylus sp. indet. Vaughan *et al.*, 1921, p. 123.

INCORRECT REFERENCES TO *Spondylus bostrychites*:

Spondylus bostrychites Guppy. Guppy, 1873, p. 87 (reprinted Harris, 1921, p. 219); Dall, 1903, p. 1586; Woodring, 1925, p. 76, pl. 9, figs. 5–7; Palmer, 1938, p. 6(150) (in part, Bowden specimen only), pl. 1(16), fig. 1 only (Bowden Formation, Jamaica; probably = *S. americanus* Hermann, 1781).

Spondylus bostrychites Guppy. Dall, 1915, p. 124, pl. 19, fig. 4 (Tampa Limestone, Florida; = *S. chipolanus tampaensis* Mansfield, 1937).

Spondylus bostrychites Guppy. Cooke, 1919, p. 144, pl. 11, figs. 11a, 11b (Anguilla Limestone, Lesser Antilles; = *S. scotti* Brown and Pilsbry, 1913, *fide* Woodring, 1982, p. 601; however, specimens illustrated by Cooke have a strong similarity to *S. chipolanus* Dall, 1898).

Spondylus bostrychites Guppy. Trechmann, 1930, p. 211 (Manchioneal Beds, Jamaica; = *S. chiriquiensis* Olsson, 1922, *fide* Palmer, 1938, p. 155).

Spondylus bostrychites Guppy. Anderson, 1929, p. 158 (Tubará Group, Colombia; = *S. colombiensis* Weisbord, 1929).

Spondylus bostrychites Guppy. Perrilliat Montoya, 1963, p. 10, pl. 2, figs. 2, 6 (Agueguexquite Formation, Mexico; = *S. americanus* Hermann, 1781).

Spondylus bostrychites Guppy. Ferreira, 1965, p. 5, figs. 7–10 (Pirabas Limestone, Brazil; appears to be *S. chipolanus tampanensis* Mansfield, 1937[2]).

Spondylus bostrychites Guppy. H. Vokes, 1986, p. 174, text-fig. 1 (Moín Formation, Costa Rica; = *S. chiriquiensis* Olsson, 1922).

> *Testa subregularis, rotundata, ventricosa, margine latiusculo, valide denticulato; extus radiatim costata, costis 5 ad 6 spiniferis; area cardinali alterius valvae angustissima, alterius latiori.*

> Nearest to *S. imperialis* [Chenu, 1843], easily distinguishable by the area of one valve being very narrow, and that of the other being rather broader, though still narrow. (Sowerby, 1850, p. 53)

Diagnosis.—Shell shape pectiniform, ornamented with alternating coarser and finer spinose ribs; valves

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[1] What Deshayes says is [translated]: "GAIDEROPE. *Gaideropa.* We used to name thus, or we used to give the name of 'donkey's foot', which is synonymous, to a rather common shell, that the ancients placed in the spiny oysters, and which is placed today in the genus Spondyle, under the denomination of *Spondylus gaderopus* [*sic*]. See SPONDYLE."

[2] In 1887, C. A. White described *Spondylus pinguisculus* (p. 47, pl. 9, figs. 22, 23) from the same Pirabas Limestone locality. Unfortunately the White species is based upon an internal mold lacking any trace of the external ornamentation. The name has forty years priority over the Mansfield name and, if the Pirabas species proves to be the same as the Tampa one, would supersede it.

unusually symmetrical, rarely any trace of an attachment area.

Description.—Shell rounded, pectiniform, subequivalved with the lower (right) valve slightly more inflated than the upper (left) one; attachment area on lower valve small or absent, marked occasionally by small area of raised concentric lamellae; remainder of surface of right valve and all of the left with radial ribbing consisting, on well-preserved valves, of ribs of four different strengths: the strongest, primary ribs most prominent and bearing large, elongate flattened or fluted spines, the ribs of secondary strength with distantly spaced, nodose spinules; the tertiary riblets occurring in groups of two to four, commonly three, separating the primary and secondaries, and often relatively smooth; quaternary riblets visible only on exceptionally well-preserved valves, submicroscopic and exceedingly numerous, often being present on the sides and upper surfaces of the primary, secondary, and tertiary ribs. Well-preserved valves also with ribbing crossed by fine raised growth lines that form small raised spinose flutings on the rib tops. Commonly seven primary ribs on the lower (right) valve and six on the upper (left) one. Cardinal area of the lower valve somewhat broader than that of the narrow, often linear, upper one; both coarsely striated. Auricles moderately large, with radial ribbing that may be obscured by strong, raised growth lamellae. Adductor scar gently arched to almost straight dorsally, broadly rounded on lateral and ventral sides; ventral internal valve margins crenulated by termination of external radial ornament.

Lectotype.—BMNH LL 9946 (selected by Palmer, 1938).

Type locality.—Locality TU 1219 (here restricted), Gurabo Formation, Río Amina, bluffs on east side of river immediately upstream from ford that is 2 km west of Potrero and about 3 km downstream from "La Represa" (= locality USGS 8516; see Saunders, Jung, and Biju-Duval, 1986, text-fig. 34).

Material.—Over 100 valves, many paired; plus numerous immature and/or fragmentary specimens, from many localities, mostly in the shallow-water facies of the Gurabo Formation.

Measurements (in mm).—

	height	*length*	*diameter (paired valves)*	*specimen locality*
BMNH LL 9946[1]	100	101.5	—	unknown[3]
BMNH LL 25706[2]	89	81	62	unknown[3]
BMNH LL 25707[2]	94	90	—	unknown[3]
BMNH LL 25708[2]	94	90	—	unknown[3]
BMNH LL 25709[2]	62	58	—	unknown[3]
BMNH LL 25710[2]	55	55	—	unknown[3]
USNM 450387	114	88	—	TU 1278
NMB G 16963	80	75	57	NMB 16821

[1] lectotype; [2] paralectotypes; [3] Heneken Collection, "San Domingo".

Remarks.—Although there are rare specimens of *S. bostrychites* Guppy, 1867, from the Cercado Formation (one pair from loc. TU 1222, near Moncion) and from the Mao Adentro Member of the Mao Formation on the Río Gurabo (locs. TU 1440, NMB 15822; see Saunders, Jung, and Biju-Duval, 1986, text-figs. 4, 5), the vast majority of the specimens have been taken in the shallow-water facies of the Gurabo Formation. In our collections and those of the Naturhistorisches Museum, the species is most abundant along the Río Gurabo above the ford, in beds that Maury (1917, p. 437) referred to her Zones D (loc. TU 1215 = NMB 15842–15858; see Saunders, Jung, and Biju-Duval, 1986, text-figs. 4, 5) and F (locs. TU 1277, 1296 = locs. NMB 15864–15875; see Saunders, Jung, and Biju-Duval, 1986, text-figs. 4, 5), at "Bluff 1" (of Maury, 1917, p. 426, where she noted it was "common") on the Río Mao (locs. TU 1293, NMB 16910; see Saunders, Jung, and Biju-Duval, 1986, text-fig. 29). and at the ford on the Río Amina (locs. TU 1219, NMB 16807; see Saunders, Jung, and Biju-Duval, 1986, text-fig. 34). Although the NMB team was not able to collect the latter locality to any great degree, in the TU collections from locality TU 1219 alone we have 20 adult valves (three paired) and 40 immature valves. Inasmuch as this is certainly one of the localities where the original Heneken Collection[3] was made, locality TU 1219 is here offered as a restriction of the type locality, which was only "San Domingo".

The species of *Spondylus* are all discouragingly similar and one species may be distinguished from another only with great difficulty. One of the most striking characteristics exhibited by *Spondylus bostrychites* is the *lack* of an attachment area. Most species are marked by a relatively large area of concentric foliations in the umbonal area of the right valve. As may be seen from the various specimens figured, this is not usually developed in *S. bostrychites*. Of all of the specimens in the TU collections only three show any trace of this attachment area.

The significance of the lack of attachment area would seem to be that, unlike the majority of spondylid species, which attach to some hard substrate — corals, rocks, etc., *S. bostrychites* did not affix itself to any hard surface but "floated" on a silty bottom. Waller (written communication, April 2, 1990) has suggested that the species may be an opportunistic cementer, with settling spat cementing themselves to tiny hard objects on the silty bottom when such objects may be found. The same life-style has been documented for the large oyster *Hyotissa haitensis* (Sowerby, 1850), which occurs

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[3] The Heneken Collection was sent to the Geological Society of London in 1848 and was the basis for the molluscan descriptions of Sowerby (1850) and Guppy (1876).

together with *S. bostrychites* at many localities (see Meeder, 1987, p. 11).

Specimens from several other formations throughout the western Atlantic have been cited as *S. bostrychites*. In our opinion, all of these, with the possible exception of the Puerto Rican specimens listed but not figured by Maury (1920, p. 22) and Hubbard (1920, p. 97), both of which were based on incomplete molds, prove to be other species. In particular, the examples from the Bowden Formation, Jamaica, which have been figured by Woodring (1925, pl. 9, figs. 5–7) and Palmer (1938, pl. 16, fig.1), show the attachment area (see Pl. 1, fig. 4). They are here assigned to the Recent species *S. americanus* Hermann, 1781.

Comparisons.—The Recent Caribbean species *Spondylus erinaceus* Reeve, 1856 (pl. 11, fig. 39), superfically resembles *S. bostrychites* in the general aspect of the surface ornament, but differs in having only five primary radial ribs (in contrast to the six or seven of *S. bostrychites*) adorned with palmate scales rather than spines, with five (rarely six) well-developed scaly ridges devoid of any sort of spine formation between them. The shell also tends to be attached to coralliferous surfaces and, consequently, to develop a relatively strong dorsal triangular area above the hinge region on the right valve. This latter feature seems to be the principal difference between the two forms. Nevertheless, *S. erinaceus* with its globose, symmetrical shells, well shown in the illustration given by Garcia (1989, pl. 1) may be the descendant of *S. bostrychites*. Certainly, no other species comes as close.

Occurrence.—Unnamed formation: López area (TU 1445). Cercado/Gurabo formations: Río Cana area (TU 1354; NMB 16817, 16818, 16821, 16824, 16861, 16862, 16865, 16867, 16868, 16878); Río Gurabo area (TU 1209, 1210, 1211, 1213–1215, 1222, 1231, 1277, 1278, 1279, 1296, 1338, 1368, 1369, 1416; NMB 15804, 15806, 15807, 15809, 15815, 15836, 15842–15844, 15846, 15848, 15851, 15853, 15855, 15856, 15862–15868, 15871, 16808, 16809, 16811); Río Mao area (TU 1225, 1293; NMB 16910); Río Amina area (TU 1219, 1220, 1248, 1370, 1371, 1411, 1412, 1455; NMB 16805, 16807); Santiago area (TU 1205, 1206, 1207, 1227A, 1250, 1380, 1404, 1405, 1449, 1453; NMB 17268). Mao Formation: Río Gurabo (TU 1440; NMB 15822).

Distribution.—Unnamed formation (López area), Cercado and Gurabo formations, and Mao Adentro Member of the Mao Formation, Dominican Republic. Other occurrences in the Caribbean fossil record are uncertain, but the specimen from the Imperial Formation (Pliocene) of California reported by Hanna (1926) may well be this species.

Spondylus lucasi Maury

Plate 2, figures 2, 3

Spondylus lucasi Maury, 1920, p. 23, pl. 5, fig. 1.

> Shell oval, oblique, small for the genus. The cardinal area is defective and broken, but shows traces of the isodont hinge of *Spondylus*. The sculpture consists of [?eight] stronger, low, primary, radiating, rounded threads bearing spines at intervals, and between every two of these primaries are eight to ten or twelve much more delicate radiating lines. The central one of these is slightly stronger than the rest. It does not stand out sharply but the eye can discern that it is a shade thicker. The fine radii between the primaries nearly always alternate in strength, the finest lines of all being visible only with a lens. All of the fine radii are ornamented with minute scales, giving them a beaded appearance, especially on the anterior part of the valve. (Maury, 1920, p. 23)

Diagnosis.—Shell shape pectiniform, ornamented by numerous finely spinose radial ribs; approximately every seventh of these slightly stronger and with longer spines.

Description.—Shell, a left valve, slightly suboval, rounded in outline; a small rounded umbo; auricles moderately short and narrow, having surface ornament of fine radial ribbing similar to that on the entire valve with microscopically small spines and raised growth lamellae. Valve ornament of seven primary radial ribs bearing relatively strong radial spines, usually six or seven in number and distantly spaced, although the anterior primary rib bears but one such spine. Between each pair of primaries, on the median surface of the valve, there are three moderately small secondary radials with a slightly weaker tertiary between each of the stronger ribs. The tertiary radials tend to increase in strength with growth, becoming indistinguishable from the secondaries toward the valve margin, so that there appear to be seven secondary ribs between each pair of primaries. Surface of all secondary and tertiary radials marked by closely approximate laciniate projections of growth lamellae. Interspaces between ribs narrow, flat-bottomed, with three rows of microscopic spinelike projections, one medial in position and the others on the slightly raised margins of the adjacent radials.

Lectotype.—AMNH 22514 (here designated).

Type locality.—Reeds' locality 370, east shore of Guánica Harbor, Puerto Rico [see Maury, 1920, pp. 1, 7; data on label with specimen].

Material.—A single left valve from locality TU 1211.

Measurements (in mm).—

	height	*length*	*locality*
AMNH 22514[1]	33[2]	28[2]	see above
USNM 450389	54.5	53	TU 1211

[1] lectotype; [2] estimated, badly broken.

Remarks.—A single left valve from locality TU 1211 (Río Gurabo; see Saunders, Jung, and Biju-Duval, 1986, text-fig. 5) is here identified as *Spondylus lucasi* Maury, 1920, originally described from the Guánica Limestone (= Ponce Limestone) and the Quebradillas Limestone of Puerto Rico. The Ponce Limestone, from the south coast, although originally described as Oligocene in age is now considered to be early Miocene; the Quebradillas Limestone, from the north coast, is now considered Pliocene. Although slightly larger than the type of *S. lucasi*, the Dominican specimen agrees so completely in all details of the ornamentation of that form as figured by Maury (see Pl. 2, fig. 3), as to leave little doubt that it represents the second record of its occurrence in the Caribbean fossil fauna.

Comparisons.—The shell of *Spondylus lucasi* Maury, 1920, has a much more evenly patterned ornament than *S. scotti* Brown and Pilsbry, 1913, as figured by Woodring (1982, pl. 97, figs. 8–10), from the early Miocene La Boca Formation of Panama, with which he tentatively [p. 601] synonymized *S. lucasi*.

Jung (1965, pl. 55, figs. 2, 3 and 1971, pl. 1, figs. 4, 5) has figured specimens from the early Miocene Cantaure Formation and the early middle Miocene Grand Bay Formation, respectively, that he compares to *S. lucasi*. Both seem better assigned to *S. scotti*.

Spondylus lucasi and the older *S. scotti* are similar only to the extent that both have relatively fine radial ribs, in contrast to such species as *S. bostrychites* Guppy, 1867, in which the ribs are much wider (compare Pl. 1, fig. 3b, and Pl. 2, fig. 2b). In *S. scotti*, there are many more major radials (17 in the type specimen) with fewer secondary radials between each pair (four to eight in the type specimen) than in *S. lucasi*, which has only seven or eight primary ribs, with about seven secondary ribs between each pair of primaries.

In the Recent fauna of the Indo-Pacific the species *S. anacanthus* Mawe, 1823, is perhaps the most nearly similar to this unusual species, which is marked by having a much more regular surface ornament than is typical for most species of *Spondylus*.

Occurrence.—Gurabo Formation: Río Gurabo (TU 1211).

Distribution.—Gurabo Formation, Dominican Republic. Ponce Limestone, Early Miocene; Quebradillas Limestone, Pliocene; Puerto Rico.

Spondylus gumanomocon Brown and Pilsbry
Plate 3, figures 1–4

Spondylus Americanus Lamarck. Gabb, 1873, p. 257 (not of Lamarck, 1819, nor of Hermann, 1781).

Spondylus gumanomocon Brown and Pilsbry, 1913, p. 514 (footnote); Maury, 1917, p. 191(355); Pilsbry, 1922, p. 413, pl. 43, figs. 4 (paralectotype), 5 (lectotype); Palmer, 1938, p. 9(153), pl. 1(16), figs. 3, 4 (lectotype); pl. 2(17), figs. 2, 4 (paralectotype); Pflug, 1961, p. 13.

[?] *Spondylus gumanomocon* Brown and Pilsbry. Maury, 1920, p. 23; Hubbard, 1920, p. 97; Olsson, 1922, p. 207(379), pl. 21(24), fig. 1.

Spondylus guamanomocon Pilsbry and Johnson [*sic*]. Vaughan *et al.*, 1921, p. 153.

Spondylus carmenensis Hodson *in* Hodson, Hodson, and Harris, 1927, p. 41, pl. 25, figs. 1–3.

> A species resembling *S. varians* Sowb. (*S. delessertii* Chenu [1845]). The upper valve is Pectiniform, orbicular, of moderate thickness, with low radial ribs, the principal ones irregularly spinose, spines short; cardinal area small and short, as in *S. americanus* [Hermann, 1781]. Lower valve very ponderous, with a long, level (not receding) cardinal area, and a very long, straight (or sometimes laterally curved) beak, the cavity of which is deeply excavated in young shells, nearly solidly filled in old ones. Sculpture like the upper valve, except that it is more or less extensively foliated towards the beak .... This is the form identified by Gabb as *Spondylus americanus*. (Brown and Pilsbry, 1913, p. 514)

Diagnosis.—Shell very massive, irregular in shape, with lower (right) valve greatly enlarged. Radial ornament of alternating larger and smaller spinose ribs.

Description.—Shell attaining large size (over 150 mm in height), attached by the umbo of the right valve, which tends to become more elongate than the relatively pectiniform, less-inflated left one, especially as the high, triangular cardinal area increases in height with shell growth. Hinge line straight, with narrow cardinal area marked by a much shorter ligamental pit than that extending the full height of the area of the right valve. Sculpture of concentric, foliated ribbing strong on the upper portion of the right valve, and often extending the full length of the shell, weaker on the upper, left valve. Radial ribbing variable, commonly three to five strong spinose primaries with two to five secondary and tertiary ribs between each pair. However, the relative strength of these ribs varies greatly, with the secondaries on some specimens becoming as strong as the primaries and developing spines of equal strength; in contrast, the tertiaries may weaken so as to be microscopic or, occasionally, divaricate as growth proceeds to the point that the number of tertiary ribs on a valve may differ between each pair of primaries.

Lectotype.—ANSP 2869 (selected by Pilsbry, 1922, pl. 43, fig. 5).

Type locality.—Mao Formation, Samba Hills, south of Guayubin (here restricted), Dominican Republic.

Material.—In addition to the type lot of five valves, five paired valves, plus seven more or less complete adults and numerous fragments and juveniles, almost all from the Mao Adentro Member of the Mao Formation.

Measurements (in mm).—

	height	*length*	*diameter (paired valves)*	*locality*
ANSP 2869[1]	175	115	—	unknown[6]
ANSP 72724A[2]	154	103	—	unknown[6]
ANSP 72724B[2]	96.5	94	—	unknown[6]
ANSP 72724C[2,3]	126	97.5	—	unknown[6]
ANSP 72724D[2]	162	123	—	unknown[6]
USNM 450390	81	56	47	TU 1221
PRI 21986[4]	74	51	50	Hodson 2436
PRI 21987[5]	80	76	43	Hodson 2436

[1] lectotype; [2] paralectotypes; [3] specimen figured by Pilsbry (1922) and Palmer (1938) as "paratype"; [4] holotype of *S. carmenensis* Hodson; [5] paratype of *S. carmenensis* Hodson; [6] Gabb Collection, "Santo Domingo".

Remarks.—The specific name *S. gumanomocon* was given by Brown and Pilsbry (1913) to material in the Gabb Collection, which Gabb had identified as *S. americanus* Lamarck, 1819. The exact locality of Gabb's five specimens remains unknown. Although we have specimens from the Río Gurabo and the Río Mao, the majority of our shells were collected in the Samba Hills just south of Guayubin (locs. TU 1221, 1245), an area that Gabb almost certainly collected. In the narrative of his travels in Santo Domingo he says, concerning the Samba Hills, near Guayubin: "They are barely fifty feet high immediately adjoining the Guayubin River, though twice that a mile or two east, and they almost disappear very soon after crossing the river. The horizontal beds continue to their southern base undisturbed, and where the road first reaches rising ground it climbs a few feet up the face of a sort of bluff, the exposed edges of a nearly horizontal sandstone, full of *Oysters* and *Spondylus*" (Gabb, 1873, p. 155).

This description fits our localities TU 1221 and 1245 (4.5 and 5 km south of the bridge at Guayubin, respectively) perfectly, for here the *only* shelled fossils are "*Ostrea*" *haitensis* Sowerby, 1850, and *Spondylus gumanomocon* (other mollusks are represented by molds). Although we are reasonably sure this is the area that Gabb's material came from, there is one difference between his material and ours: all of his shells are single valves, gray in color, and most of ours are paired valves, yellowish in color. So Gabb probably collected near our localities but not at them. For this reason, we have not restricted the type locality to one of our locality numbers.

Although the majority of specimens of *S. gumanomocon* come from the Mao Adentro Limestone Member of the Mao Formation, the species is not confined to those beds. Maury (1917, p. 355) cited the species as occurring at "Zone D, Río Gurabo at Los Quemados" (= locs. TU 1215, NMB 15842–15858; see Saunders, Jung, and Biju-Duval, 1986, text-figs. 4, 5) and both we and the Naturhistorisches Museum team collected the species at this locality. This is not unexpected as the locality is a coral reef in the Gurabo Formation. The Naturhistorisches Museum team also collected a single valve at Cañada de Zamba, in the Río Cana drainage (loc. NMB 16818; see Saunders, Jung, and Biju-Duval, 1986, text-fig. 15) in the coralline facies of the Gurabo Formation. Furthermore, they collected one specimen from the Cercado Formation, just above the mouth of Arroyo Bellaco (loc. NMB 16853; see Saunders, Jung, and Biju-Duval, 1986, text-fig. 15) near the coral reef in that tributary, and a second specimen from the Cercado Formation just below the contact with the Gurabo Formation on the Río Cana (loc. NMB 16842; see Saunders, Jung, and Biju-Duval, 1986, text-fig. 15).

The species *S. carmenensis* Hodson *in* Hodson, Hodson, and Harris, 1927 [p. 41, pl. 25, figs. 1–3], described from the "Oligocene" of the Buchivacoa District, State of Falcón, Venezuela, but probably coming from the Miocene La Puerta Group[4], agrees in shape and ornamentation with *S. gumanomocon*, and was synonymized by Palmer (1938, p. 155). We see no reason to disagree.

Comparisons.—Gabb (1873, p. 257) identified this species as *Spondylus americanus* Lamarck, 1819 (= *S. americanus* Hermann, 1781). Specimens of that species in the Tulane collections reveal a much more spinose ornamentation with all radials — primary, secondary, and tertiary—having spines that tend to be narrowly and elongately pointed. Given the inherent variability of species of *Spondylus*, and the fact that many of the molluscan species present in the fauna of the Mao Formation are still living in the western Atlantic or Caribbean area today, the two forms may ultimately prove to be the same. Certainly it seems probable that *S. gumanomocon* and *S. americanus* are part of the same lineage.

Occurrence.—Cercado/Gurabo formations: Río Cana area (NMB 16818, 16842, 16853); Río Gurabo (TU 1231 [? = TU 1215]; NMB 15837). Mao Formation:

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[4] The type locality was given subsequently by Hodson and Hodson (1931, p. 5) as southeast of Dabajuro, and expanded by Palmer (1938, p. 154), to "about 10 miles east and 4 miles south of Dabajura [*sic*]". The type locality for the La Puerta Formation (now Group) is the La Puerta syncline, southeast of Dabajuro. The *Lexico Estratigrafico de Venezuela* (1970, p. 672) indicates only the La Puerta Group in the Buchivacoa District. It is the lateral equivalent of the Socorro, Urumaco and Codore formations, just to the east, and the exact stratigraphic level is uncertain.

Guayubin area (TU 1221, 1245, 1281); Río Gurabo area (TU 1208, 1366; NMB 15822, 15825); Río Mao (TU 1336).

Distribution.—Coralline facies of the Cercado Formation and the Gurabo Formation, Mao Adentro Limestone Member of Mao Formation; Dominican Republic. ?La Puerta Group, Venezuela; Miocene. Unknown formation, Costa Rica; Pliocene.

NEOGENE PALEONTOLOGY IN THE NORTHERN DOMINICAN REPUBLIC
13. The Class Echinoidea (Echinodermata)

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ABSTRACT

Nine echinoid species are reported from the Miocene and Pliocene of the Dominican Republic. Four species are still living in the Caribbean and two of the others closely resemble living species. For this reason it is suggested that living conditions in the Miocene and Pliocene were very similar to those now present in the region. One new species is described from the early Pliocene: *Clypeaster maoadentroensis*.

RESUMEN

Se describen nueve especies de equinoidos del Mioceno y Plioceno en la República Dominicana. Cuatro especies están todavía viviendo en el mar Caribe, y dos de los otros se parecen mucho a especies actuales. Por esta razón, se cree que el ambiente natural en el Mioceno y Plioceno se parece mucho a él de hoy en la región. Se describe un especie nueva del Plioceno temprano: *Clypeaster maoadentroensis*.

INTRODUCTION

Only a few fossil echinoids have been described from the Dominican Republic (Jackson, 1922). The present collection, for the most part made by Peter Jung, John Saunders, and Emily and Harold Vokes, is important not only because of the number of specimens but also because they were collected from measured sections, making it possible to know with certainty their age relative to each other. The fauna is of particular interest because of the close similarity of the fossil echinoids to those now living in the Caribbean. This similarity makes it possible to suggest the living habits and habitats of these fossil species.

Background information on the collecting localities has been presented in detail by Saunders, Jung, and Biju-Duval (1986), and faunal monographs on many of the faunal groups present have been published previously in this series (*e.g.*, Jung, 1986; Foster, 1986; Foster, 1987; Cairns and Wells, 1987; Logan, 1987; Bold, 1988; E. Vokes, 1989; H. Vokes, 1989; Jung and Petit, 1990). A map showing collected sections in the Cibao Valley of the northern Dominican Republic that appears in all of these publications (*e.g.*, Saunders, Jung, and Biju-Duval, 1986, text-fig. 3) is reproduced here as Text-figure 1.

ACKNOWLEDGMENTS

I thank Peter Jung, John Saunders, Emily and Harold Vokes not only for collecting these fossil echinoids but for permitting me to study them. They also read the manuscript, and I thank them for their suggestions. Additional reviews were undertaken by M. McKinney (University of Tennessee, Knoxville, TN) and Graig Shaak and Douglas Jones (Florida State Museum, University of Florida, Gainesville, FL). Peter Hoover was of great assistance in the preparation of the manuscript for publication. Without his help the paper would not have been published.

The photography was done by Arnold Powell and the artwork by Mary Parrish.

PREVIOUS WORK

Jackson (1922, p. 6) studied a small collection of fossil echinoids from the Dominican Republic that is now in the USNM. In this collection, he identified seven species, two of them, *Clypeaster concavus* Cotteau, 1875 and *Brissopsis antillarum* Cotteau, 1875, from beds he considered Oligocene. Four he considered Miocene, including *Cidaris* sp. a of Jackson (1922),

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Table 1.—Distribution of northern Dominican Republic echinoid species, by formation and age.

age	*unit*	*species*
early Pliocene	Mao Fm., Mao Adentro Mbr.	*Echinometra lucunter* (Linnaeus, 1758) *Clypeaster maoadentroensis*, new species
	Gurabo Fm.	*Moira atropos* (Lamarck, 1816) *Brissopsis jimenoi* Cotteau, 1875 *Schizaster doederleini* (Chesher, 1972) *Clypeaster caudatus* Jackson, 1922
late Miocene	Cercado Fm.	*Clypeaster* cf. *C. sunnilandensis* Kier, 1963 *Encope aberrans imperforata* Kier, 1963
late early Miocene	Baitoa Fm.	*Mellita* sp.

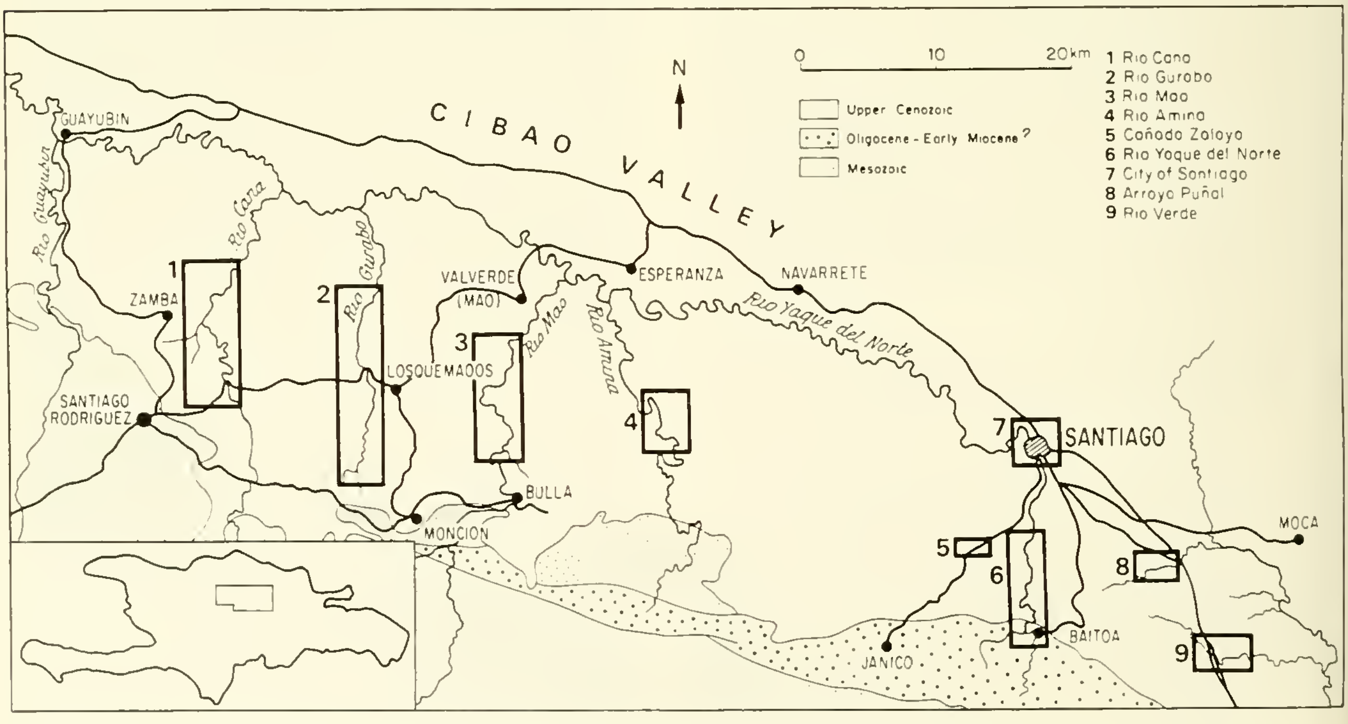
Cidaris melitensis Wright, 1855, *Echinopedina cubensis* Cotteau, 1881, and *Clypeaster caudatus* Jackson, 1922. One species, *Clypeaster dalli* (Twitchell *in* Clark and Twitchell, 1915), he considered Miocene or Pliocene.

Jackson had five specimens from the Cevicos Limestone that he referred to *Clypeaster concavus*, but four of them are only fragments and can not be specifically identified with any certainty. The one whole specimen is aberrant, having only four petals, and may be *C. concavus*, although its oral surface is not as concave as is typical in this species. No specimens of this species are present in the new collections.

The specimen from the Cevicos Limestone that Jackson identified as *Brissopsis antillarum* is badly crushed, making positive identification impossible. It is not conspecific with the specimen in the present collections referred to *Brissopsis jimenoi* Cotteau, 1875. The posterior petals in Jackson's specimens are straight, whereas in *B. jimenoi* they are confluent adapically but diverge distally.

The Dominican Republic specimens that Jackson referred to *Cidaris* sp. a and *Cidaris melitensis* are based only on spines. Many cidarid spines are in the present collection but are not described. The Dominican Republic specimen from the Gurabo Formation that Jackson referred to *Echinopedina cubensis* was considered to be a different species by Lambert (*in* Sánchez Roig, 1949, p. 39), who made it the holotype of a new species, *Hebertia jacksoni* Lambert *in* Sánchez Roig, 1949. However, this specimen is very badly weathered, with all the tuberculation removed and the peristome broken away. It cannot be generically identified.

Jackson's *Clypeaster caudatus* is well-represented in the present collections and one of the new specimens



Text-figure 1.—Locality map for the sections measured and described by Saunders, Jung, and Biju-Duval (1986). The TU collections were made in these same areas but in intervening areas also. See Appendix 4 of that work for a complete description of all TU localities.

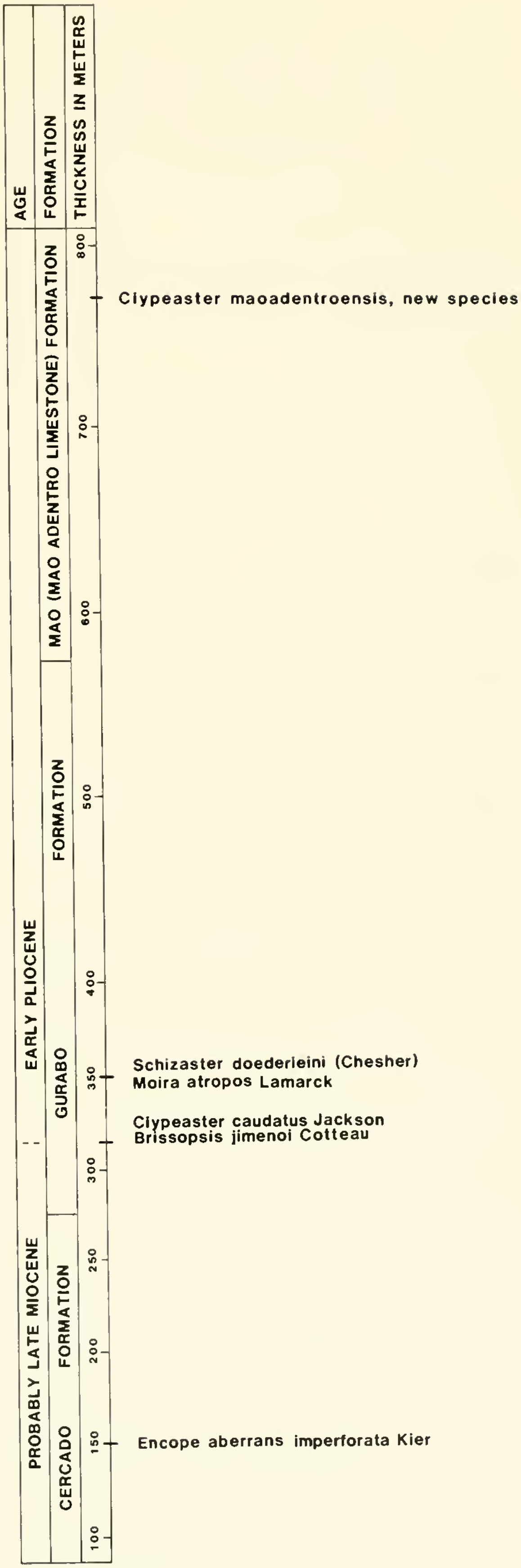
is illustrated (Pl. 5, figs. 1, 2). The specimen he referred to *Clypeaster dalli* is consubspecific with specimens of that species from the Pleistocene Caloosahatchee Formation and post-Caloosahatchee beds in Florida (Kier, 1963, p. 29). Kier considered *C. dalli* to be a subspecies of *C. rosaceus* (Linnaeus, 1758).

BIOSTRATIGRAPHY

Nine species of echinoids can be identified from the Neogene of the Dominican Republic (Table 1). Six occur in the Río Cana section (Text-fig. 2): one in the Cercado Formation, four in the Gurabo Formation, and one in the Mao Adentro Limestone. The oldest species, *Encope aberrans imperforata* Kier, 1963, occurs in the Cercado Formation 150 m above the base of the Río Cana section in beds considered of probable late Miocene age (Saunders, Jung, and Biju-Duval, 1986, text-fig. 16). This subspecies has been reported elsewhere (Kier, 1963, p. 35) from the post-Caloosahatchee beds and the Tamiami Formation (Buckingham Limestone Member) of Florida. Dubar (*in* Oaks and Dubar, 1974) dates the Caloosahatchee as early to medial Pleistocene and the Buckingham Limestone Member of the Tamiami as medial to late Pliocene.

Four species occur near the base of the Gurabo Formation (317–350 m above the base of the Río Cana section) in beds considered by Saunders, Jung, and Biju-Duval (1986, text-fig. 16) to be of early Pliocene age. *Brissopsis jimenoi* Cotteau, 1875 is reported from beds in Cuba considered of Miocene age, but this age determination was made in 1875 and it is not known from what formation the specimens were collected. *B. jimenoi* is very similar and may be synonymous with *Brissopsis elongata* Mortensen, 1907, now living in the Caribbean.

Clypeaster caudatus Jackson, 1922 was originally reported from the Mao Adentro Limestone or Gurabo Formation of the Dominican Republic. Sánchez Roig (1949, p. 80) reported the species as occurring in the Oligocene of Cuba, but most modern workers consider Sánchez Roig's "late Oligocene" of Cuba as Miocene. I have not been able to compare the Cuban specimens with those from the Dominican Republic so I can not confirm this identification. Gordon (1963, p. 636) considered *C. caudatus* to be a a synonym of *C. cubensis* Cotteau, 1875, which is known from the Miocene of Cuba and lower or middle Miocene of Puerto Rico. The petals in *C. caudatus* are less inflated than in the specimens Gordon referred to *C. cubensis*, and the two species are probably distinct. *C. caudatus* is also very similar to *Clypeaster rosaceus* (Linnaeus, 1758), known from the Miocene to Recent of the Caribbean region. Specimens of *C. caudatus* also occur in the northern Dominican Republic at Arroyo López. Poddubiuk (1985) argues that *C. rosaceus* is derived from *C. cub-*



Text-figure 2.—Occurrence of echinoids in the Río Cana section.

ensis and *C. caudatus* and discusses evolutionary changes in morphology in the lineage.

Moira atropos (Lamarck, 1816) lives today in the Caribbean and has been found as fossil in the Pliocene of South Carolina and Venezuela. *Schizaster doederleini* (Chesher, 1972) now lives in the Caribbean and has never before been found as a fossil.

The youngest species in the Río Cana section, *Clypeaster maoadentroensis*, n. sp., occurs low in the Mao Adentro Limestone, approximately 765 m above the base of the section. Saunders, Jung, and Biju-Duval (1986, text-fig. 16) consider these beds to be of late early Pliocene age. This species is quite distinct from *C. caudatus*, which occurs lower in the section in the Gurabo Formation. I know of no well-dated species of *Clypeaster* Lamarck, 1801, with which it has clear affinities.

Three species do not occur in the Río Cana section. *Mellita* sp. is present in the Baitoa Formation, which is considered older than the Cercado Formation. Eames *et al.* (1962, text-fig. 5) place the Baitoa in the middle or late Burdigalian or late early Miocene. In the Baitoa, *Mellita* is represented only by immature specimens whose affinities with other species are uncertain. *Clypeaster* cf. *C. sunnilandensis* Kier, 1963 occurs in the Cercado Formation (of probable late Miocene age). The specimens are only fragments but are quite similar to, though probably not conspecific with, specimens of *C. sunnilandensis* from the Pliocene of Florida. *Echinometra lucunter* (Linnaeus, 1758) is found in the Mao Adentro Limestone (of late early Pliocene age, according to Saunders, Jung, and Biju-Duval, 1986, text-fig. 16). This species lives today in the West Indies and off the west coast of Africa. It has been found previously as fossil from Jamaica, and from the Pleistocene of Angola and Florida.

Fragments of sand dollars occur at many horizons in the measured sections at Río Cana (Saunders, Jung, and Biju-Duval, 1986, text-figs. 15, 16). They are found in the Cercado Formation at localities NMB 16836, 16839, and 16842, approximately 228 to 241 m above the base of the section. They also occur in this section in the Gurabo Formation at localities NMB 16818 and 16858, 315–322 m above the base. Higher in the section, they occur in the Mao Adentro Limestone at locality NMB 16873, 690 m above the base. In the Río Gurabo section (Saunders, Jung, and Biju-Duval, 1986, text-figs, 5, 6), fragments of sand dollars occur below the base of the Gurabo Formation at localities NMB 15904, 15906, 15907, 15910, 15911, 15914, and 15915, which are 110–132 m above the base of the section. Finally, they occur in the Río Yaque del Norte section (Saunders, Jung, and Biju-Duval, 1986, text-fig. 21) at La Barranca at locality NMB 17268.

PALEOECOLOGY

Because so many of the Dominican Republic echinoid species are still extant, it is feasible to predict how the fossil echinoids lived. *Encope aberrans imperforata* Kier, 1963 is very similar to *Encope aberrans aberrans* Martens, 1867, which according to Serafy (1979, p. 76) lives from Cape Hatteras south to the Bahama Islands and throughout the Gulf of Mexico at depths from 12–90 m. In the Gulf of Mexico, Serafy reports that it lives on bottoms of crushed shell and quartz sand.

Brissopsis jimenoi Cotteau, 1875 is very similar to, and may be synonymous with *Brissopsis elongata* Mortensen, 1907, which lives along the coasts from Venezuela to Panama, and Belize and Puerto Rico at depths from 13–72 m. Kier (1975, p. 16) found this species living buried 40–100 mm in mud at depths of 12–18 m.

Clypeaster caudatus Jackson, 1922 is extinct, but is very similar to *Clypeaster rosaceus* (Linnaeus, 1758), now living in the Caribbean at depths from intertidal to 285 m. In the Florida Keys (Kier and Grant, 1965, pp. 26, 27), this species is abundant in 1–15 m, living on sand patches in or near fields of turtle grass.

Schizaster doederleini (Chesher, 1972) and *Moira atropos* (Lamarck, 1816) occur in the Gurabo Formation at the same locality. They also are found living together today in the Caribbean. Kier (1975, p. 14) reports the two species living buried 40–100 mm in mud at a depth of 12–18 m off Belize. Elsewhere *M. atropos* has been reported from the coast of North Carolina south to Brazil from littoral depths to 145 m.

Clypeaster maoadentroensis, n. sp., is quite distinct from any living species. Clypeasterids today are confined to tropical or subtropical regions and commonly are littoral–sublittoral, rarely occurring as deep as 500 m (Mortensen, 1948, p. 17). Among living species of *Clypeaster* Lamarck, 1801, *Clypeaster* cf. *C. sunnilandensis* Kier, 1963 most resembles *C. subdepressus* (Gray, 1825), which according to Serafy (1979, p. 66) is known from North Carolina southward through the Greater and Lesser Antilles, the Gulf of Mexico, and southward along the coasts of Central and South America to Brazil. It lives at depths from 5–210 m, but is most common in less than 50 m. Kier and Grant (1965, p. 28) found it most abundant between 5 and 12 m on sandy areas with little grass.

Echinometra lucunter (Linnaeus, 1758) lives today from Florida to Brazil and off the west coast of Africa. It is most common in shallow water less than 3 m deep (Kier and Grant, 1965, p. 18) and commonly lives in niches in rock.

In summary, seven of the Dominican Republic species are alive today or are very similar to species that live today. All of these living species occur in shallow water in the West Indies. Presumably, the conditions where the fossils lived were similar to those now in the Caribbean.

The most striking aspect of the Dominican Republic echinoid faunas is the large number of Miocene and Pliocene species that are still extant or are very similar to species now living. Three of the six early Pliocene species: *Echinometra lucunter* (Linnaeus, 1758), *Moira atropos* (Lamarck, 1816), and *Schizaster doederleini* (Chesher, 1972), are still alive; and a fourth, *Brissopsis jimenoi* Cotteau, 1875, may be synonymous with a living species, *B. elongata* Mortensen, 1907. The early Pliocene *Clypeaster caudatus* Jackson, 1922 is very similar to the living *C. rosaceus* (Linnaeus, 1758). Only one early Pliocene species, *Clypeaster maoadentroensis*, n. sp., is clearly distinct from any living species.

Of the two late Miocene species, only *Encope aberrans imperforata* Kier, 1963 is still extant, although subspecifically differentiated. The second, *Clypeaster* cf. *C. sunnilandensis* Kier, 1963 is very similar to the living *C. subdepressus* (Gray, 1825). The early Miocene *Mellita* sp. appears to be distinct from any living species.

The longevity of the Dominican Republic species is in sharp contrast to the Neogene echinoid faunas of the southeastern United States. Only two of the 16 species of echinoids that can be identified with certainty from the Pliocene of the eastern United States are still alive and both these species are subspecifically differentiated: *Lytechinus variegatus plurituberculatus* Kier, 1963 and *Encope aberrans imperforata* Kier, 1963. I suspect that the longevity of the Dominican Republic species is probably an indication that the environmental conditions in the region remained relatively the same, whereas they changed in the southeastern United States.

SYSTEMATIC PALEONTOLOGY

INTRODUCTION

The type specimens are housed in the Naturhistorisches Museum, Basel, Switzerland (NMB) and the U. S. National Museum of Natural History (USNM). The localities are either those of the NMB or of Emily and Harold Vokes of Tulane University, New Orleans, LA (TU). The stratigraphic and geographic location of all the NMB localities and some of the TU localities are plotted on maps and sections in Saunders, Jung, and Biju-Duval (1986). Other abbreviations used in this section include: Museum of Comparative Zoology, Harvard University, Cambridge, MA (MCZ). Many measured taxonomic characters of echinoids can be expressed in terms of percent of test length, herein abbreviated as %L.

SYSTEMATICS

Genus ECHINOMETRA Gray, 1825

Echinometra lucunter (Linnaeus, 1758)
Plate 4, figures 1–4

Echinus lucunter Linnaeus, 1758, p. 665.
For a synonymy, see Mortensen, 1943, p. 357.

Kier and Grant (1965) and McPherson (1969) describe aspects of the biology of this species.

Five specimens can be referred to this species. They are identical in all respects to Recent specimens of this species from the Florida Keys (see Pl. 4, figs. 1–4 for comparison of one of the fossil specimens with a Recent specimen). The fossil and Recent specimens share a similar number of plates relative to size, similar number of pore pairs in each ambulacrum, similar tuberculation, and tests of similar elongated shape.

Type material.—Figured specimen, USNM 375449.

Occurrence.—*Echinometra lucunter* occurs at locality TU 1438 in the Mao Adentro Limestone (Pliocene), in a roadcut 0.5 km south of the bridge at Guayubin, on the road to Sabaneta.

Distribution.—*Echinometra lucunter* lives today in the West Indies from Florida to Brazil and off the west coast of Africa. Arnold and Clark (1934, p. 140) report it as a fossil from Jamaica, Dartevelle (1953, p. 38) found it in the Pleistocene of Angola, Kier (1963, p. 19) found it in the Pleistocene Caloosahatchee Formation of Florida, where Donovan and Gordon (1989) also reported it in the Pleistocene Falmouth Formation.

Genus CLYPEASTER Lamarck, 1801

Clypeaster maoadentroensis, new species
Plate 4, figures 5–7; Text-figures 3, 4A

Etymology.—The species is named for the formation where the holotype was collected.

Material.—One moderately well-preserved specimen, which is somewhat weathered dorsally but whose test appears to be undistorted.

Shape and size.—Test, 98 mm long, 84 mm wide, and 44 mm high; greatest width central, greatest height slightly posterior to center, with test sloping more sharply posteriorly than anteriorly. Petals only very slightly inflated. Ventrally, test depressed deeply only in immediate vicinity of peristome.

Apical system.—Monobasal, five genital pores, center of apical system located slightly posterior to center at distance from anterior margin equal to 53 %L.

Ambulacra.—Petals long, extending almost to margin of test; anterior petal III slightly longer than other petals, length = 44 %L, petal IV = 39 %L, petal V = 42 %L; width of petals = 23–25 %L. Poriferous zone at greatest width = 5.5 %L, or 39 percent of the width of interporiferous zone at its greatest width. Petals closing distally with poriferous zone of same petal almost in contact; petal III with 80 pore pairs (in both zones), petal IV with 84, and petal II with 82. Distinct ambulacral groove extending ventrally from near margin to peristome.

Peristome.—Situated slightly posterior to center with center of peristome located at distance from anterior margin equal to 54 %L. Size of opening uncertain because of fracturing around peristome.

Periproct.—Located near posterior margin, opening wider than high with width = 5.4 %L, height = 5.1 %L. Sutures not clear enough to determine which plates enclose periproct.

Diagnosis.—Species characterized by smooth dorsal surface with petals only slightly inflated, pore pairs widely separated from each other, resulting in fewer pore pairs in petals, ventral surface depressed only in vicinity of peristome.

Type material.—Holotype, NMB M9746.

Comparison with other species.—This species is distinguished from *Clypeaster caudatus* Jackson, 1922, which occurs lower in the Río Cana section by its longer petals, wider poriferous zones, and in having the pore pairs in its petals more widely separated from each other in the same poriferous zones, resulting in fewer pore pairs in each petal. For example, a specimen of *C. caudatus* (NMB catalogue number unknown) with a petal II that is 39 mm long has 120 pore pairs, whereas the holotype of *C. maoadentroensis*, having a slightly longer petal (43.2 mm), has only 80 pore pairs. The greatest distance between two adjacent outer pores (measured along the length of the petal) near the midlength (Text-fig. 4A) of petal III in the holotype of *C. maoadentroensis* is 1.3 mm, but is only 0.8 mm in *C. caudatus* (Text-fig. 4B) in petal III of a specimen of similar size. Furthermore, the peristome in *C. maoadentroensis* is slightly posterior to the center, whereas it is central in *C. caudatus*. Finally, the ventral surface is depressed only around the peristome in *C. maoadentroensis* instead of over much of the ventral surface in *C. caudatus*. Although the relative inflation of the petals, position of the peristome, and shape of the test are characters that vary considerably within a species of *Clypeaster*, the distance between pore pairs in a poriferous zone is fairly constant, and therefore a reliable character for specific differentiation.

Of all the other species of *Clypeaster* from the West Indian region, *C. maoadentroensis* most resembles *Clypeaster duchassaingi* Michelin, 1855 from the "formations madréporiques" of Guadeloupe. *C. maoadentroensis* differs in having its apical system posterior to the center of the test, as opposed to anterior in *C. duchassaingi*, in having its posterior petals extending much nearer the posterior margin, a more posteriorly situated peristome, a blunter posterior margin, and a narrower anterior.

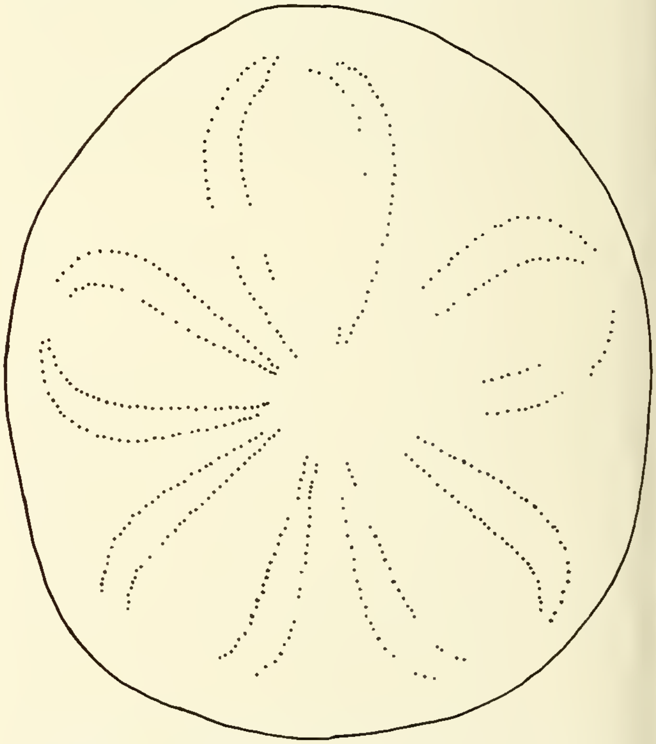
Occurrence.—Early Pliocene, Mao Adentro Limestone, locality NMB 17022, Río Cana section (Saunders, Jung, and Biju-Duval (1986, text-fig. 15). E. Vokes (written commun., 1984) considers this formation to be middle Pliocene in age.

Clypeaster caudatus Jackson, 1922
Plate 5, figures 1, 2; Text-figure 4B

Clypeaster caudatus Jackson, 1922, p. 36; pl. 3, figs. 1, 2; Sánchez Roig, 1949, p. 80, pl. 10, fig. 2; ?Gordon, 1963, p. 636.

Eight specimens and four fragments can be referred to this species, whose holotype is also from the Dominican Republic. They are similar to the holotype in having only slightly inflated petals, which close distally with their poriferous zones meeting at the end of each petal. Their tests are also relatively wide (84 to 94 %L) and their ventral surfaces are deeply depressed around the peristome.

Gordon (1963, p. 636) considered this species a synonym of *Clypeaster cubensis* Cotteau, 1875. I have compared the Dominican Republic specimens with the specimens that Gordon referred to *C. cubensis* from the Miocene Ponce Limestone of Puerto Rico. Although they are very similar, the Dominican Republic specimens have less inflated petals. Whether or not



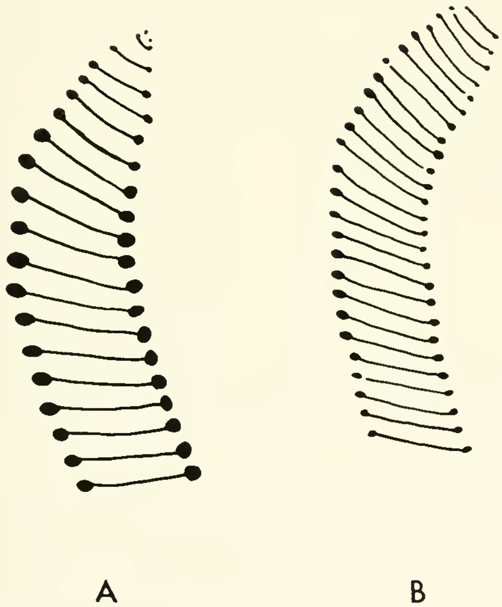
Text-figure 3.—*Clypeaster maoadentroensis*, n. sp., dorsal view of holotype, NMB M9746, ×1.

this difference is significant will not be known until more specimens can be studied. As pointed out by Kier (1963, p. 29), the extent of inflation of the petals is very variable in *Clypeaster rosaceus* (Linnaeus, 1758), a species quite similar to *C. caudatus*.

Type material.—Holotype, USNM 328235; paratype, USNM 328236; figured specimen, NMB M9747.

Occurrence.—According to Jackson (1922, p. 36), the holotype of *Clypeaster caudatus* came from float from the Gurabo Formation, or the Mao Adentro Limestone, Río Gurabo, near Los Quemados, Dominican Republic. The new material is from locality NMB 16858 (Saunders, Jung, and Biju-Duval, 1986, text-figs. 15, 16) in the Río Cana section 320 m above the base of the section near the base of the Gurabo Formation, from beds considered to be of early Pliocene age; and localities NMB 17272, 17274 (Saunders, Jung, and Biju-Duval, 1986, text-figs. 24, 26) in the Arroyo López section, beds B and D. The Vokes' material came from locality TU 1215, Gurabo Formation, Río Gurabo, from bluffs on both sides, from the ford on the Los Quemados–Sabaneta road, upstream to approximately 1 km above the ford (= locs. USGS 8539–8543; Maury's Zone D), and locality TU 1444, Gurabo Formation, Río Yaque del Norte, east bank, at López, appoximately 0.5 km upstream from the mouth of Arroyo López, between the middle and lower hard limestone ledges.

Distribution.—*Clypeaster caudatus* was reported by Sánchez Roig (1949) from El Jobo, near Puriales, Guantanamo, Oriente Province, Cuba. He attributed a late Oligocene age to the specimen, but it would probably now be considered Miocene.



Text-figure 4.—Comparison of left poriferous zone of petal III of *Clypeaster maoadentroensis* (A) and *C. caudatus* (B) showing greater width separating pores of a pore pair in *C. maoadentroensis* and greater distances between adjacent pore pairs. A, holotype, NMB M9746; B, figured specimen, NMB M9747, ×3.

Clypeaster cf. **C. sunnilandensis** Kier, 1963
Plate 6, figures 1, 2

cf. *Clypeaster sunnilandensis* Kier, 1963, pl. 3, fig. 3, pls. 12, 13.

The three fragments recovered appear to be very similar to *C. sunnilandensis* from the Pliocene Tamiami Limestone of Florida. The test of one of the fragments is wider more anteriorly than in specimens of *C. sunnilandensis* and the test appears to be lower. These specimens probably represent a new species, but with only three fragments, none of which show the ventral surface, it is not possible to make this determination.

Type material.—Figured specimens, USNM 375450, 375451.

Occurrence.—The form here compared to *Clypeaster sunnilandensis* was recovered from locality TU 1223, Cercado Formation, roadcut 5.3 km north of the plaza at Monción, on the road to Los Quemados.

Distribution.—*Clypeaster sunnilandensis* is known from the Pliocene Tamiami Limestone of Florida.

Genus **ENCOPE** J. L. R. Agassiz, 1841

Encope aberrans imperforata Kier, 1963
Plate 6, figure 3

?*Encope wiedenmayeri* Jeannet, 1928, p. 17.
?*Encope michelini* J. L. R. Agassiz. Cooke, 1961, p. 17.
Encope michelini imperforata Kier, 1963, p. 33, pl. 5, fig. 1; pl. 6, figs. 3, 4, text-figs. 25–30, table 2; Phelan, 1972, pp. 117, 125, 126.

One specimen showing its dorsal surface appears to belong to this subspecies, originally assigned to *Encope michelini* J. L. R. Agassiz, 1841. Subsequently Phelan (1972) revised the genus and showed that *E. aberrans* Martens, 1867 should be maintained as a species separate from *E. michelini*, and that *E. michelini imperforata* should be referred to *E. aberrans*.

E. aberrans imperforata was based on specimens from the Plio-Pleistocene Caloosahatchee and Tamiami formations of Florida. This subspecies is similar in all respects to the living *E. aberrans aberrans* except that its posterior closed lunule is quite small or absent, whereas it is always fully developed in the living species. The specimen from the Dominican Republic also has a smaller posterior lunule. Although its posterior petals are longer than the other petals, and its test narrower than normally found in *E. aberrans*, I have seen a few modern specimens of *E. aberrans* that are as narrow and have posterior petals longer than the anterior.

The specimens from the Miocene or Pliocene of Venezuela that Jeannet (1928, p. 17) referred to *Encope wiedenmayeri* Jeannet, 1928, and Cooke (1961, p. 17) referred to *Encope michelini* J. L. R. Agassiz, 1841, may be consubspecific with *E. aberrans imperforata*. More specimens are needed before this assignment can be made with any certainty.

Type material.—Florida specimens: holotype, USNM 648167; figured specimens, USNM 648168–648172; Dominican Republic figured specimen, NMB M9748.

Occurrence.—*Encope aberrans imperforata* has been recovered in the present collections from locality NMB 16857 (Saunders, Jung, and Biju-Duval, 1986, text-figs. 15, 16), late Miocene from the Río Cana section, 150 m above the base.

Distribution.—Florida: Plio-Pleistocene post-Caloosahatchee beds, and Caloosahatchee and Tamiami formations (see Kier, 1963, p. 35 for exact localities). Specimens questionably consubspecific with *E. aberrans imperforata* have been reported from the Miocene or Pliocene of Venezuela (Jeannet, 1928; Cooke, 1961).

Genus **MELLITA** J. L. R. Agassiz, 1841

Mellita species

Plate 6, figures 4, 5

Eight small specimens can be referred tentatively to this genus. Although they have five ambulacral notches and their periprocts are outside the basicoronal plate, characters (Kier, 1963, p. 44) commonly found in *Leodia* Gray, 1852, they have more affinities with *Mellita*, including: (1) a posterior lunule that extends far anteriorly between the posterior petals; (2) paired interambulacra separated from the basicoronal row by one pair of ambulacral plates; (3) the first pair of post-basicoronal plates in the paired interambulacra elongated; and (4) lunules formed by the closing of marginal notches.

These specimens appear to represent a new species but because no large specimens are present it seems inadvisable to erect one. They differ from *Mellita aclinensis* Kier, 1963, from the Plio-Pleistocene of the southeastern United States, in having a wider posterior lunule and the periproct not partly within the basicoronal interambulacral plate. They differ from *Mellita quinquiesperforata* (Leske, 1778), now living in the Caribbean, in having five instead of four ambulacral notches, and their periproct more posterior and outside of the basicoronal plate. No small specimens of *Mellita caroliniana* (Ravenel, 1841) from Plio-Pleistocene beds in South Carolina are available, so it is difficult to compare these specimens to this South Carolina species. However, the periproct in *M. caroliniana* is within the basicoronal plate (Kier, 1972, fig. 4), whereas in the Dominican Republic specimens it is posterior to it.

Type material.—Figured specimen, USNM 375452.

Occurrence.—Late early Miocene, locality TU 1253, Baitoa Formation, roadcut on the west side of road from Santiago de los Caballeros to Baitoa, 1 km north of the village of Baitoa (= loc. USGS 8559). Locality TU 1362 (Saunders, Jung, and Biju-Duval 1986, text-fig. 21), Baitoa Formation, trail that leads to top of bluff, east side of Río Yaque del Norte, just downstream from Baitoa. Locs. NMB 16943, 17282, 17283, 17290 (Saunders, Jung, and Biju-Duval, 1986, text-fig. 25), López section of Río Yaque del Norte.

Genus **MOIRA** A. Agassiz, 1872

Moira atropos (Lamarck, 1816)

Plate 7, figures 3, 4

Spatangus atropos Lamarck, 1816, p. 32.
For synonymies, see Mortensen, 1951, p. 329, and Serafy, 1979, p. 91.

The single specimen recovered in this study is indistinguishable from specimens of this species now living from the coast of North Carolina and Bermuda through the Caribbean, Gulf of Mexico, and south to Brazil. Although the specimen is distorted and partially covered with a hard matrix, enough of the test is visible that it can be referred with certainty to *M. atropos*. Its petals are like those in Recent specimens, deeply sunken but constricted dorsally where the interambulacra almost meet above them. The petals of the fossil and Recent specimens have similar length and shape, and ambulacrum III is similar. Furthermore, the shape of their tests are the same, as are the positions of their apical system and peristome. The positions of both the peripetalous and lateroanal fascioles are the same, although because of preservation it is not possible to determine which plates the fascioles occur on in the fossil specimen.

Type material.—Figured specimen, USNM 375453.

Occurrence.—Early Pliocene, Gurabo Formation, locality TU 1354, Cañada de Zamba, a tributary on the west side of the Río Cana, approximately 2.5 km east of the village of Zamba, which is 7 km north of Cruz de Santiago (Santiago Rodriguez), on the road to Guayubin; or 4.5 km (airline) below the ford at Caimito (see Saunders, Jung, and Biju-Duval, 1986, text-fig. 15).

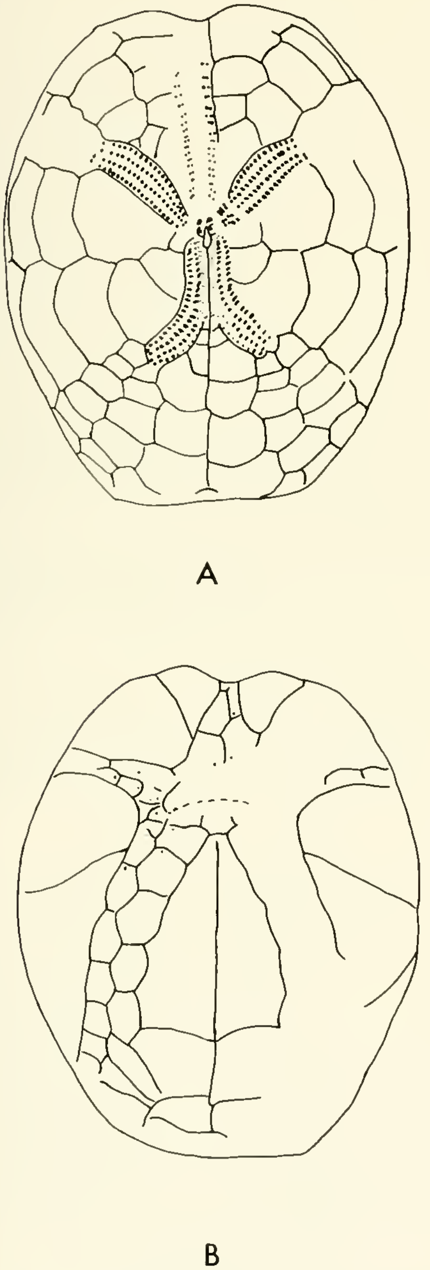
Distribution.—*Moira atropos* (Lamarck, 1816) has been found (Cooke, 1959, p. 74) in beds now considered of Pliocene age in the Intracoastal Waterway canal in Horry County, South Carolina, one-half to 1 mi southwest of the bridge on US 17 near Nixons Crossroads, about 15 mi northwest of Myrtle Beach (loc. USGS 18759). Cooke (1961, p. 22) reports the species from the Pliocene San Gregorio Formation, Río Seco area, Falcón, Venezuela.

Genus **BRISSOPSIS** J. L. R. Agassiz, 1840

Brissopsis jimenoi Cotteau, 1875
Plate 7, figures 1, 2; Text-figures 5A, 5B

Brissopsis jimenoi Cotteau, 1875, p. 6; Cotteau, 1881, p. 33, pl. 3, figs. 5–9; Cotteau, 1897, p. 79, pl. 24, figs. 5–9; Jackson, 1922, p. 81; Jeannet, 1928, p. 12, pl. 1, fig. 35; Sánchez Roig, 1949, p. 225; Kier, 1984, p. 87, pl. 46, figs. 1, 2.

Material.—Only a single specimen is available. It was originally covered with a sandy silt matrix, with most of its spines still attached to the test, showing that the test was covered at or very soon after death. The test is flattened and weathered, obscuring the fascioles.



Text-figure 5.—*Brissopsis jimenoi* Cotteau, A, dorsal view; B, ventral view, NMB M9747, ×1.

Shape and size.—Test, 65 mm long, 54 mm wide (83 %L), height, 25 mm (38 %L).

Apical system.—Central, located at distance from anterior margin to center of genital pores equal to 50 %L. Four genital pores, ethmolytic with genital plate 2 extending far posteriorly.

Ambulacra.—Anterior ambulacrum not petaloid, in groove extending from apical system to peristome; pore pairs largest adapical to peripetalous fasciole; minute between fasciole and phyllode; 56 plates in ambulacrum. First enlarged pore pairs in plate 7.

Anterior petals (II and IV) curved convexly anteriorly with their greatest width near end of petal; depressed in groove. Span of ends of petals = 42.6 %L. Short, with length slightly greater than one-half distance from apical system to ambitus; length = 21 %L; greatest width = 8.1 %L; 44 petaloid pore pairs in each petal; pore pairs in anterior poriferous zones reduced in size adapically. First petaloid pore pair in plate 12.

Posterior petals (V and I) confluent for three-fifths distance from apical system to end of petals, sharing common groove; curving away from each other distally; short, length = 25 %L; greatest width = 6.3 %L; 48 pore pairs. Petaloid pore pairs in posterior poriferous zones greatly reduced in size from apical system for three-fifths length of petal. First petaloid pore pair in plate 19.

Peristome.—Anterior, distance from anterior edge of peristome to anterior margin = 24 %L; width of opening = 21 %L; height = 7 %L.

Periproct.—Inframarginal, large, width = 15 %L, height = 12 %L, occurring within plates 5–9.

Fascioles.—Only short tract of peripetalous fasciole preserved in lobe extending anteriorly in anterior ambulacrum (III), crossing plate 7 at distance from apical system = 36 %L.

Oral plate arrangement.—Labrum extending to second adjoining ambulacral plate (Text-fig. 5B), with length = 6.6 %L; sternal plate (first plate of plastron) length = 41 %L (estimated), combined width = 31 %L; episternal plate (second plate of plastron) length = 14 %L, combined width = 32 %L.

Type material.—Lectotype in the Cotteau Collection, Université Claude Bernard, Lyon, France. Dominican Republic figured specimen, NMB M9749.

Remarks.—This Dominican Republic specimen appears to be conspecific with the holotype of *B. jimenoi*. The two specimens are of similar shape, have similar petals, and labrum and sternal plates of similar dimensions. Because the Cuban holotype is a cast, description of the Dominican Republic specimen herein is justified; it exhibits features not visible on the holotype.

Comparison with other species.—This species differs from *Brissopsis aguayoi* Sánchez Roig, 1952, from the Oligocene–Miocene of Cuba in its larger, lower and longer anterior petals. It is distinguished by its shorter petals from *Brissopsis antillarum* Cotteau, 1875 from the Miocene Anguilla Formation of Anguilla and the Miocene La Vela Formation in Venezuela. Its anterior petals extend little over one-half the distance from the apical system to the margin, but in *B. antillarum* these petals extend two-thirds this distance. Furthermore, the test in *B. jimenoi* is more elongate, and lower.

B. jimenoi has a much lower test and less divergent and more curved petals than the specimen from the Miocene of Costa Rica that Durham (1961, p. 484) referred to *Brissopsis*, n. sp.

This species is very similar and may be synonymous with *Brissopsis elongata* Mortensen, 1907, now living in the Caribbean. The two species are similar in the following features (the dimensions for *B. elongata* are from Chesher, 1968):

1. Width of the test: 83 %L in *B. jimenoi*; mean of 82.3 %L in *B. elongata*, with a range from 77–86 %L.
2. Labrum extends to the second adjoining ambulacral plate in both species.
3. Same number of adjoining ambulacral plates along the plastron plates with the sixth ambulacral plate occurring at the suture between the first and second plates of the plastron.
4. Posterior petals confluent proximally, very divergent distally. Although many specimens of *B. elongata* do not have their posterior petals as divergent, Chesher (1968, pl. 15, fig. a) shows a specimen with petals of similar shape to those in *B. jimenoi*.
5. In both species, the first petaloid pore pair in an anterior petal is in plate 12, and the first in a posterior petal is in plate 19.
6. The peristome is in a similar position. In *B. jimenoi*, it is located at a distance from the anterior margin equal to 24 %L; in *B. elongata* it is at 25 %L with a range of 23–28 %L.
7. The periproct in *B. jimenoi* is enclosed by interambulacral plates 5–9; in *B. elongata* by interambulacral plates 5–8.
8. The span of the ends of the anterior petals is 42.6 %L in *B. jimenoi*, 48.8 %L in *B. elongata* with a range of 39–56 %L.
9. The peripetalous fasciole crosses ambulacrum III at a distance from the apical system of 36 %L in *B. jimenoi*. In *B. elongata* the mean of the distance is 38.9 %L with a range of 34–43 %L.
10. The length of the first plastron plates in *B. jimenoi* is 41 %L in both *B. jimenoi* and *B. elongata*.
11. Although the apical system in *B. jimenoi* is more posterior than in most specimens of *B. elongata*, with a distance equal to 50 %L versus a mean of 38 %L in *B. elongata* (no range given by Chesher), some specimens of *B. elongata* have their apical system as posterior. In three specimens from Belize in the USNM, the distance ranges from 44 to 52 %L.

Although these species appear identical, I hesitate to place them in synonymy. Nothing is known of the pedicellariae in *B. jimenoi*, and with only two specimens known of *B. jimenoi* (each from a different locality), it is not possible to make a statistical comparison of populations of the two species. Furthermore, the position of most of the length of the fascioles is unknown on the fossil specimens. This feature has been shown by Chesher to be very important systematically in *Brissopsis*. Finally *B. elongata* is junior to *B. jimenoi*, and it would be unfortunate to synonymize this well-known living species with a fossil species based on a holotype which is only an internal mold.

Jackson (1922, p. 83) referred a Dominican Republic specimen to *Brissopsis antillarum* Cotteau, 1875. This specimen in the USNM (uncatalogued) is from the Cevicos Limestone, Arroyo La Mora, west of Cevicos. It is badly crushed and can not be specifically identified with any certainty.

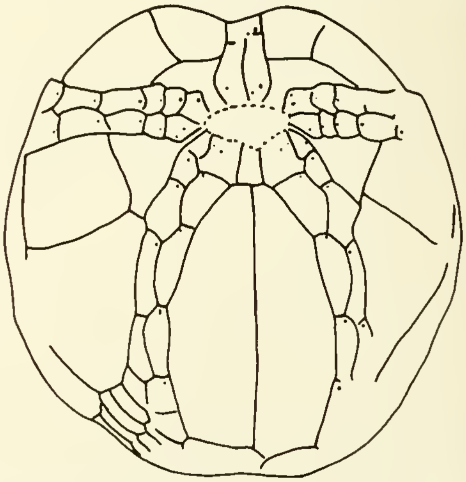
Occurrence.—Early Pliocene, near base of Gurabo Formation, locality NMB 16824 (Saunders, Jung, and Biju-Duval, 1986, text-figs. 15, 16) 317 m above base of Río Cana section.

Distribution.—Cuba, Miocene?, San Martin Cienfuegos, Las Villas Province. Jeannet's (1928, p. 12) specimen from the middle Miocene of Trinidad may or may not belong to this species.

Genus SCHIZASTER J. L. R. Agassiz, 1835

Schizaster doederleini (Chesher, 1972)

Plate 7, figure 5; Plate 8, figures 1–6; Text-figure 6



Text-figure 6.—*Schizaster doederleini* (Chesher), oral view, figured specimen, USNM 375456, ×2.

Paraster doederleini Chesher, 1972, pp. 10–25, figs. 1–9; Kier, 1975, p. 9, pls. 7, 8, figs. 1–5, text-figs. 7, 8.
Schizaster orbignyanus A. Agassiz, 1880. Serafy, 1979, fig. 37A.

Twenty-four Dominican Republic specimens can be referred to this species, which now lives in the Caribbean off Belize and Florida, and in the Gulf of Mexico off the Dry Tortugas. Their dimensions are very similar to those of a living population of this species from Belize (Table 2). The specimen that Serafy (1979, fig. 37A) referred to *Schizaster orbignyanus* A. Agassiz, 1880 is *S. doederleini*.

The fossil specimens differ only in having slightly shorter petals with a narrower span. Furthermore, the fossil specimens are similar to the Recent specimens in having very small anterior genital pores, similar number of pore pairs in ambulacrum III within the peripetalous fasciole (a fossil specimen 35.6 mm long has 56 pore pairs, a Recent specimen 36.7 mm long has 58), and similar number of petaloid pore pairs. In both the fossil and Recent specimens the peripetalous fasciole crosses plate 4 in ambulacrum III, plate 11 or 12 in ambulacrum IV, and in both populations the labrum extends back (Text-fig. 6) to the posterior portion of the first adjoining ambulacral plate on the anterior portion of the second. Finally, both have the periproct within interambulacral plates 5–8.

Type material.—Holotype, USNM E11376; paratypes, MCZ 8397c, 8397d; figured specimens, USNM E13735, 13749, 13743–13750, E30468. Dominican Republic fossil figured specimens, USNM 375454, 375455, 375456.

Comparison with other species.—This species is easily distinguished from any fossil species known from the region. It differs from *Schizaster delgadoi* (Sánchez Roig, 1953) from the Miocene of Cuba by its much smaller test, with more central apical system, shorter posterior petals, wider anterior petals that distally curve anteriorly instead of the reverse, wider ambulacrum III, and more posterior peristome. It differs from *Schizaster fernandezi* Sánchez Roig, 1952, also from the Miocene of Cuba, in its more central apical system, and wider ambulacrum III, which has more enlarged pore pairs, 50 in a specimen 26 mm long as opposed to only 28 in a specimen of the same size of *S. fernandezi*.

Table 2.—*Schizaster doederleini* (Chesher): comparison of northern Dominican Republic fossils with Recent specimens from Carrie Bow Cay, Belize.

	mean percent of length	
	fossil (min/max)	*Recent (min/max)*
width	90.3 (87–94)	96 (92–99)
height	73.1 (69–80)	73.8 (70–80)
apical system to anterior margin	53 (49–59)	53 (48–57)
apical system to fasciole on ambulacrum III	50 (46–53)	53 (48–56)
length of anterior petal	31.7 (30–33)	33 (34–38)
width of anterior petal	11.2 (10.8–12.3)	12 (9–14)
length of posterior petal	15 (14.1–16.3)	16 (14–19)
width of posterior petal	8.4 (7.7–10.0)	9 (7–11)
peristome to anterior of test	24.4 (19.4–27.2)	20 (15–25)
span of anterior petals	51 (47–55)	58 (55–62)

It differs from *Schizaster cartagensis* (Sánchez Roig, 1949) from the Oligocene–Miocene of Cuba by its much shorter and wider petals, and from *Schizaster rojasi* Sánchez Roig, 1952, in having wider petals, and a higher test with its greatest width more posterior. Its posterior petals are shorter and the anterior petals more curved anteriorly than in *Schizaster sanctmariae* Sánchez Roig, 1949 also from the Oligocene–Miocene of Cuba. Of all the Oligocene–Miocene Cuban species, *S. doederleini* most resembles *Schizaster munozi* Sánchez Roig, 1949, from which it differs in having shorter, wider posterior petals and wider interior petals.

S. doederleini is easily distinguished from the Pleistocene *Schizaster eustatii* (Engel, 1961) from the Caribbean island of St. Eustatius by having many more pore pairs in the dorsal part of ambulacrum III within the peripetalous fasciole. Only 32 pore pairs occur in this region in *S. eustatii*, whereas in a specimen of similar size of *S. doederleini*, 50 pore pairs are present. Furthermore, the anterior petals in *S. eustatii* curve posteriorly, whereas in *S. doederleini* they curve anteriorly.

Occurrence.—*Schizaster doederleini* is known as fossil from the early Pliocene, near the base of the Gurabo Formation, locality NMB 16862 (Saunders, Jung, and Biju-Duval, 1986, text-figs. 15, 16), Río Cana section, 350 m above the base; locality TU 1354 (at approximately same stratigraphic level in Gurabo Formation as loc. NMB 16862), Cañada de Zamba, a tributary on the west side of the Río Cana, approximately 2.5 km east of the village of Zamba, which is 7 km north of Cruz de Santiago (Santiago Rodriguez), on road to Guayubin; or 4.5 km (airline) below the ford at Caimito.

Distribution.—This species has been reported by Chesher (1972) and Serafy (1979) living off Colombia and Florida, but Kier (1975, p. 11) suggests that Chesher's Colombian specimens probably belong to another species.

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EXPLANATION OF PLATE 1

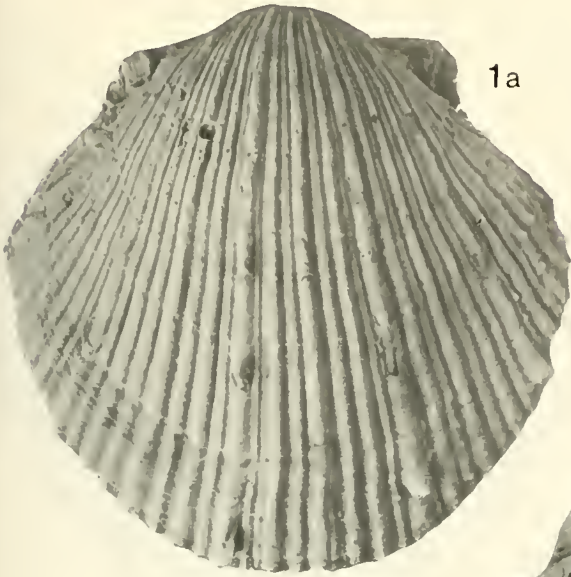
Figure Page

1–3. ***Spondylus bostrychites*** Guppy 8

1. Left valve, BMNH LL 9946 (lectotype), ×¾. Gurabo Formation, locality unknown. Height 100 mm, length 101.5 mm. **a**, exterior view; **b**, interior view.
2. BMNH LL 25706 (paralectotype). Gurabo Formation, locality unknown. Height 89 mm, length 81 mm, diameter of paired valves 62 mm. **a**, exterior of right valve, ×1; **b**, dorsal view of paired valves, ×2.
3. Right valve, USNM 450387 (hypotype). Gurabo Formation, Río Gurabo area, locality TU 1278. Height 114 mm, length 88 mm. **a**, exterior view, ×¾; **b**, enlargement of portion of valve, ×3.

4. ***Spondylus americanus*** Hermann 10

Right valve, USNM 450388 (hypotype), ×2. Bowden Formation, Jamaica, locality TU 705. Height 31.8 mm, length 34.6 mm.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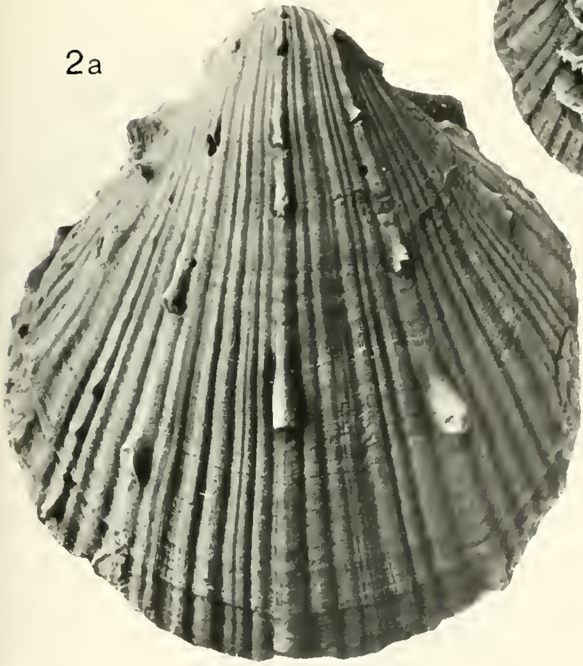
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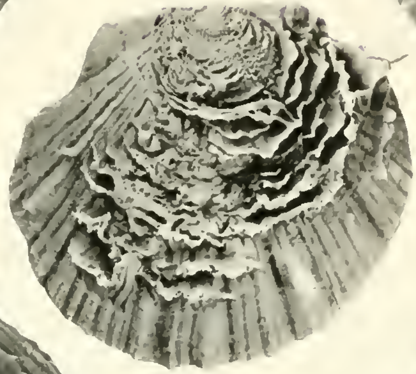
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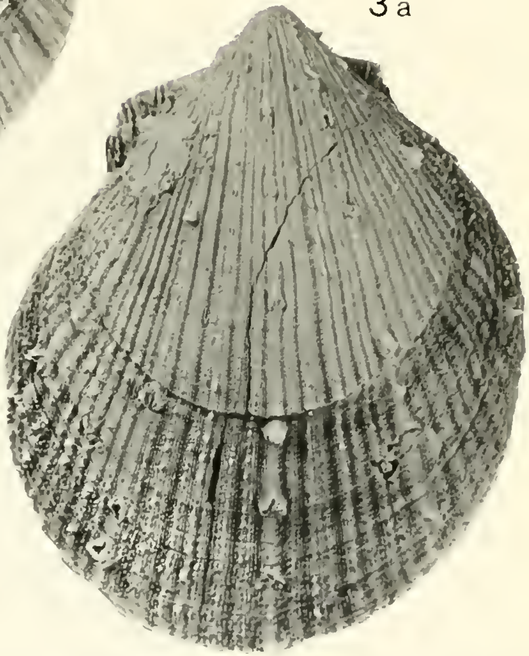
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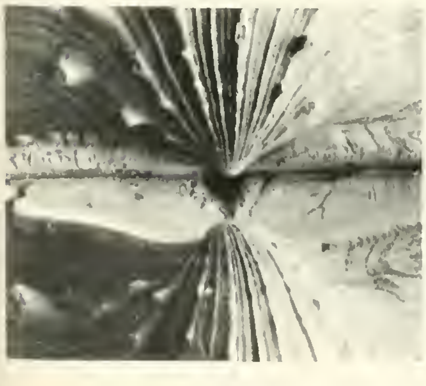
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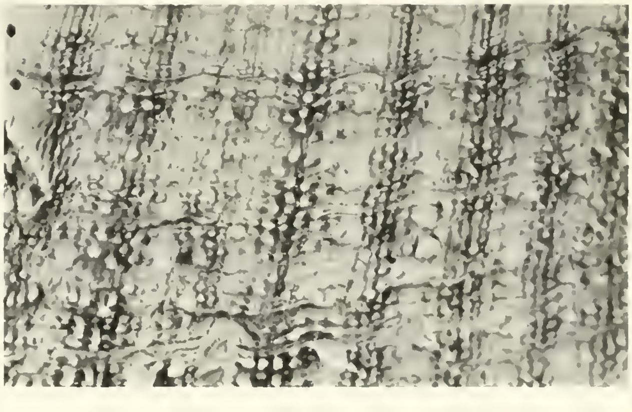
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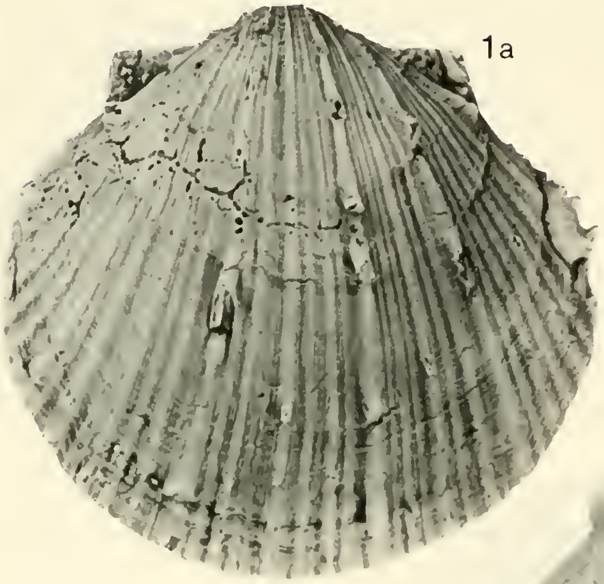
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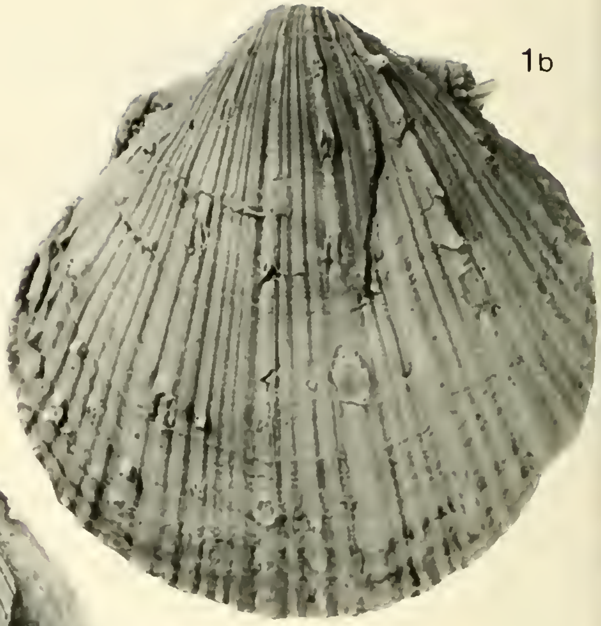
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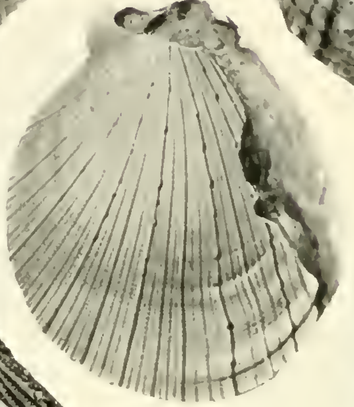
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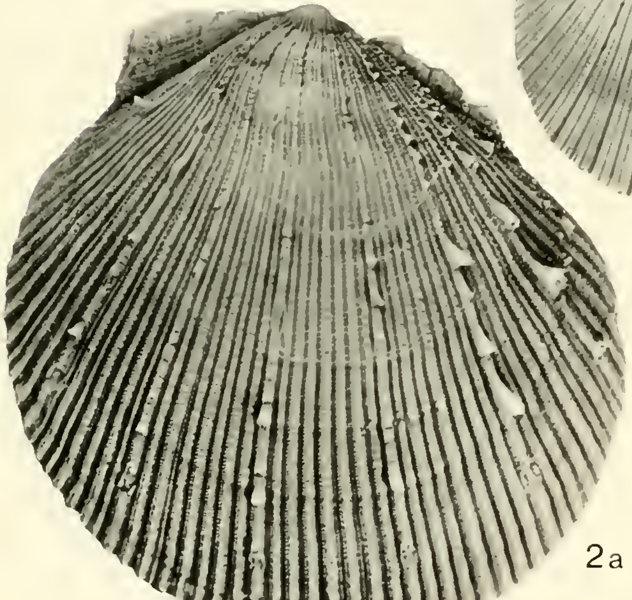
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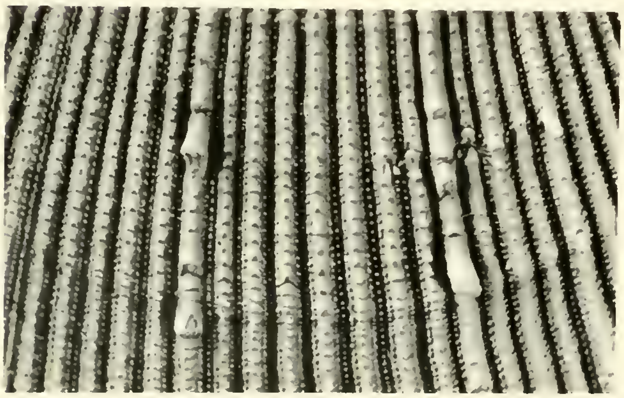
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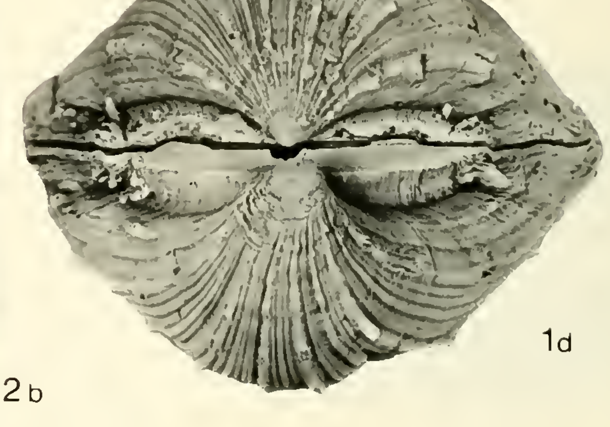
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EXPLANATION OF PLATE 2

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1.	***Spondylus bostrychites*** Guppy	8
	NMB G 16963 (hypotype), ×1. Río Cana, Gurabo Formation, locality NMB 16821. Height 80 mm, length 75 mm, diameter of paired valves 57 mm. **a**, exterior view of left valve; **b**, exterior view of right valve; **c**, anterior view of paired valves; **d**, dorsal view of paired valves.	
2–3.	***Spondylus lucasi*** Maury	10
	2. Left valve, USNM 450389 (hypotype). Río Gurabo, Gurabo Formation, locality TU 1211. Height 54.5 mm, length 53 mm. **a**, exterior view, ×1½; **b**, enlargement of portion of valve, ×3.	
	3. Left valve, AMNH 22514 (lectotype), ×1½. Guánica Limestone (= Ponce Limestone), Puerto Rico. Height 33 mm, length 28 mm (from Maury, 1920, pl. 5, fig. 10).	

EXPLANATION OF PLATE 3

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1–4.	***Spondylus gumanomocon*** Brown and Pilsbry	11

1. Right valve, ANSP 2869 (lectotype), ×¾. ?Mao Formation, locality unknown. Height 175 mm, length 115 mm.
2. Left valve, ANSP 72724B (paralectotype), ×¾. ?Mao Formation, locality unknown. Height 96.5 mm, length 94 mm.
3. Right valve, ANSP 72724C (paralectotype), ×¾. ?Mao Formation, locality unknown. Height 126 mm, length 97.5 mm.
4. USNM 450390 (hypotype), ×1. Guayubin, Mao Formation, locality TU 1221. Height 81 mm, length 56 mm, diameter of paired valves 47 mm. **a**, anterior view of paired valves; **b**, exterior view of left valve; **c**, exterior view of right valve.

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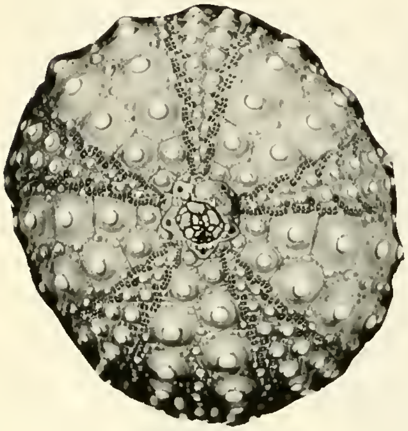
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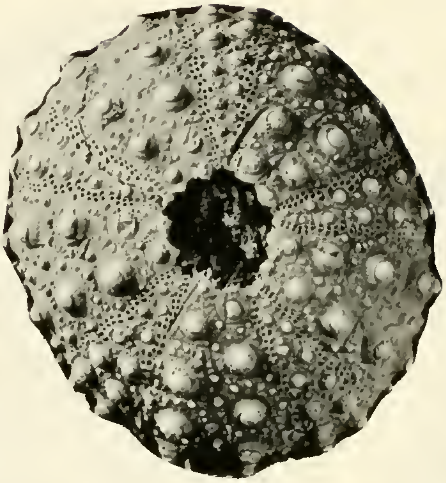
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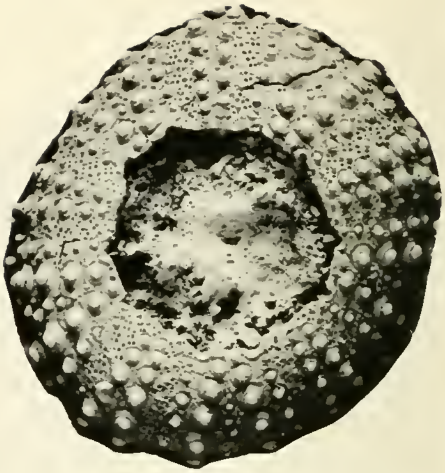
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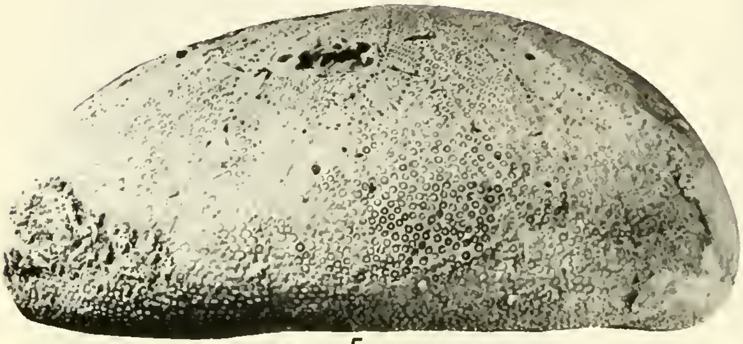
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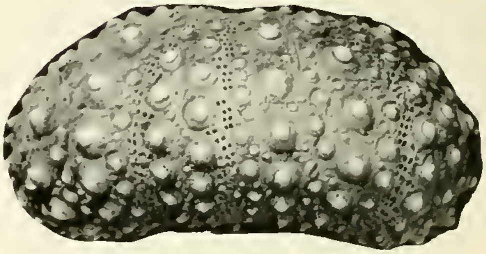
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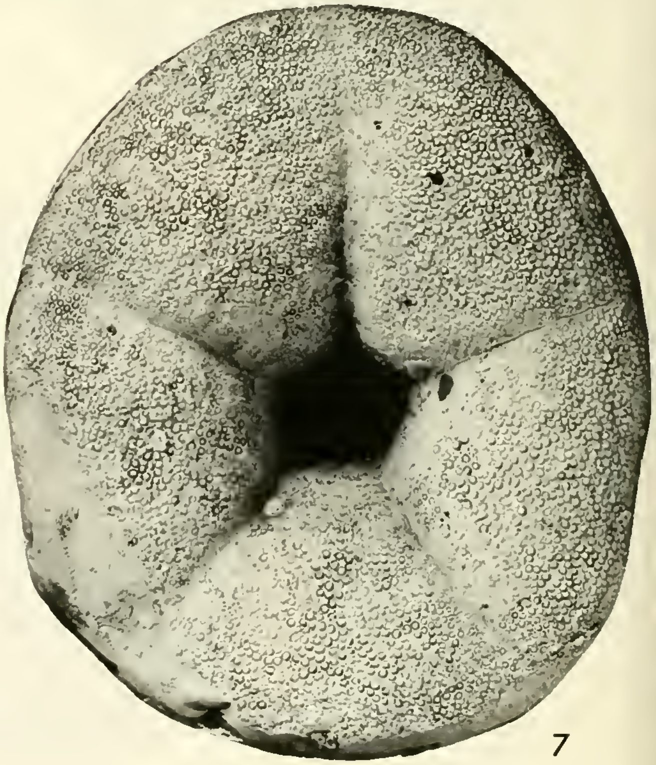
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1–4.	**Echinometra lucunter** (Linnaeus, 1758)	17
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	2–4. Dorsal, ventral, and right side views of figured specimen (USNM 375449) from locality TU 1438 in the Pliocene Mao Adentro Limestone, in a roadcut 0.5 km south of the bridge at Guayubin on the road to Sabaneta, ×2.	
5–7.	***Clypeaster maoadentroensis***, new species	17
	Left side, dorsal, ventral views of the holotype (NMB M9746) from locality NMB 17022, early Pliocene, Mao Adentro Limestone, 765 m above the base of the Río Cana section (Saunders, Jung, and Biju-Duval, 1986, text-figs. 15–16), ×1.	

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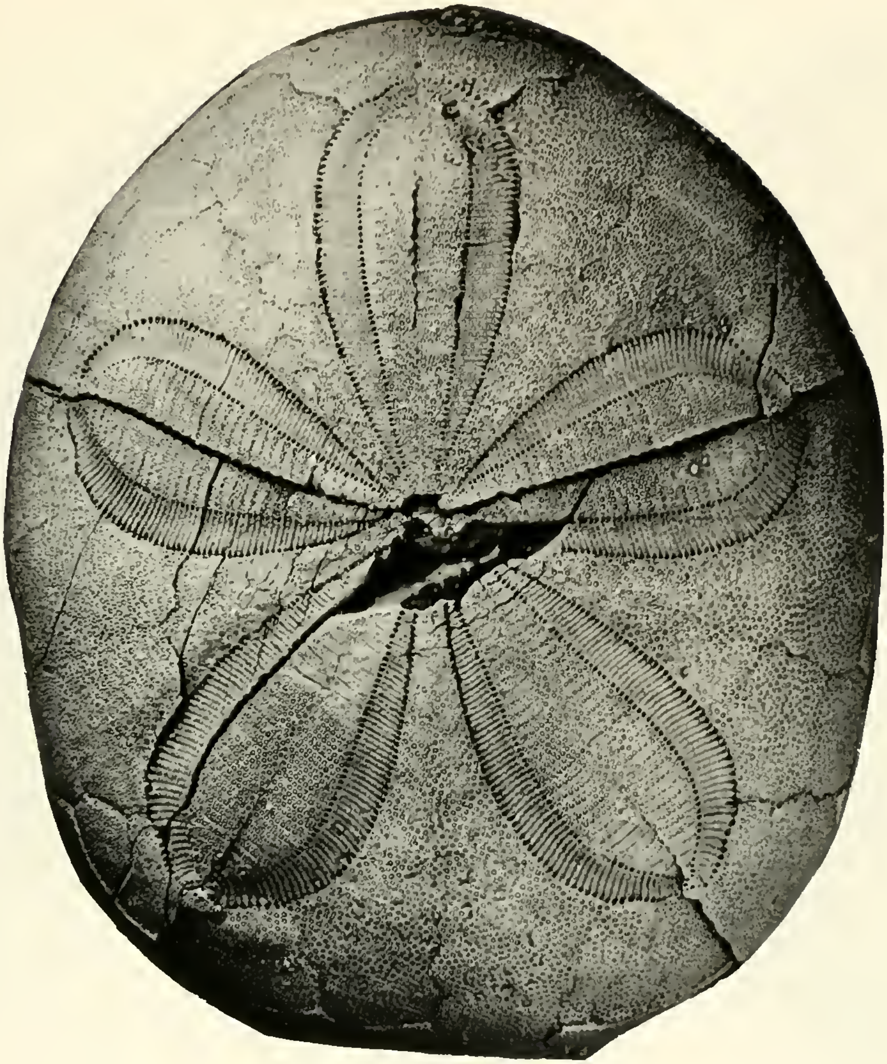
1, 2.	***Clypeaster caudatus*** Jackson, 1922 Dorsal and right side views of figured specimen (NMB M9747) from locality NMB 17274, bed B, Arroyo López section (Saunders, Jung, and Biju-Duval, 1986, text-fig. 26), ×11.	18



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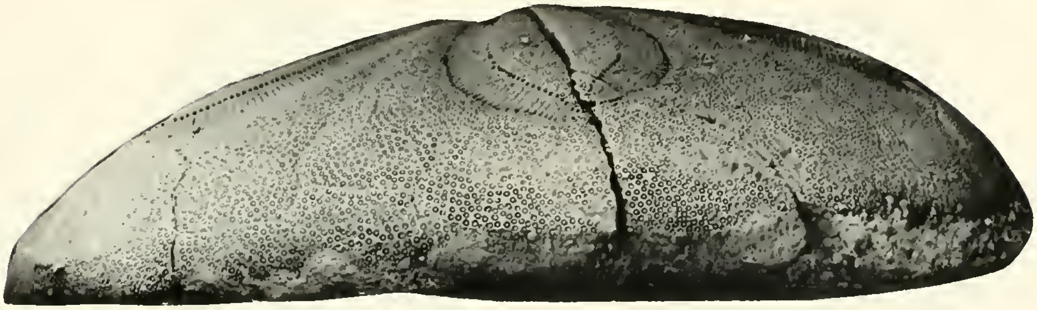

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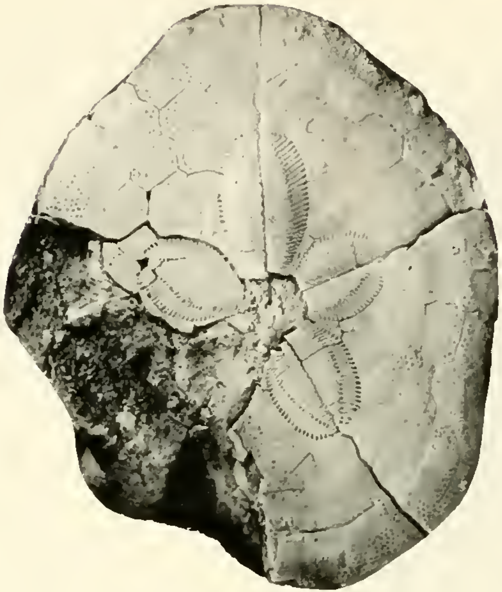

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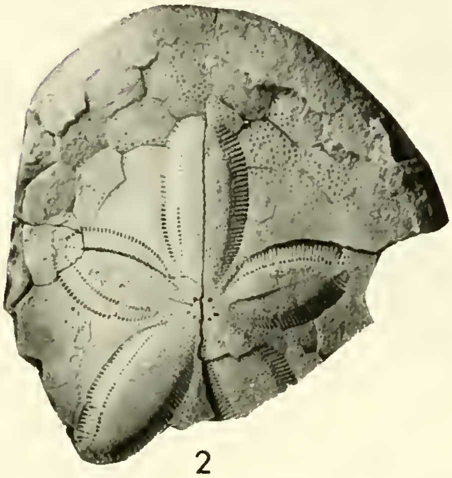

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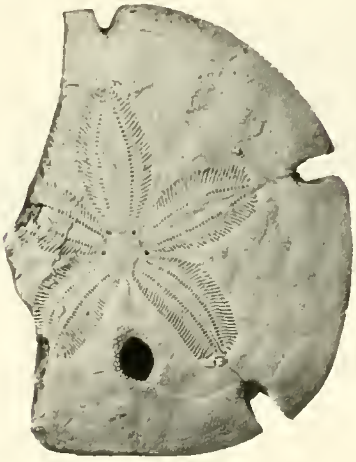

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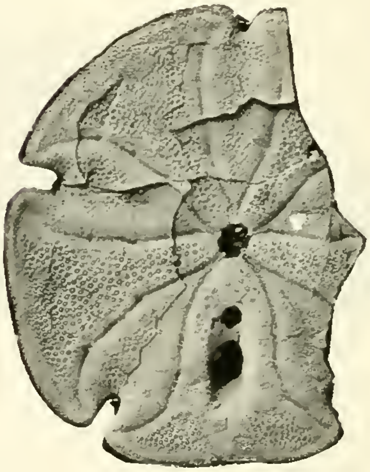

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EXPLANATION OF PLATE 6

Figure Page

1, 2. ***Clypeaster*** cf. ***C. sunnilandensis*** Kier, 1963 19

1. Dorsal view of figured specimen (USNM 375450) from the late Miocene Cercado Formation at locality TU 1233, roadcut 5.3 km north of plaza at Monción, on road to Los Quemados, ×1.
2. Dorsal view of figured specimen (USNM 375451) from same locality as above, ×1.

3. ***Encope aberrans imperforata*** Kier, 1963 19

Dorsal view of figured specimen (NMB 9748) from locality NMB 16857, late Miocene from the Río Cana section (Saunders, Jung, and Biju-Duval, 1986, text-figs. 15, 16), ×1.

4, 5. ***Mellita*** species 20

Dorsal and ventral views of figured specimen (USNM 375452) from early Miocene, Baitoa Formation, locality TU 1362 (Saunders, Jung, and Biju-Duval, 1986, text-fig. 21), ×2.

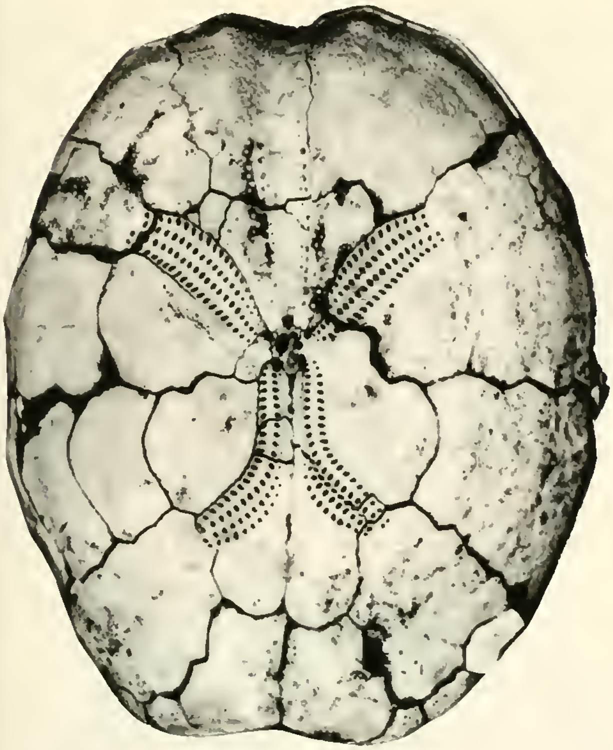
EXPLANATION OF PLATE 7

Figure Page

1, 2. ***Brissopsis jimenoi*** Cotteau, 1875 21
Dorsal and ventral views of figured specimen (NMB M9749) from the early Pliocene, near base of the Gurabo Formation, at locality NMB 16824 (Saunders, Jung, and Biju-Duval, 1986, text-figs. 15, 16), 317 m above the base of the Río Cana section, ×1.

3, 4. ***Moira atropos*** (Lamarck, 1816) 20
Dorsal and ventral views of figured specimen (USNM 375453) from locality TU 1354, early Pliocene, Gurabo Formation (Saunders, Jung, and Biju-Duval, 1986, text-fig. 15), ×2.

5. ***Schizaster doederleini*** (Chesher, 1972) 22
Dorsal view of figured specimen (USNM 375454) from locality TU 1354, early Pliocene, Gurabo Formation (Saunders, Jung, and Biju-Duval, 1986, text-fig. 15), ×3.



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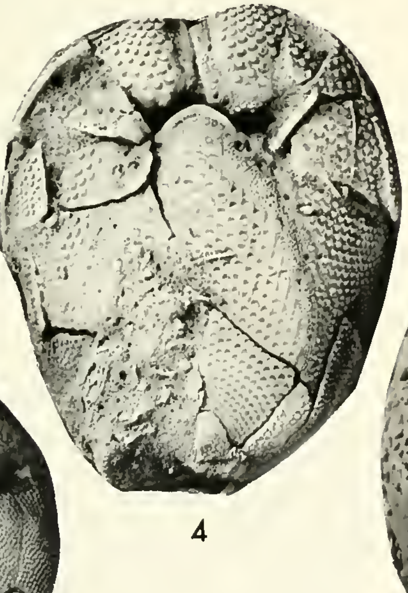

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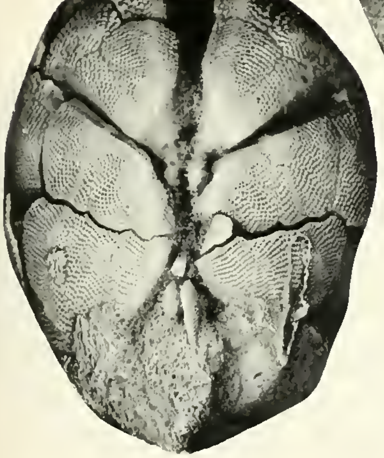

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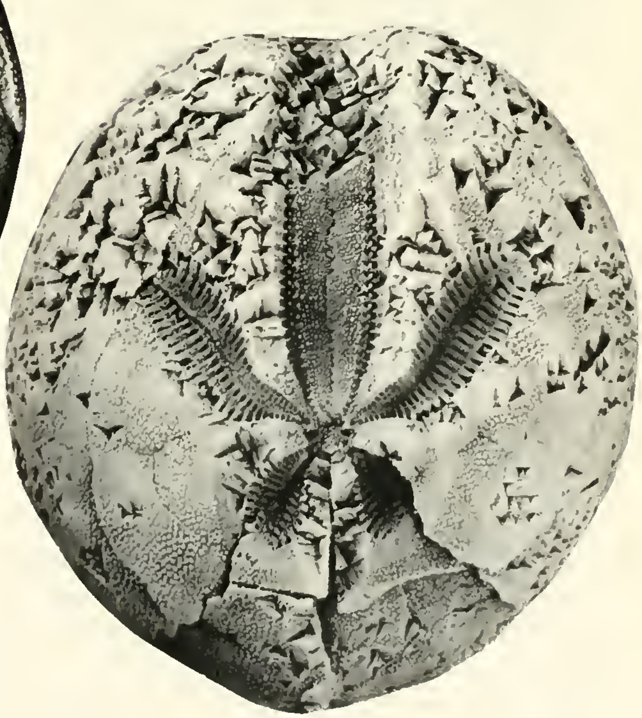

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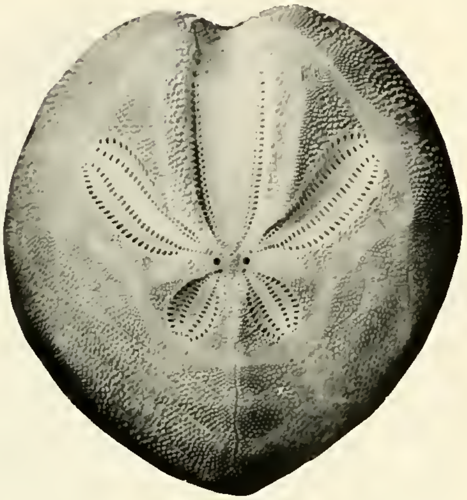

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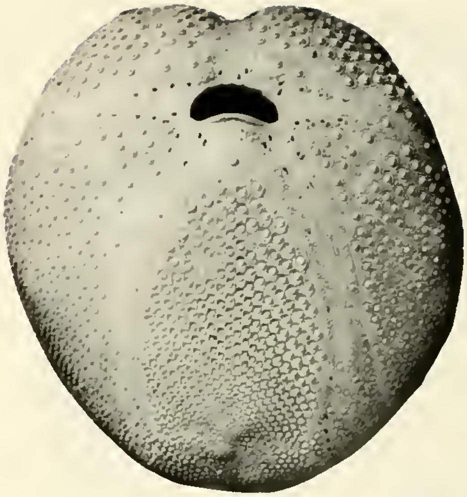

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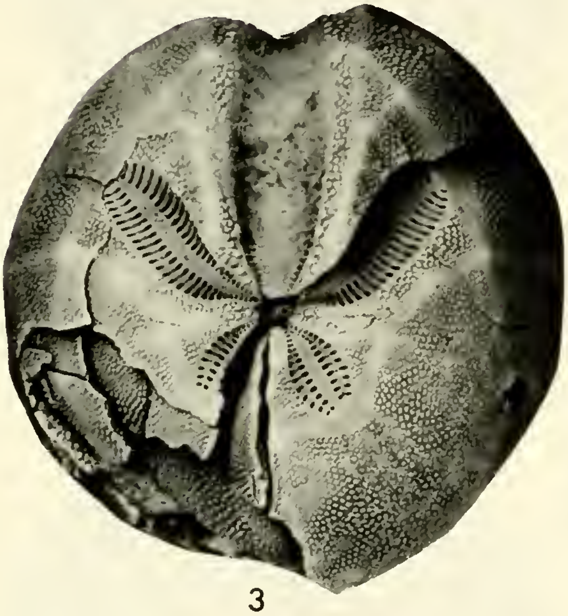

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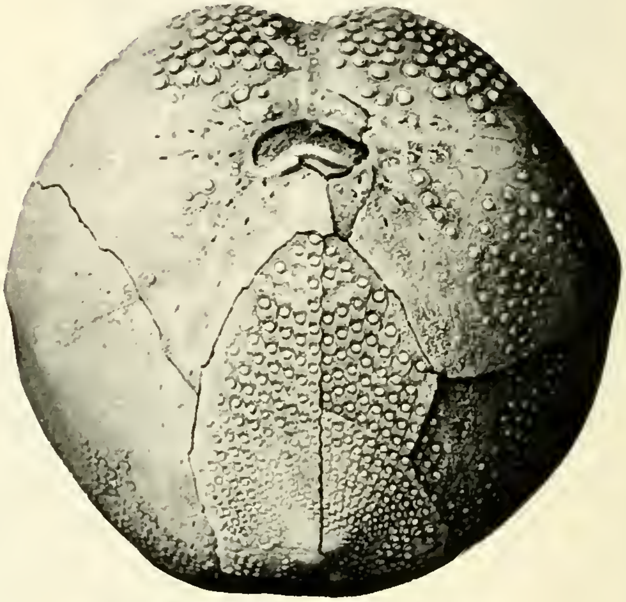

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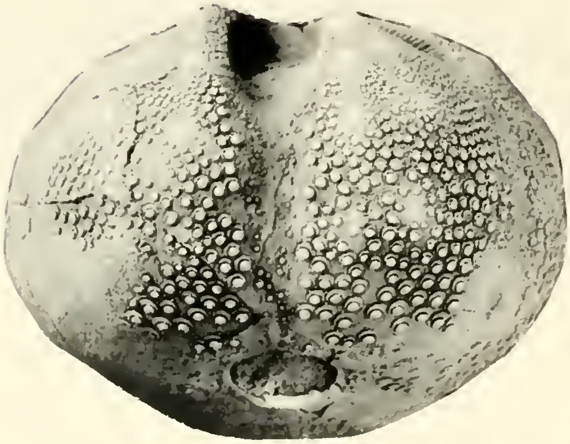

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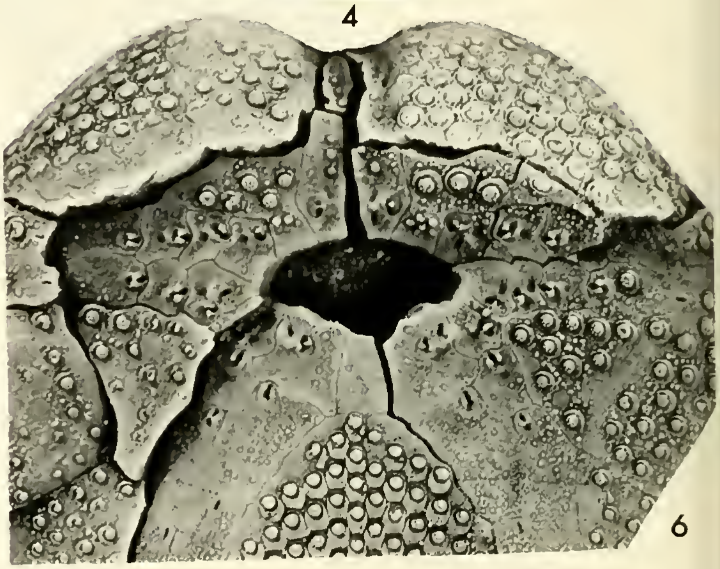

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EXPLANATION OF PLATE 8

Figure Page

1–6. ***Schizaster doederleini*** (Chesher, 1972) 22

1, 2. Dorsal and ventral views of figured specimen (USNM 30468), Recent, from depth of 15 m in mud fields west of Water Cay, Belize (Kier, 1975, fig. 1), ×2.

3–5. Dorsal, ventral, and front views of figured specimen (USNM 375455) from locality TU 1354, early Pliocene, Gurabo Formation (Saunders, Jung, and Biju-Duval, 1986, text-fig. 15), ×3.

6. View of peristome of figured specimen (USNM 375456) from locality TU 1354, ×4.5.

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Note: Page numbers are in light face; plate numbers are in **bold face** type; the page numbers on which principal discussions occur are in *italics*.

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