PORTER M. KIER

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Echinoids from
the Yorktown
Formation
of Virginia
and Their
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ABSTRACT

Porter M. Kier. Upper Miocene Echinoids from the Yorktown Formation of Virginia and Their Environmental Significance. *Smithsonian Contributions to Paleobiology*, number 13, 41 pages, 7 figures, 10 plates. 1972.—Five echinoid species are described from the upper Miocene part of the Yorktown Formation of Virginia: *Echinocardium orthonotum* (Conrad), *Arbacia improcera* (Conrad), *Psammechinus philanthropus* (Conrad), *Mellita aclinensis* Kier, and *Spatangus glenni* Cooke. The assemblage probably lived in shallow, warm-temperate waters, *E. orthonotum* deeply buried near shore, *S. glenni* shallowly buried offshore, and *M. aclinensis* with its test just covered near shore. *Arbacia improcera* and *P. philanthropus* presumably lived together intertidally and near shore, *P. philanthropus* living in holes in the indurated sediments or on the sand with its test covered with debris, whereas *A. improcera* probably was easily visible with nothing covering its test. Specimens formerly referred to *E. orthonotum* from the middle Miocene Choptank Formation from Maryland are referred to *E. marylandiense*, new species. *Echinocardium gothicum* (Ravenel), from the Bear Bluff Formation of South Carolina, is considered a junior subjective synonym of *E. orthonotum*.

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Porter M. Kier

Upper Miocene Echinoids from the Yorktown Formation of Virginia and Their Environmental Significance

Introduction

Although three species of echinoids have been described from the Yorktown Formation (upper Miocene lower Pliocene), these species were based on few specimens. Now that a large collection of echinoids from this formation has been studied, these species are redescribed herein and two additional species reported. This collection was made by Mr. Warren Blow, presently with the Paleontology and Stratigraphy Branch of the United States Geological Survey, who started collecting fossils from the Yorktown Formation eight years ago. Since that time, he has accumulated hundreds of echinoids, which he has presented to the National Museum of Natural History, Smithsonian Institution (under the catalog numbers of the United States National Museum: USNM). Many of these specimens were collected in fragments that Blow painstakingly reassembled. He collected four large slabs containing hundreds of echinoids preserved within the sediment. Some of the specimens are extraordinarily well preserved with their apical systems, spines, pedicellariae, anal plates, and lanterns still intact, and many have their original color. Specimens of one of the species have food particles or fecal

pellets still preserved in their tests. The study of this large collection permits a more definitive description of the species, resulting in a better understanding of their relationship to other species, and some interpretation of the environment in which they lived.

The echinoid assemblage consists of: *Echinocardium orthonotum* (Conrad), *Arbacia improcera* (Conrad), *Psammechinus philanthropus* (Conrad), *Mellita aclinensis* Kier, and *Spatangus glenni* Cooke. The first three species had been described previously from the Yorktown, but *Echinocardium orthonotum* was thought to include also specimens from the middle Miocene Choptank Formation from Maryland. These Maryland specimens are distinct and are referred to a new species described herein, *Echinocardium marylandiense*. Four specimens of *Mellita aclinensis* are present, a species known heretofore only from the upper Miocene Tamiami Formation in Florida, and one specimen of *Spatangus glenni*, previously known only from upper Miocene or Pliocene deposits in South Carolina.

Acknowledgments

I thank Warren C. Blow for collecting and preparing most of the echinoids described in this paper and for his great generosity in presenting the specimens to the National Museum of Natural History. These echin-

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oids are some of the best-preserved fossil echinoids known, and their availability to science is due to his patient and preserving efforts. I am much indebted to J. E. Hazel of the United States Geological Survey, (USGS), who not only critically read the manuscript but also provided much of the information on the paleoclimatology of the Miocene of the region of the deposition of the Yorktown Formation and provided a comparison with the present climate of this area. Druid Wilson, also of the United States Geological Survey, collected many of the South Carolina specimens discussed in this paper and provided much information on the stratigraphy of the beds from where they were collected. Blake W. Blackwelder, who is now studying the mollusks of the Bear Bluff Formation, gave me his preliminary opinions on the age of this formation, and Richard E. Grant of the United States Geological Survey and David L. Pawson of the National Museum of Natural History, Smithsonian Institution, reviewed the paper and made many pertinent suggestions. Lauck W. Ward provided valuable information on the relative age of the Virginia localities.

Thomas F. Phelan not only did the photography but also made the remarkable reconstruction of a disassociated lantern of *Psammechinus philanthropus* figured on Plate 2: figures 7, 8. Larry Isham, the scientific illustrator for the Department of Paleobiology in the National Museum of Natural History made the locality map and the superb reconstruction of the living habits of the Miocene echinoids on Figure 2.

Horace Richards of the Academy of Natural Sciences of Philadelphia lent specimens and searched for one of Conrad's lost types, and Norman F. Newell provided locality data on one of the type-specimens in the American Museum of Natural History (AMNH).

Stratigraphy

The Yorktown Formation consists of fossiliferous, silty sands and sandy silts that crop out in southeastern Virginia and northeastern North Carolina, from the Rappahannock River in Virginia to the Neuse River in North Carolina. Most of the echinoids (representing all the species) came from four localities, two of which have been dated by Hazel (1971a). He has just completed a biostratigraphic study of the ostracodes of the Yorktown, identifying 230 species and dividing

the formation into three ostracode assemblage zones. The oldest zone, the *Pterygocythereis inexpectata* Zone, and the middle *Orionina vaughani* Zone are considered by Hazel to be late Miocene, and his uppermost zone, the *Puriana mesacostalis* Zone, is considered by him to be early Pliocene. The two echinoid localities, and probably the third and fourth at and near Mogart's Beach, belong to Hazel's *Orionina vaughani* Zone. This zone approximates Mansfield's (in Gardner, 1943) *Turritella alticostata* Zone, which Mansfield also considered to be late Miocene. Gibson (1967) likewise considers these beds as late Miocene.

Warren C. Blow and Lauck W. Ward (personal communication, 1971) have made extensive collections from these four localities and believe that, on the basis of the molluscan assemblages, they are roughly equivalent in age.

Paleoenvironment

CLIMATE.—Hazel (1971b) has also made a paleoclimatological study of the Yorktown Formation based on the ostracodes, and he concludes that the climate was more equable and warmer in the winter during the deposition of the Yorktown than it now is in the same region. Fifty-nine of the ostracode species found in the Yorktown are still living, and, as a result, Hazel is able to make well-substantiated estimates of the Yorktown climate. The *Orionina vaughani* Zone (where the echinoids occur) contains 40 surviving ostracode species. These ostracodes indicate that bottom temperatures averaged no cooler than 12.5°C in the coldest month and that the summer maximum averaged below 20°C in the older part of the zone and less than 25°C in the middle and younger parts. Hazel believes that, during deposition of the *Orionina vaughani* Zone, the yearly range in bottom temperature was only about 5°C to 10°C. This equable thermal regime is markedly different from that of any province and concomitant climate zone now extant along the Atlantic coast of the United States. The temperatures varied from about 12°C to 15°C in the winter to about 17.5°C to 20°C and finally to 20°C to 25°C in summer. This particular thermal regime, Hazel believes, is indicative of warm-temperate conditions analogous to that represented by the Lusitanian Province of western Europe. A warm-temperate zone is not present along the Atlantic coast of North America today (Dana,

1853; Hall, 1964; Hazel, 1970). The offshore climate of the study region today is mild-temperate with the bottom temperature in inner sublittoral waters averaging about 5°C to 7.5°C in the coldest month and about 20°C to 25°C in the warmest month.

The Yorktown echinoids, like the ostracodes, indicate a past climate warmer than now. *Psammechinus philanthropus* (Conrad) is very similar to the living *P. miliaris* (Müller), so much so that small specimens of both species are almost indistinguishable. This living species occurs in cold-temperate to subtropical waters off European coasts from Trondheimfjord to the northwestern coast of Africa. *Spatangus glenni* Cooke is very similar to *S. purpureus* Müller, also occurring in the same waters and in the Mediterranean. *Mellita aclinensis* Kier has been found in the Tami-ami Formation of Florida, probably deposited in subtropical waters; it is very similar to *M. quinquesperforata* (Leske), now living in mild-temperate to tropical waters along the eastern coast of America from Nantucket to the Brazilian coast as far south as Santos. *Mellita quinquesperforata*, primarily a tropical-subtropical species, is scarce north of Cape Hatteras. *Arbacia improcera* (Conrad) resembles *A. punctulata* (Lamarck), which lives in mild-temperate to tropical waters from Cape Cod through the Caribbean and in Yucatan. *Echinocardium orthonotum* (Conrad) is not useful in evaluating past climate because it resembles the living species *E. cordatum* (Pennant), which is virtually cosmopolitan in cold-temperate to tropical waters.

Although some of these living species range into cooler waters, they all occur in subtropical regions, suggesting that the fossil echinoids they resemble lived in waters warmer than the mild-temperate waters now occurring off the coast of Virginia.

LIVING HABITS OF THE ECHINOIDS.—Most of the fossil species are very similar to species now living, and it is therefore possible to make well-substantiated assumptions on the living habits of these fossil echinoids (see Figure 1).

Arbacia improcera resembles *A. punctulata* (Lamarck) living off the coast of Virginia. Presumably its living habits were similar to *A. punctulata*, which is found in its greatest numbers in shallow water 5 to 20 feet deep on rock or sand bottoms. This species according to Sharp and Gray (1962) and Kier and Grant (1965:17–18) is highly variable in its response to light, with some specimens remaining exposed to

the full light of the sun and others seeking cover. Like *A. punctulata*, *A. improcera* probably lacked sucking disks on its adapical tubefeet and, therefore, was unable to cover itself with debris. It presumably did not excavate holes in the rocky shores (no living *Arbacia* can). It has many porepairs on the adoral surface, and the large number of tubefeet extending from them would have made it possible for the animal to cling tenaciously to intertidal rocks that were exposed to wave action. These tubefeet had sucking disks, as indicated by the presence of a ridge between the pores of each porepair, for the attachment of muscles used to retract these prehensile tubefeet (Nichols, 1959a:421; Chesher, 1968:17).

Psammechinus philanthropus (Conrad) is strikingly similar to *P. miliaris*, and presumably it lived similarly in the littoral zone on rock or sand. It probably lived with *Arbacia improcera*, but it doubtless had sucking disks on its adapical tubefeet (they occur in *P. miliaris*), and, therefore, it may have had its test covered with algae and other foreign debris. Some individuals might have lived in holes burrowed into rock.

Mellita aclinensis Kier is very like *M. quinquesperforata* (Leske) and presumably lived like it in shallow water on a firm sand bottom. It would have been slightly buried, with not more than 20 to 30 mm of sediment on top of its test.

Spatangus glenni is very similar to *S. purpureus* Müller now living off the British Isles. Owing to the research of Nichols (1959a, 1959b, 1962), the living habits of this British species are well known. *Spatangus glenni* shares enough morphological features with *S. purpureus* to suggest that the fossil species lived like the Recent ones in shallow water, that is, offshore, burrowing approximately 2 cm into coarse sediment. *Spatangus glenni* has a bilobed subanal fasciole that is also present in *S. purpureus*, where it is used to maintain, in the sediment, two horizontal tubes lying parallel to each other and originating at each lobe of the fasciole. These tubes provide a drain-away for the waste products of respiration and defecation, which are transported to the posterior region of the echinoid by cilia. This current is greatly enhanced and directed away from the test down the twin tubes by the densely ciliated small spines in the subanal fasciole. According to Nichols (1962:116), two tubes are necessary in *S. purpureus* because the echinoid lives in coarse sediment that is subject to

caving. The extra tube provides oxygen for the echinoid while it reopens a blocked tube. Long prehensile tubefeet found within the fasciole are used to excavate these tubes and to plaster their sides with mucus. The presence of large pores within the fasciole of *S. glenni* indicates that it also had these tubefeet.

Commonly, spatangoids that burrow deeply in the substrate have a tube extending from the dorsal surface of the test to the top of the substrate. This tube provides a channel for water currents that are directed over the respiratory tubefeet of the petals. *Spatangus purpureus* (and *S. glenni* as indicated by the presence of large tubercles) has large spines on the adapical surface that help keep an opening to the surface when the echinoid is burrowed only slightly, but both species lack the structures necessary to maintain a long tube. The porepairs in the anterior ambulacrum of *S. glenni* are very small and lack any protuberances between the pores of a pair for the attachment of the muscles that are used to retract the long tubefeet necessary to excavate and maintain a tube; however, *S. purpureus*, in spite of the lack of a dorsal tube, is able to burrow because it lives in coarse substratum that has large interstices through which the currents can pass.

Because the subanal fasciole in *S. glenni* is less strongly bilobed than in *S. purpureus* and there are fewer adapical tubercles, resulting in fewer large spines, *S. glenni* was probably able to burrow slightly less deeply than *S. purpureus*.

Although *Echinocardium orthonotum* is also a spatangoid, it probably lived somewhat differently than *Spatangus glenni*. It is very similar and has all the functional morphological features of the living *E. cordatum* (Pennant). Considerable research has been done on this living species; Nichols (1959a) in particular has studied its living habits and compared them to *S. purpureus*. Although *S. purpureus* (and presumably *S. glenni*) burrows only to a level 2 cm beneath the surface of the substratum, *E. cordatum* burrows much deeper, to a depth of 10 to 20 cm. According to Nichols, *E. cordatum*, because it commonly lives near shore on sandy beaches, must burrow deeply in order to avoid being left high and dry by the receding tide, whereas *S. purpureus* lives far enough offshore to be unaffected by tides. *Echinocardium cordatum* builds and maintains a long breathing tube to the surface and has an inner fasci-

ole on its dorsal surface in order to draw water down the funnel and across the respiratory petals. Likewise, *E. orthonotum* has an inner fasciole and presumably also has constructed a funnel. Because *Echinocardium cordatum* and *E. orthonotum* do not have bilobed subanal fascioles as do *S. purpureus* and *S. glenni*, they could construct only one sanitary tube for the removal of waste products instead of two as in the two species of *Spatangus*. Finally, although *E. cordatum* lives on beaches near shore, it is not found in areas subject to heavy wave or current action.

In summary (Figure 1), *Arbacia improcera* and *Psammechinus philanthropus* would be living in the intertidal and littoral zones on rock or sand, *P. philanthropus* in holes in the rock or covered with debris, but *A. improcera* would be easily visible with its test uncovered. Living also near shore, deeply buried in the sand, would be *Echinocardium orthonotum* with a long funnel extending above its test to the surface of the substratum and a single tube extending posteriorly. The sand dollar, *Mellita aclinensis*, would be found near shore at a depth of 3 to 15 meters with its test slightly buried. Finally, farther offshore *Spatangus glenni* would be burrowed only a few centimeters in the sand, with no funnel to the surface, but with its adapical spines holding open a passage to the respiratory tubefeet, and with two tubes extending posteriorly.

CONDITION OF DEPOSITION.—These echinoids are remarkably well preserved. Most of the regulars still have the parts of their lanterns intact inside their tests, and many pedicellariae are present with the specimens. Many specimens of *Psammechinus philanthropus* still have food or fecal pellets preserved in their tests (Plate 2: figure 2).

Because lanterns and pedicellariae are lost after the death of the animal, it must be assumed that the echinoids were covered with sediment at, or soon after, death; otherwise, currents or the action of predators would have broken up the tests and disassociated the lanterns and pedicellariae. Echinoids, however, do not occur in the sediment in their living positions. Large slabs have been collected that contain many specimens of *P. philanthropus* and *E. orthonotum* (Plate 9: figure 3), and these specimens are jumbled with the tests in haphazard position. It is, therefore, probable that these echinoids, while alive, were caught up by storm currents and waves and covered by sediment. Possibly this deposition took

FIGURE 1.—The probable life positions of the five echinoid species from the Yorktown Formation: These fossil species are so like species now living that it is possible to make well-substantiated predictions of their living habits. The figures of *Spatangus* and *Echinocardium* are based on the figures and descriptions of Nichols (1959a) for *Spatangus purpureus* Müller and *Echinocardium cordatum* (Pennant).

place near shore in shallow water perhaps 5 to 20 meters deep because the most common specimens are *P. philanthropus* and *E. orthonotum*, both species that are assumed to have lived near shore.

POST-DEPOSITION CONDITIONS.—Many of these echinoids still have their color, and many of the tests do not have the interstices of their plates filled with secondary calcite. This unusual preservation indicates that little leaching and recrystallization has occurred in the sediments since their deposition. The presence of organic material still preserved in the food or fecal pellets indicates restricted bacterial activity.

Relation to Other Fossil Echinoid Faunas

The Yorktown echinoid assemblage has affinities with echinoid assemblages from the upper Miocene or Pliocene of South Carolina and Florida. *Echinocardium orthonotum* of the Yorktown is considered herein a senior synonym of *E. gothicum* (Ravenel), described by Ravenel (1848) and Tuomey and Holmes (1855) from Grove Plantation on the Cooper River in South Carolina. This species also occurs in spoil deposits in the Intracoastal Waterway canal, which Druid Wilson (personal communication, 1970) considers, on the

basis of the mollusks, to be late Miocene and equivalent in age to the beds at Grove Plantation. *Spatangus glenni*, which is found in the Yorktown, is found also in these canal deposits. B. W. Blackwelder (personal communication, 1971), who is currently studying the mollusks, believes that these deposits are from the Bear Bluff Formation of Dubar (1969), which Dubar considers probably to be Pliocene.

The Yorktown species *Arbacia improcera* is very similar and may be conspecific with *A. sloani* (Clark) from upper Miocene beds in the Duplin Marl at Bostick Landing, Pee Dee River, South Carolina.

The Yorktown echinoid assemblage is also somewhat similar to the echinoids of the upper Miocene Tamiami Formation of Florida. *Mellita acinensis* is found in both assemblages, and the Yorktown *A. improcera* is probably synonymous with the Tamiami *A. crenulata* Kier.

Localities

Most of the echinoids collected by Warren C. Blow came from the four localities in Virginia indicated in Figure 2 and described by him below. Hazel (1971a)

FIGURE 2.—The localities (1-4) where Warren C. Blow collected most of his echinoids from the Yorktown Formation.

has studied the ostracodes from localities 3 and 4 and considers them to be from his *Orionina vaughani* Zone of the Yorktown Formation. Both Warren Blow and Lauck W. Ward, who also has collected extensively in the Yorktown, consider all four localities to be in this zone.

LOCALITY 1 (USGS locality 25113).—Future Homemakers of America-Future Farmers of America [FHA-FFA] girls camp, approximately 3.6 miles NNE of Smithfield, south bank of James River, Isle of Wight County (see Virginia quadrangle 7.5' Mulberry Island, 1965). A block of cemented coquina containing numerous specimens of *Echinocardium orthonotum* (Conrad) was found adjacent to 23-foot-high face of outcropping Yorktown Formation at a point between 100 and 300 yards ESE of the present camp staircase. This material undoubtedly was derived from a distinctive 1- to 2-foot-thick ledge of cemented coquina occurring approximately 21 feet above the beach, which terminates the Yorktown Formation along Mogarts Beach. Collectors: Edward E. Bottoms and Warren C. Blow. Species: *Echinocardium orthonotum* (Conrad), *Psammechinus philanthropus* (Conrad).

LOCALITY 2.—Hunt club, south bank of James River, approximately 0.65 miles ESE of FHA-FFA girls camp at Mogarts Beach, Isle of Wight County (see Virginia quadrangle 7.5', Mulberry Island, 1965). This locality begins at the mouth of a deep ravine (distinguishable by its two small lakes), approximately 100 feet WNW of the club house, and continues ESE along the base of the bluffs overlooking the James River for approximately 200 yards.

USGS 25114: Echinoids collected in situ in very macrofossiliferous, aqua, silty sand between the beach level and not more than 6 feet above the beach. Collectors: Warren C. Blow and others from 1963–1967. Species: *Arbacia improcera* (Conrad), *Psammechinus philanthropus* (Conrad), and *Spatangus glenni* Cooke.

USGS 25115: In situ in sparsely macrofossiliferous, aqua, silty sand, approximately 6.5 to 8.5 feet above beach level. Collectors: R. H. Bailey, B. Dyer, R. V. Blow, and W. C. Blow, 1965–1967. Species: *Echinocardium orthonotum* (Conrad).

USGS 25116: 100 yards ESE of ravine between 0 and 0.5 feet above beach level. Collectors: Richard H. Bailey and W. C. Blow, 1967. Species: *Spatangus glenni* Cooke.

USGS 25117: 158 yards ESE of ravine, 3 feet above beach level. Collector: W. C. Blow, 1968. Species: *Spatangus glenni* Cooke.

LOCALITY 3.—Rice's Pit just N of the intersection of the Fox Hill Road (Virginia Highway 167), and the Harris Creek Road, Hampton City (see Virginia quadrangle 7.5', Hampton, 1965).

USGS 24810: Western wall of pit approximately 350 feet NNW of the upper SW corner; approximately 36 feet below local topography. Collectors: B. Dyer and W. C. Blow, 1969. Species: *Echinocardium orthonotum* (Conrad).

USGS 25122, 25123: In situ from very macrofossiliferous, buff, silty sand of the upper 6 to 7 feet of the Yorktown Formation (approximately 6 to 12 feet below local topography along central portion of the southern half of the western wall of pit). Collectors: W. C. Blow, Barbara Grocys. Species: *Arbacia improcera* (Conrad), *Psammechinus philanthropus* (Conrad), *Mellita acinensis* Kier, and *Echinocardium orthonotum* (Conrad).

LOCALITY 4.—Lone Star Cement pit, 0.5 mile N of Chuckatuck, Nansemond County (see Virginia quadrangle 7.5', Chuckatuck and Beens Church, 1965).

USGS 24493: Western wall of pit approximately 300 yards from NW corner 1 to 3 feet above lake level, 24 feet below top of section. Collectors: W. C. Blow and R. V. Blow, 1967. Species: *Psammechinus philanthropus*, *Echinocardium orthonotum* (Conrad).

USGS 24626: Western wall of pit, eastern face of cut 33. Collector: W. C. Blow, 1968. Species: *Echinocardium orthonotum* (Conrad).

USGS 25119: Float of maroon chunks of semi-hardened, silty sand collected between the south-central and northernmost extent of the western wall of the pit. Collector: W. C. Blow, 1964. Species: *Echinocardium orthonotum* (Conrad).

USGS 25120: Approximately 3 to 5 feet above the lake level (22 to 24 feet below local topography) along the central portion of the western wall of the pit. Collectors: W. C. Blow and E. E. Bottoms, 1964. Species: *Echinocardium orthonotum* (Conrad).

USGS 25121: Material collected in situ (generally from a fine blue-gray hash) along the south-central and northern half of the western wall of pit, approximately 0 to 3 feet above lake level or 24 to 27 feet below local topography. Collectors: W. C. Blow and others, 1963–present. Species: *Arbacia improcera*

(Conrad), *Psammechinus philanthropus* (Conrad), *Mellita acclinensis* Kier, and *Echinocardium orthotum* (Conrad).

Arbacia improcera (Conrad)

PLATE 1

Echinus improcerus Conrad, 1843a:310.

Psammechinus improcerus.—Stefanini, 1912:705.

Coelopleurus improcerus.—Clark and Twitchell, 1915:180, pl. 84: figs. 4a–c.

Arbacia improcera.—Cooke, 1941:11, pl. 1: figs. 7–9.—Cooke, 1959:20, pl. 4: figs. 1–3.—Kier, 1963: pl. 1: fig. 6.

For many years only one specimen has been available (in addition to the missing holotype), but five additional specimens are now extant. The dimensions of five of these specimens are as follows:

Diameter	6.7	18.5	32.7	29.5	36.5
Height	3.5	6.9	16.0	13.2	15.0
Diameter of peristome	—	9.5		13.3	16.4
Greatest width of ambulacrum	1.3	3.6	7.1	6.2	7.4
Height of interambulacral plate at ambitus	—	1.4	2.7	2.5	2.7
Width of interambulacral plate at ambitus	1.3	3.8	6.7	6.0	6.7
Number of interambulacral plates in single row	8.9	12.0	14.0	13.0	15.0
Number of porepairs in single poriferous zone	—	37.0	52.0	51.0	57.0
Greatest width of apical system	2.8	5.9	8.3	—	10.0

COMPARISON WITH OTHER SPECIES.—*Arbacia improcera* may be conspecific with *A. sloani* (Clark) from upper Miocene beds in the Duplin Marl at Bostick Landing, Pee Dee River, South Carolina. Only one specimen of *A. sloani*, the holotype, is known, and it is similar in most of its dimensions to *A. improcera*, having the diameter of its peristome 50 percent of the diameter of its test (D), width of an ambulacrum at the ambitus 20 percent D, height of an interambulacral plate at the ambitus 2.0 percent D, width 5.5 percent D, greatest width of the apical system 7.3 percent D, number of interambulacral plates in single row 14, and number of porepairs in a single poriferous zone 55. Cooke (1959:21) considered that the two species were very similar and might be synonymous, but he also noted that they differed, with *A. improcera* having a lower test and a more rugose

ornamentation. The only specimen of *A. improcera* that he had available is lower than the holotype of *A. sloani*, which has a height 41 percent of its diameter as opposed to 53 percent in *A. sloani*. One of the recently acquired specimens of *A. improcera*, however, has a height equal to 49 percent D. This difference from *A. sloani* is slight and, until more specimens have been found, its significance cannot be evaluated. Although Cooke considered the ornamentation in the naked adapical interambulacral areas different in the two species, I can see no distinguishing dissimilarities (compare Plate 1: figure 5 to Plate 2: figure 1). When more specimens are available, it should be possible to determine whether these two species are separate or synonymous, but, until then, it seems best not to attempt to make this decision.

Arbacia improcera differs from *A. rivuli* Cooke from the late Miocene(?) in South Carolina in having its adapical interambulacra more naked. In *A. improcera* only a single row of tubercles occurs on each column of interambulacral plates down to a point near the ambitus, whereas in *A. rivuli* a second row extends almost to the apical system. *Arbacia improcera* differs from *A. waccamaw* Cooke also from the late Miocene(?) in South Carolina in having wider and lower adapical interambulacral plates.

Arbacia improcera may be conspecific with *A. crenulata* Kier from the late Miocene Tamiami Formation of Florida. When I described *A. crenulata*, only one specimen of *A. improcera* was available for comparison. On this specimen the ornamentation was decidedly different from that of *A. crenulata*. In *A. crenulata* the ornamentation consists of fine crenulations, whereas in the single specimen of *A. improcera* they were granules; however, on the new specimens of *A. improcera* these granules commonly are joined together into crenulations. These two species are probably synonymous, but more specimens are needed in order to know the extent of the variation of this ornamentation within one population.

Arbacia improcera is similar in the following dimensions to *A. punctulata* (Lamarck), now living off the coast of Virginia: height, diameter of peristome, width of ambulacrum, width of apical system, number of interambulacral plate, and number of porepairs. It differs in having only two large tubercles on each interambulacral plate at the ambitus, whereas there are three in specimens of the same size in *A.*

punctulata. Moreover, in *A. improcera* the naked zones in the interambulacra extend farther adorally.

LOCALITIES.—Blow's localities 2 (USGS 25114), 3 (USGS 25122), 4 (USGS 25121), J. T. Williams' marl pit, Smith County, 0.5 mile below the dam at Suffolk waterworks, collected by M. W. Twitchell. USGS 24817, exposed face of high bluff (approximately 500 feet NW of cemetery), south bank of Nansemond River, 0.5 mile downstream from Virginia Highways 10 and 32 bridge, Suffolk City, Virginia, from fossiliferous, bluff, silty sand, 3 feet above beach level, collected by Brian Dyer and Warren C. Blow; Bank of Nansemond River rising from tidal flats at Suffolk, Virginia, collected by W. C. Mansfield. The holotype came from the James River near Smithfield.

TYPE-SPECIMENS.—Location of holotype not known; figured specimens: USNM 166487, 17449.

Psammechinus philanthropus (Conrad)

FIGURE 3; PLATE 2: FIGURES 2–8; PLATE 3; PLATE 4: FIGURES 1, 3; PLATE 5: FIGURES 1, 3

Echinus philanthropus Conrad, 1843a:310.—Conrad, 1846:220.

Psammechinus philanthropus.—Meek, 1864:2.—Stefanini, 1912:705.—Clarke and Twitchell, 1915:181, pl. 84: figs. 6a–c.—Cooke, 1941:16.—Cooke, 1959: 16, pl. 3: figs. 1, 2.

Echinus ruffini Forbes in Lyell, 1845a:426, figs. 1a–d [and Lyell, 1845b:560, 2 figs.].—Desor, 1858:121.—Emmons, 1858:306, figs. 239a–d.—Stefanini, 1912:705.

MATERIAL.—Hundreds of extremely well-preserved specimens have been collected by Robert V. Blow and Warren C. Blow. Many of them are on two large slabs. These specimens are arranged haphazardly, indicating that they are not in life position, but the presence of lanterns, apical systems, and spines on many of the specimens indicates that they were buried soon after death. Because in the past only a few specimens have been available, this species has never been adequately described. The description and statistics below are based on 30 specimens from the same locality (Blow locality 4, USGS 24493).

SHAPE AND SIZE.—Diameter (D) varying from 14.0 to 39.3 mm, mean 21.1 (SD 5.4, CV 25.6, N=30), height varying from 46 to 61 percent D (SD 3.5, CV 6.6, N=30), height not varying with size of specimen; marginal outline of test circular to slightly subpentag-

onal with apices at ambulacra; test slightly depressed at peristome.

APICAL SYSTEM.—All oculars exert (Figure 3), genital 2 larger than other genital plates, one or two tubercles on each genital, periproct oblique with long axis passing through genital 2 and ocular V.

AMBULACRA.—Narrow, width 23–26 percent D, mean 24.8 (SD 0.7, CV 3.1, N=30); plates trigeminate, 15 compound plates in single poriferous zone of smallest specimen 14.0 mm in diameter, 20 in specimen 21 mm in diameter, 26 in largest 39.3 mm in diameter, with a mean 18.8 plates (SD 2.5, CV 13.3, N=30).

INTERAMBULACRA.—Plates low, at ambitus 1.2 compound ambulacral plates for each interambulacral plate; 13 plates in single column of smallest specimen 14.0 mm in diameter, 16 in specimen 21.0 mm, 22 in largest 39.3 mm in diameter, mean 15.6 (SD 2.1, CV 13.2, N=30).

PERISTOME.—Pentagonal with apices in interambulacra, large, diameter varying from 36 to 52 percent D, mean 44.8 (SD 3.1, CV 6.8, N=30).

TUBERCULATION.—Ambulacra; two vertical rows of primary, imperforate, noncrenulate tubercles in each

FIGURE 3.—*Psammechinus philanthropus* (Conrad): Apical system of USNM 174452 from Blow's locality 4 ($\times 10$). (A photograph of this region is on Plate 3: figure 4.)

area (Plate 3: figure 2) with two inner rows almost equally developed at ambitus in larger specimens (Plate 5: figure 1); in small specimens only two rows at ambitus, inner tubercles slightly developed (Plate 4: figure 1); primary tubercles occupy most of height of plate.

INTERAMBULACRA.—In large specimens at ambitus 5–8 imperforate, noncrenulate tubercles arranged in 1–2 irregular horizontal rows (Plate 5: figure 3), in small specimens two vertical rows of tubercles at ambitus with a single large tubercle in middle of each plate with a smaller tubercle on either side (Plate 4: figure 3); as echinoid increases in size, these smaller tubercles increase in size relative to the central tubercle until they are of equal size and the two vertical rows are no longer distinguishable.

PEDICELLARIAE.—Tridentate and ophicephalous pedicellariae found (Plate 2: figures 3–6).

LANTERN.—Preserved on most specimens (Plate 2: figures 7, 8).

COLOR.—Preserved on all specimens, dark brown band running down center of ambulacra; lighter or a dark brown band running down center of interambulacra.

COMPARISON WITH OTHER SPECIES.—This species is very similar and obviously closely related to *Psammechinus miliaris* (Müller), now living along the European coasts from the Trondheimfjord and Iceland to the northwestern coast of Africa. I measured the diameter, height, diameter of peristome, width of ambulacrum, and number of interambulacral and ambulacral plates of a collection of both species and tested them statistically to see whether or not they differed significantly. No significant difference is present in the height of the test, width of ambulacra, and number of ambulacral plates, but the two species differ in the diameter of their peristomes and the number of interambulacral plates. *Psammechinus philanthropus* has a larger peristome and more interambulacral plates than *P. miliaris*, with a peristome whose diameter is 44.8 percent the diameter of the test as opposed to 39.7 percent in *P. miliaris*, and an average of 15.6 interambulacral plates in each half-column as opposed to 16.1 in the living species. A student *t* test was run on the difference of these means, and they are significant to .001.

The tuberculation of *P. philanthropus* (Plate 5: figures 1, 3) differs in large specimens in having at least five tubercles on each interambulacral plate at

the ambitus of approximately equal size, whereas in *P. miliaris* one tubercle is larger than all the others (Plate 5: figures 2, 4). This difference, however, is not present in small specimens. Specimens of the two species 14 mm in diameter are indistinguishable in their tuberculation. The small *P. philanthropus* (Plate 4: figures 1, 3) has one larger tubercle on each plate just as in *P. miliaris* (Plate 4: figures 2, 4); however, the difference in size of the peristome is persistent in all the specimens regardless of their size.

The test of *P. philanthropus* has brown bands running down the ambulacra and interambulacra, whereas in *P. miliaris* the test is generally green with dark green bands. This difference is probably significant, but perhaps the present color of the fossil specimens is not the same as it was originally.

Most previous authors have considered Forbes' *Echinus ruffini* a synonym of *P. philanthropus*. The type (probably in the Lyell Collection) came from a locality near Williamsburg, Virginia, where beds of Yorktown age are known to occur, and although Forbes' illustrations are not very clear, his specimen appears to be *P. philanthropus*.

Cooke (1959:16) considered *P. exoletus* McCrady a synonym of *P. philanthropus*; however, the type-specimen, which is lost, was only a small fragment, and it is not possible from the illustration of it to see enough specific characters to be able to determine whether or not it belongs to *P. philanthropus*. The fragment came from "Smith's," Goose Creek, South Carolina, from beds that Cooke (1941:16) considered to be the Pliocene Waccamaw Formation but that later (1959:16) he thought were late Miocene (Duplin Marl).

TYPE-SPECIMENS.—Location of holotype not known; it is not with Conrad's other types at the Academy of Natural Sciences of Philadelphia (H. G. Richards, 1971, personal communication); figured specimens: USNM 562264, 559495 (formerly Johns Hopkins University T1001), USNM 174450, 1774451, 1774452, 174453, 174454.

STRATIGRAPHIC POSITION AND GEOGRAPHIC LOCALITIES.—Upper Miocene Yorktown Formation. Virginia: Holotype from James River near Smithfield; south side of James River at J. A. Mogarts' residence 5 miles N of Smithfield, USNM 166501, collected by W. M. Twitchell; Rock Wharf road on Days farm 1.5 miles NE of Smithfield, collected by W. M. Twitchell; Bluff W of Days Point from uppermost

bed, James River, USGS 14065, collected by W. C. Mansfield and C. W. Mumm; Yorktown, USNM 373038, collected by Julia Gardner; 2.5 miles NW of Suffolk, about 0.5 mile below Calhoun Bridge (on right bank of creek), USGS 10198, collected by W. C. Mansfield. Warren C. Blow collected specimens from his localities 1-4 at USGS 25113, 25114, 25121, 25122. The holotype of *Echinus ruffini* Forbes came from Burwell's Mill near Williamsburg. All the above localities are probably in Hazel's *Orionina vaughani* Zone, according to Warren C. Blow (1971, personal communication).

Mellita acclinensis Kier

PLATE 6; PLATE 7: FIGURE 1

Mellita acclinensis Kier, 1963:40-45, figs. 36-41; pl. 15: figs. 1-3; tpls. 3,4.

Leodia caroliniana Cooke [not Ravenel], 1959:47.

Three specimens are referred to this species, which previously was known from the late Miocene Tamiami Formation in Florida. The Virginia specimens differ only in their larger size. The Florida specimens are less than 73 mm long, whereas the Virginia specimens are 128-147 mm long. Because echinoids commonly occur together in groups of individuals of the same age, the Florida population probably was only more juvenile. The figured Florida specimens have wider lunules, but this is because they are smaller, and in smaller specimens the lunules are wider relative to their length. A larger fragment from Florida is figured herein (Plate 6: figure 3) showing the narrower lunules typical of the larger specimens from Virginia. The dimensions of the Virginia specimens are as follows (in mm):

	USNM 174457	USNM 174458	USNM 174468
Length	128	130	147
Width	135	129	148
Height	16.0	12.3	-
Length of petals:			
III	-	33.0	-
II	-	30.5	-
I	-	38.2	-
Width of petals:			
III	-	13.1	-
II	14.2	12.7	-
I	-	12.5	-
Number of porepairs in single poriferous zone of petals:			
III	-	88	-

	USNM 174457	USNM 174458	USNM 174468
II	-	90	-
I	-	107	-
Width (maximum) of interporiferous zones:			
III	-	-	-
II	4.8	4.7	-
I	-	4.1	-
Distance of apical system from anterior margin:	62.2	60.2	-
Length of posterior lunule:	26.4	32.2	-
Distance of peristome from anterior margin:	64.6	62.0	71.0

Considerable evidence suggests that *M. acclinensis* is the ancestor of *M. quinquesperforata* (Leske). The species differ mainly in that *M. acclinensis* has six lunules and *M. quinquesperforata* commonly has five; however, as pointed out by Cerame-Vivas and Gray (1964), some specimens of *M. quinquesperforata* have been found with six lunules. Probably the species evolved from the form with six lunules in the late Miocene and Pliocene to a form commonly with five lunules in the Recent. (Two specimens were collected by Richard H. Bailey and Warren C. Blow from Hazel's (1971a) *Puriana mesacostalis* Zone of the Yorktown Formation at Colerain Landing, North Carolina, which Hazel considers to be early Pliocene.)

Although there is a sand dollar, *Leodia sexiesperforata* Leske, with six lunules living today off the southeastern United States, I do not believe that it is a descendent of *M. acclinensis*. The presence of six lunules in *Leodia* is not really the important morphological character distinguishing *Leodia* from *Mellita*. Cerame-Vivas and Gray (1964) assumed this when they considered that *L. sexiesperforata*, the type-species of *Leodia*, should be referred to *Mellita*. *Leodia sexiesperforata* differs from *M. quinquesperforata*, the type-species of *Mellita*, in having its posterior lunule not extending far anteriorly between the posterior petals, in having its paired interambulacra separated from the basicoronal row by two pairs of ambulacral plates, in having its periproct slightly indenting the basicoronal plate, and in having a short pair of post-basicoronal plates in the paired interambulacra.

Cooke (1959:47) tentatively referred a specimen from the Yorktown Formation at Days Point to *L. caroliniana* (Ravenel), but this specimen is *M. acclinensis*. The test of *M. acclinensis* is much flatter than

this South Carolina species, which has a sharper margin, and the lunules are commonly, but not always, narrower.

Although the holotype of *L. caroliniana* has been lost, there are many specimens in the national collections from localities near the type-locality (Grove Plantation, Cooper River), from beds of the same age and slightly younger, that appear to be conspecific with Ravenel's holotype. These specimens are very variable in the shape of their petals and lunules, and they include specimens that have longer and curved posterior petals with narrow lunules, as in the specimen figured by Ravenel (1842), and the straight posterior petals and short lunules of the specimen figured by Tuomey and Holmes (1857: pl. 1: figs. 4a-c).

Leodia caroliniana should be referred to *Mellita* not *Leodia* because the periproct occurs partially within the basicoronal plate (Figure 4), the posterior lunule extends far anteriorly between the posterior petals, the paired interambulacra are separated from the basicoronal row by one pair of ambulacral plates, the

FIGURE 4.—*Mellita caroliniana* (Ravenel): plate arrangement around the peristome of USNM 174465 from beds considered to be probable late Miocene by Cooke (1959:80) ($\times 1.3$). Dredged from the Intercoastal Waterway canal 1 to 1.5 miles SW of the bridge on US Highway 17 near Nixon's Crossroads about 15 miles NE of Myrtle Beach, Horry County, South Carolina (collected by L. C. Glenn).

first pair of post-basicoronal plates in the paired interambulacra are elongate, and the lunules are formed by the closing of marginal notches and not by resorption of the test. It resembles *Encope* in its thick test and in the fact that a few specimens have five instead of four genital pores, but the presence of the periproct in the basicoronal plate separates it from *Encope*, in which the periproct is more posterior and occurs between post-basicoronal plates. *Mellita caroliniana* in general appearance strongly resembles the living *E. emarginata* (Leske), suggesting that *Mellita* and *Encope* may have had a common ancestor. This resemblance caused Cooke (1942:20, pl. 3: figs. 14, 15; 1959:49) to refer these South Carolina specimens, together with a few from North Carolina, to *E. emarginata*.

TYPE-SPECIMENS.—Holotype: USNM 648136; figured paratypes: USNM 648189–648193; figured specimens: USNM 174457, 174458.

STRATIGRAPHIC POSITION AND LOCALITIES.—Florida: Tamiami Formation (barnacle-echinoid-oyster facies = Murdock Station Member of Hunter, 1968:442–443), spoil banks from group of pits (sec. 29, T. 41 S, R. 23 E) about 1 mile SW of Acline, Charlotte County.

Virginia: Yorktown Formation, *Orionina vaughani* Zone, at Blow locality 3, USGS 25122; one from Blow's locality 4 (USGS 25121); and one specimen in a collection made by G. A. Cooper, J. Cooper, Druid Wilson, and H. B. Roberts; specimen referred to by Cooke (1959:47) probably from same zone at Days Point, James River, W of mouth of Pagan Creek, about 4 miles N of Smithfield, USGS 16920.

North Carolina: Yorktown Formation, *Puriana mesacostalis* Zone; Colerain Landing, west bank of Chowan River, Bertie County, in a buff, silty sand approximately 100–150 yards S of the Colerain Beach Club, from layer containing *Pecten eboreus* Conrad, occurring approximately 7 feet above beach level, USGS 25118.

Echinocardium orthonotum (Conrad)

FIGURE 5; PLATE 8: FIGURES 3–7; PLATE 9

Spatangus orthonotus Conrad, 1843b:327.

Amphidetus orthonotus.—Tuomey and Holmes, 1855: pl. 2: figs. 1–1c.

Echinocardium orthonotum.—Clark, 1904: 430 [not pl. 119: figs. 1a–c, which is *Echinocardium marylandiense* Kier,

new species].—Stefanini, 1912:706.—Clark and Twitchell, 1915: 213, pl. 97: figs. 2a–c [2a, b with image reversed], pl. 98: figs. 1a–c [not pl. 98: figs. 2a–c, which is *E. marylandiense* Kier, new species].—Cooke, 1942:60.—Cooke, 1959:78 [not pl. 33: figs. 1–5, which are *E. marylandiense* Kier, new species].

Amphidetus virginianus Forbes in Lyell, 1845a: 425, 2 figs. *Echinocardium virginianum*.—Desor, 1858:408.

Amphidetus gothicus Ravenel, 1848:4, figs. 1, 2.—McCrary in Tuomey and Holmes, 1855:7, pl. 3: figs. 3, 3a–f.

Echinocardium gothicum.—Stefanini, 1912:707.—Clark and Twitchell, 1915:214.—Cooke, 1942:60.—Cooke, 1959:79, pl. 33: figs. 7–10.

Amphidetus ampliflorus McCrary in Tuomey and Holmes, 1855:6, pl. 3: figs. 2, 2a.

Echinocardium ampliflorus.—Stefanini, 1912:707.

MATERIAL.—Over 100 specimens, most of which were on a single slab (Plate 9: figure 3). The specimens lack their spines, but, considering their thin, fragile tests, they must have been buried at, or soon after, death. The tests are arranged in haphazard fashion, indicating that they are not in living position. The description and statistics below are from 25 specimens from this slab.

SHAPE AND SIZE.—Largest specimen 75.0 mm long, smallest 28.3, mean 42.8 (SD 11.5, CV 26.9, N=25); test wide, width 80–97 percent L, mean 86.1 (SD 3.9, CV 4.5, N=24), greatest width anterior of center; test high with height 47–61 percent L, mean 53.3 (SD 4.2, CV 7.8, N=21), greatest height posterior of apical system; posterior truncation oblique with periproct slightly visible from above.

APICAL SYSTEM.—Four genital pores, ethmolytic with genital 2 extending far posteriorly; located at distance from anterior margin to center of genital pores equal to 40–52 percent L, mean 45.5 (SD 2.9, CV 6.4, N=24).

AMBULACRA.—Anterior ambulacrum not petaloid (Plate 9: figure 1), in groove from apical system to peristome, at margin depth of groove equal to 3.2 percent L; porepairs within internal fasciole oblique with adapical pore of pair larger than adoral, small node between pores of each pair; pores in plates between internal fasciole and phyllode very small, single or slit-like; 7 or 8 pores in single poriferous zone from internal fasciole to peristome.

Anterior paired petals very wide, with large porepairs outside of internal fasciole and 4–5 large porepairs within internal fasciole in posterior poriferous zones, none in anterior poriferous zones within internal fasciole, petals only slightly depressed, nar-

rowing distally; 11–13 (mean 11.7) large porepairs outside of internal fasciole in petal IIa, 7–8 (mean 7.6) large porepairs outside of internal fasciole in petal IIb.

Posterior paired petals with no large porepairs within internal fasciole, 10–12 (mean 11.1) large porepairs in petal Va outside of internal fasciole, 9–11 (mean 10.5) in petal Vb outside of internal fasciole; outer poriferous zones of anterior and posterior petals forming almost continuous arc; ambulacral plates beyond petals with single pores except within anal fasciole, where 2 porepairs in each single poriferous zone.

INTERAMBULACRA.—22–24 plates in interambulacrum 5, 15–17 in interambulacrum 1, 13 in 2 from internal fasciole to peristome.

PERISTOME.—Located at distance from anterior margin to anterior edge of peristome equal to 23–32 percent L, mean 27.5 (SD 1.8, CV 6.4, N=21); opening wider than high with width 15–23 percent L, mean 19.6 (SD 2.1, CV 10.6, N=16).

PERIPROCT.—Located high on posterior truncation, opening slightly wider than high with width 16.5 percent L (SD 2.4, CV 14.7, N=14), height 12–20 percent L, mean 14.6 (SD 2.5, CV 17.4, N=13); located between plates 5–8.

ORAL PLATE ARRANGEMENT.—Labrum wide (Figure 5), extending across almost entire width of peristome, extending very short distance posteriorly, length

FIGURE 5.—*Echinocardium orthonotum* (Conrad): Labrum of USNM 174466 from Blow's locality 1 ($\times 5$).

of labrum 5–8 percent L, mean 6.7 (SD 0.8, CV 11.9, N=9); plastron extending to posterior margin, length 53–60 percent L, mean 57.1 (SD 1.9, CV 3.3, N=13) width 26–32 percent L, mean 28.6 (SD 1.8, CV 6.4, N=9); first plate of interambulacra 1, 4 very narrow. Ambulacra widening near peristome, phyllodes with 5 pores in ambulacrum III, 9–10 in II, 7 in I.

FASCIOLAS.—Internal fasciole prominent, greatest width of tract 1.6 mm in specimen 66 mm long or 2.4 percent L, fasciole crossing ambulacral plates 7a and 7b in ambulacrum III, 19a–20a and 17b in ambulacrum II, 22a and 24b in ambulacrum I, 11a–12a or b in interambulacrum 5, 8a–9a or b in 1, 7a or 7b in 2; greatest width of area circumscribed by internal fasciole anterior of apical system, width 26–35 percent L, mean 30.6 (SD 2.4, CV 8.1, N=24). Subanal fasciole occurring on posterior truncation below periproct, area circumscribed by fasciole 15.0 mm wide on specimen 66 mm long or 22 percent L, maximum width of tract 1.1 mm wide on specimen 66 mm long or 1.6 percent L; crossing plates 3–5 of interambulacrum 5, plates 6a–8a of ambulacrum I, plates 6d–8b of ambulacrum V. Anal fasciole extending adapically from subanal fasciole (Plate 8: figure 6).

COMPARISON WITH OTHER SPECIES.—This species has been considered in the past as including specimens from the Choptank Formation in Maryland and the Yorktown Formation in Virginia. Cooke (1959: 79) noted that there were some differences between specimens from the two localities and suggested that two species might be represented, but he had only two poorly preserved specimens from the Yorktown and could not be certain that they were distinct. Study of a large number of specimens now available shows clearly that the Choptank specimens are specifically distinct from the Yorktown specimens. A student *t* test was run on dimensions of the two populations, and nine dimensions differed very significantly. These results are in Table 1. A *P* test was run to eliminate all those characters whose variances were too high to permit a valid *t* test. *Echinocardium orthonotum* differs from *E. marylandiense*, new species, in having a narrower, less angular, and lower test, a narrower and less posteriorly situated peristome, wider periproct, longer and narrower plastron, shorter labrum, narrower fascioles, a narrower area circumscribed by the internal fasciole, and less prominent nodes on the interambulacral plates.

TABLE 1.—Differences between *Echinocardium orthonotum* and *Echinocardium marylandiense*

Characters measured	Mean percent of length of test		Significance of difference by <i>t</i> test (two-sided)
	<i>orthonotum</i>	<i>marylandiense</i>	
Width of test	86.1	97.9	.001
Height of test	53.3	59.0	.001
Distance from anterior edge of peristome to anterior margin	27.5	31.6	.001
Width of peristome	19.6	23.0	.001
Width of periproct	16.5	12.8	.001
Length of plastron	57.1	52.0	.001
Width of plastron	28.6	34.8	.001
Length of labrum	6.7	9.2	.001
Width of area circumscribed by internal fasciole	30.7	39.1	.001

REMARKS.—*Echinocardium orthonotum* appears to be a senior synonym of *E. gothicum* (Ravenel) from the late Miocene or Pliocene of South Carolina. When only a few specimens of *E. orthonotum* were available

and the variation within the species not known, *E. orthonotum* appeared to be distinct from the larger specimens referred to *E. gothicum*; however, specimens of *E. orthonotum* now available from Virginia

are nearly as large as those from South Carolina referred to *E. gothicum*, and no significant differences are apparent. Unfortunately, the type-specimens of *E. gothicum* are lost. They probably were in the Museum, (now the Charleston Museum) College of Charleston, but Druid Wilson of the United States Geological Survey reports (personal communication, 1971) that he did not see them there during a visit in 1970. Several specimens, however, which are indistinguishable from Ravenel's figures of the type-specimens, have been collected in the Intracoastal Waterway canal. The specimen Cooke (1959) referred to *E. gothicum* was one of these. The others were collected by Druid Wilson in 1959 and 1962. The beds at this locality, according to Wilson (personal communication, 1971), are equivalent in age, on the basis of the molluscan fauna, to the beds at the type-locality of *E. gothicum* (Grove Plantation, Cooper River, South Carolina). Wilson considers the beds at the Grove not Waccamaw age (Pliocene), as tentatively suggested by Cooke (1936:130), but Yorktown (late Miocene), as indicated by the presence of *Ostrea disparilis* Conrad and *Margaritaria abrupta* (Conrad), which never have been collected outside of beds of Yorktown age. He also considers these South Carolina beds to be equivalent in age to the Yorktown beds, where the Virginia specimens of *E. orthonotum* were collected.

Although only four of these South Carolina specimens are well enough preserved to show many of the features of the species, their dimensions fall well within the range of the Virginia specimens of *E. orthonotum*. These dimensions include width (81–98 percent of the length), height of the test (50–57 percent L), distance of the anterior edge of the peristome from the anterior margin of the test (25–30 percent L), width of peristome (15–18 percent L), width of the area circumscribed by the internal fasciole (29–30 percent L), distance of the apical system from the anterior margin (44–47 percent L), number of large porepairs in the posterior poriferous zones of the anterior petals with the internal fasciole (5), and number of pores in the phylloides. The petals are of similar shape and the internal fasciole of similar configuration. Three of these specimens differ in having 1–3 more porepairs in each poriferous zone of the petals outside of the internal fasciole than in the Virginia specimens. It is unfortunate that more specimens are

not available from South Carolina in order to determine the significance of this difference and to afford a firmer basis for determining whether or not these two species are synonymous, but at this time the evidence is insufficient to separate them. A photograph of one of the South Carolina specimens is included on Plate 8: figure 3 for comparison with the Virginia specimens.

McCrary (in Tuomey and Holmes, 1855:6) erected another species, *Amphidetus ampliflorus*, for one specimen from the type-locality of *E. gothicum*. According to McCrary, this specimen differs from *E. gothicum* in having a lower test and its greatest width anterior instead of central. Most subsequent workers including Cooke have considered these two species to be synonymous. This slight difference in the shape of the test occurs within the variation present in the large population of specimens of *E. orthonotum* described herein from Virginia, and presumably the difference could be expected in the South Carolina specimens if they had come from a population of similar species of the same genus. Furthermore, the same variation is present among the specimens collected from the Intracoastal Waterway canal in South Carolina.

Echinocardium orthonotum is readily distinguished from most of the living species of *Echinocardium* by having its paired petals greatly expanded adapically (not contracted) so that the outer poriferous zones of the posterior petals form an arc almost joined with the posterior poriferous zones of the anterior petals. Only three living species have similar petals: *E. mortenseni* Thiéry, *E. mediterraneum* (Forbes), and *E. cordatum* (Pennant).

Of these three, *E. orthonotum* most resembles *E. cordatum*, from which it differs in having a narrower, lower test that lacks the greatly inflated area posterior to the apical system and in having its posterior truncation tilting so that the periproct is almost visible from above, whereas in *E. cordatum* the truncation is vertical or overhanging. The apical system in *E. orthonotum* is central, but it is posteriorly eccentric in the living species and the plastron is longer and narrower. The anterior ambulacrum (III) is less depressed adapically and in a shallower anterior groove at the ambitus in *E. orthonotum*, and there are large pores in the posterior poriferous zones of the anterior petals within the internal fasciole, whereas in *E. cor-*

datum these porepairs are microscopic. The area circumscribed by the anal fasciole is much wider, with width greater than height, whereas in *E. cordatum* it is much narrower, with width less than height. Finally, the plastron is less inflated.

Although *E. marylandiense* is middle Miocene, *E. orthonotum* is late Miocene, and their most similar living species is *E. cordatum*, there is no consistent evolutionary trend apparent from the oldest to the youngest. All that can be said is that the two Miocene species resemble each other more than they resemble the living species.

TYPE-SPECIMENS.—Holotype, Academy of Natural Sciences of Philadelphia 1079; figured specimens: USNM 174461, 174462, 174463, 174466, 562468 (as *E. gothicum* in Cooke, 1959: pl. 33: figs. 7–10); American Museum of Natural History (by Clark and Twitchell, 1915: pl. 97: figs. 2a–c).

STRATIGRAPHIC POSITION AND GEOGRAPHIC LOCALITIES.—Virginia: Upper Miocene, Yorktown Formation. The holotype was collected near Coggin's Point, James River, Virginia; the measured specimens described herein from Blow's locality 1, USGS 25113. Specimens also occur from all the other Blow localities, USGS 25115, 25119, 25120, 25121, 25122, 24810, 24626. W. C. Blow and B. Dyer collected specimens in situ in a partially indurated burrow approximately 5 feet above the beach on the south bank of the Nansemond River, 0.5 mile downstream from Virginia Highways 10 and 32 bridge, approximately 500 feet NW of cemetery, Suffolk City, Virginia (USGS 24816). The holotype of *Amphidetus virginianus* Forbes came from Coggin's Point, James River, Virginia, and was collected by Charles Lyell.

South Carolina: The specimens referred by Ravenel and McCrady to *E. gothicum* (Ravenel) and *E. ampliflorus* (McCrady) came from beds considered to be Yorktown in age or later at Grove Plantation E of Cooper River and 5 miles NW of Wando. The specimen figured by Cooke (1959: pl. 33: figs. 7–10) came from beds probably of the same age as Grove Plantation in the Intracoastal Waterway canal, 1 to 1.5 miles SW of the bridge near Nixon's Crossroads, Horry County, about 15 miles NW of Myrtle Beach, South Carolina. The specimens collected by Druid Wilson came from spoil from the north and south side of the Intracoastal canal SW of Little River, just E of Vereen Marina, Horry County, South Carolina (USGS 21915).

The specimen, which Cooke (1959:79) referred to this species, from the Jackson Bluff Formation (lower part of the *Cancellaria* Zone) at Jackson Bluff, Ochlockonee River, Florida, may belong to this species, but it is too poorly preserved to be identified with certainty. It definitely is not *E. marylandiense*, new species.

Echinocardium marylandiense, new species

FIGURE 6; PLATE 7: FIGURES 2, 3; PLATE 8: FIGURES 1, 2

Echinocardium orthonotum.—Clark, 1904:430, pl. 119: figs. 1a–c.—Clark and Twitchell, 1915: pl. 98: figs. 1a–c, 2a–c.—Schoonover, 1941:92–93.—Cooke, 1942:60 [the specimens from Maryland belong to this species].—Vokes, 1957: 39, pl. 30: figs. 1–3.—Cooke, 1959: pl. 33: figs. 1–5.

DIAGNOSIS.—Species characterized by petals expanding adapically, with outer poriferous zones of an anterior petal forming almost continuous arc with those of posterior petal; wide test with width equal to length, height 54–69 percent L, central apical system, width of area circumscribed by internal fasciole 37–44 percent L, prominent nodes on interambulacral plates.

MATERIAL.—Hundreds of specimens of this species have been found, particularly near Scientists' Cliffs, Calvert County, Maryland. Large slabs from there are filled with specimens (Schoonover, 1941). The description here is based on specimens from this locality, and the statistics were taken from 15 individuals.

SHAPE AND SIZE.—Largest specimen 57.0 mm long, smallest 43.5, mean 47.4 (SD 4.1, CV 8.7, N=15); test wide, nearly as wide as long with width 94–104 percent L, mean 97.9 (SD 3.0, CV 3.1, N=15), greatest width anterior of center; test high with height 54–69 percent L, mean 59.0 (SD 4.4, CV 7.4, N=14), greatest height posterior of apical system; posterior truncation oblique with periproct slightly visible from above.

APICAL SYSTEM.—Four genital pores, ethmolytic with genital 2 extending far posteriorly; located at distance from anterior margin to center of genital pores equal to 40–51 percent L, mean 46.4 (SD 2.9, CV 6.2, N=15).

AMBULACRA.—Anterior ambulacrum not petaloid (Plate 7: figure 2), in groove from apical system to peristome, at margin depth of groove equal to 3.9 percent L (SD 0.8, CV 20.3, N=14); porepairs within internal fasciole oblique with adapical pore of pair

larger than adoral, small node between pores of each pair; pores in plates between internal fasciole and phyllode very small, single or slit-like; 7 pores in single poriferous zone from internal fasciole to peristome.

Anterior paired petals very wide with large porepairs outside of internal fasciole and 3–5 large porepairs within internal fasciole in posterior poriferous zone, none in anterior poriferous zones within internal fasciole, petals only slightly depressed, narrowing distally; 9–11 (mean 9.7) large porepairs outside of internal fasciole in petal IIa, 5–8 (mean 6.4) large porepairs outside of internal fasciole in petal IIb.

Posterior paired petals with no large porepairs within internal fasciole, 9–11 (mean 9.8) large porepairs in petal Va outside of internal fasciole, 8–10 (mean 8.8) in petal Vb outside of internal fasciole; outer poriferous zones of anterior and posterior petals forming almost continuous arc; ambulacral plates beyond petals with single pores except within anal fasciole, where 2 porepairs are in each single poriferous zone.

INTERAMBULACRA.—A single prominent node on each interambulacral plate; 22–24 plates in interambulacrum 5, 15–17 in interambulacrum 1, 10–11 in 2 from internal fasciole to peristome.

PERISTOME.—Located at distance from anterior margin to anterior edge of peristome equal to 28–34 percent L, mean 31.6 (SD 1.5, CV 4.8, N=15); opening wider than high with width 21–25 percent L, mean 21–25 (SD 1.1, CV 4.8, N=14).

PERIPROCT.—Located high on posterior truncation, opening slightly higher than wide with height 10–16 percent L, mean 12.6 (SD 1.6, CV 12.6, N=12), width 11–14 percent L, mean 12.8 (SD 0.9, CV 7.0, N=13); located between plates 5–8.

ORAL PLATE ARRANGEMENT.—Labrum wide (Figure 6), extending across almost entire width of peristome, extending posteriorly two-thirds height of first ambulacral plate; length of labrum 7–11 percent L, mean 9.1 (SD 0.8, CV 9.1, N=15); plastron extending to posterior margin, length 50–55 percent L, mean 52.0 (SD 1.8, CV 3.4, N=15) width 33–36 percent L, mean 34.8 (SD 1.1, CV 3.1, N=15); first plate of interambulacra 1,4 very narrow. Ambulacra widening near peristome (Figure 6), phyllodes with 5 pores in ambulacrum III, 7–8 in II, 6 in I.

FASCIOLAS.—Internal fasciole prominent, greatest width of tract 2.9 mm in specimen 48 mm long or 6.0

FIGURE 6.—*Echinocardium marylandiense*, new species: Adoral plate arrangement of figured paratype USNM 174467 from the middle Miocene Choptank Formation, Scientists' Cliffs, Calvert County, Maryland ($\times 1.6$). (For detailed locality data, see description of species.)

percent L, fasciole crossing ambulacral plates 7a and 7b in ambulacrum III, 20a and 17b in ambulacrum II, 21a and 23b in ambulacrum I, 11a–12a or b in interambulacrum 5, 9a–10a or b in 1, 7a or 7b in 2; greatest width of area circumscribed by internal fasciole anterior of apical system, width 37–44 percent L, mean 39.1 (SD 2.1, CV 5.5, N=14). Subanal fasciole occurring on posterior truncation below periproct, area circumscribed by fasciole 14.4 mm wide on specimen 45 mm long or 32 percent L, maximum width of tract 1.7 mm wide on specimen 45 mm long or 3.7 percent L; crossing plates 3–5 of interambulacrum 5, plates 6a–8a of ambulacrum I, plates 6b–8b of ambulacrum V. Anal fasciole present but tract not clear.

COMPARISON WITH OTHER SPECIES.—*Echinocardium marylandiense* differs from *E. orthonotum* from the Upper Miocene Yorktown Formation of Virginia and Upper Miocene of South Carolina in having a wider, more angular, and higher test, a wider, more posteriorly situated peristome, a narrower periproct, shorter, wider plastron, longer labrum, wider fascioles, and a wider area circumscribed by the internal fasciole, and more prominent nodes on the

interambulacral plates. See Table 1 for the statistical expression of these differences.

Of all the living species, *E. marylandiense* most resembles *E. cordatum* (Pennant). It differs in the following characters:

1. Lower test lacking the greatly inflated area posterior to the apical system.
2. Apical system centered, whereas in *E. cordatum* it is posteriorly very eccentric.
3. Wider area circumscribed by internal fasciole.
4. Anterior poriferous zones more anteriorly situated.
5. Larger pores in posterior poriferous zones of anterior petals within internal fasciole; in *E. cordatum* these pores are microscopic, whereas in *E. marylandiense* they are distinguished easily with the naked eye.
6. Posterior truncation tilting in *E. marylandiense* so that periproct is almost visible from above, whereas in *E. cordatum* the truncation is vertical to overhanging.
7. Area circumscribed by subanal fasciole much wider, with width greater than height, whereas in *E. cordatum* it is much narrower, with width less than height.
8. Plastron less inflated and labrum with longer posterior extension.
9. Anterior ambulacrum much less depressed from apical system to margin.

TYPE-SPECIMENS.—Holotype: USNM 174460; figured specimens: USNM 174467, 498960a,b, 559489.

STRATIGRAPHIC POSITION AND GEOGRAPHIC LOCALITIES.—Middle Miocene Choptank Formation, type-specimens and measured specimens came from slabs (Schoonover, 1941) collected 2200 feet N of stairway and artesian well at Scientists' Cliffs, which in turn is 1.5 miles N of Kenwood Beach (= Governor's Run), and about 1 mile S of mouth of Parker Creek, Calvert County, Maryland. The slabs were found 18 feet above mean high tide within a vertical range of three or four inches, which extends about 12 feet along face of cliff. The slabs consist mainly of quartz sand and come from a horizon near the contact between the Calvert and Choptank Formations and 18 feet below the bottom of Shattuck's (1904) Zone 17 of the Choptank, according to Schoonover (1941). T. G. Gibson of the United States Geological Survey has studied the Foraminifera in one echinoid from these slabs and states (personal communication, 1971) that the assemblage is typical of the Choptank Formation in this area. Other localities: Jones Wharf, Patuxent River, Maryland, and specimens provisionally referred to this species from Grubin Neck, 1 mile N of Howell Point, Talbot County, Maryland.

Spatangus glenni Cooke

FIGURE 7; PLATE 10

Spatangus glenni Cooke, 1959:80, pl. 35: figs. 1-5.

One specimen appears conspecific with this species, previously described from beds considered by Cooke (1959:80) to be probably late Miocene. These appear to be the beds that Dubar (1969) designated as his Bear Bluff Formation but considered to be Pliocene(?). Its dimensions and the dimensions of the holotype are included herein (the other two specimens from South Carolina are fragments).

COMPARISON WITH OTHER SPECIES.—*Spatangus glenni* most closely resembles, of all the fossil and living species, *S. purpureus* Müller, now living in the eastern Atlantic from the North Cape and southern coast of Iceland to the Mediterranean and western coast of Africa as far south as Senegal. The species are very alike and obviously are closely related. They differ only in that *S. glenni* has fewer large adapical tubercles, a narrower subanal fasciole (30-32 percent L versus 50 percent in *S. purpureus*), and a narrower peristome. Cooke (1959:80) considered that in *S.*

FIGURE 7.—*Spatangus glenni* Cooke: Adoral plate arrangement of USNM 174464 from Blow's locality 2 ($\times 1$).

glenni "the interporiferous zones are much wider than those of *Spatangus purpureus* as figured by A. Agassiz (1873, pl. 34, fig. 3)." This figure by Agassiz, however, shows the interior of the test where the interporiferous zones are narrower than on the exterior because of the tilt of the pores toward the middle of the petal. On the exterior, the interporiferous zones have an approximately similar width in both species.

TYPE-SPECIMENS.—Holotype: USNM 562499a; paratypes: USNM 562499b, 562499c; hypotype:

USNM 174464.

STRATIGRAPHIC POSITION AND GEOGRAPHIC LOCALITIES.—The holotype and paratype came from beds considered to be late Miocene-Pliocene(?) at USGS 18759 in the Intracoastal Waterway canal in Horry County 1 to 1.5 miles SW of the bridge on U.S. Highway 17 near Nixon's Crossroads, about 15 miles NE of Myrtle Beach, collected by L. C. Glenn. The Virginia specimens came from Blow's locality 2 (USGS 25114, 25116, 25117).

TABLE 2.—*Spatangus glenni* Cooke: Dimensions of holotype from South Carolina and of USNM 174464 from Virginia

Characters measured	Holotype	USNM 174464
Length	110	98
Percent of length:		
width	90	92
height	49	46 (est.)
apical system to anterior	37	40
anterior edge of peristome to anterior of test	22	21
anterior edge of labrum to posterior of test	74	71
width of peristome	14	17
greatest width of anterior petal	12	10
greatest width of posterior petal	13	11
length of anterior petal	43	39
length of posterior petal	39	42
span of anterior petals	66	67
span of posterior petals	43	39 (est.)
greatest width of ambulacrum III	—	9
height of labrum		3.4
length of plastron	—	40
width of plastron	—	30
width of subanal fasciole	30	32
length of subanal fasciole	60 (est.)	69
width of periproct	14 (est.)	—
height of periproct	8 (est.)	—
depth anterior notch	—	7.4
Number of porepairs in single poriferous zones:		
petal II	40	38
petal I	39	36
Number of plates:		
ambulacrum III	—	54
ambulacrum II	—	102
ambulacrum I	—	102
Number of plates:		
interambulacrum 2	—	27
interambulacrum 5	—	38
interambulacrum 1	—	32

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PLATE 1

Arbacia improcera (Conrad):

- 1-3. Apical, side adoral views of USNM 174449 from Blow's locality 2 ($\times 2$).
4. Apical system of same specimen ($\times 8$)
5. Interambulacrum 2 of same specimen showing crenulations on plates ($\times 8$).

PLATE 2

Arbacia sloani (Clarke):

1. Interambulacrum 4 of holotype, USNM 166488, from the upper Miocene Duplin Marl at Bostick's Landing, Pee Dee River, Florence County, South Carolina ($\times 8$). This species is probably conspecific with *A. improcera* (Conrad) from the Yorktown Formation.

Psammechinus philanthropus (Conrad):

2. Food or fecal pellets found in USNM 174450 from Blow's locality 4 ($\times 6$).
- 3–5. Tridentate pedicellariae taken from USNM 174451 from Blow's locality 4 (figures 3, 5, $\times 70$; figure 4, $\times 140$).
6. Ophicephalous pedicellaria from same specimen ($\times 140$).
- 7, 8. Side and top views of lantern from USNM 174451 from Blow's locality 4 ($\times 7$).

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PLATE 3

Psammechinus philanthropus (Conrad):

1–3. Adapical, adoral side views of USNM 174452 from Blow's locality 4 ($\times 3$).

4. Apical system of same specimen ($\times 13$).

5–7. Adapical, side, adoral views of USNM 174453 from Blow's locality 4 ($\times 3$).

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PLATE 4

Psammechinus philanthropus (Conrad):

- 1, 3. Views of ambulacrum and interambulacrum at ambitus of USNM 174453 from Blow's locality 4 ($\times 24$). (Views of this entire specimen on Plate 3: figures 5–7).

Psammechinus miliaris (Müller):

- 2, 4. Views of ambulacrum and interambulacrum at ambitus of Recent specimen USNM 174455 collected by Mary Kier from intertidal zone on eastern coast of Isle of Arran, near Brodick, Scotland ($\times 24$).

These photographs show the great similarity between young specimens (approximately 15 mm in diameter) of these two species. In the adults figured on Plate 5, one of the tubercles in *P. miliaris* is much larger than the others, whereas this differentiation is much less in *P. philanthropus*.

PLATE 5

Psammechinus philanthropus (Conrad):

- 1, 3. Views of ambulacrum and interambulacrum at ambitus of USNM 174454 from Blow's locality 4 ($\times 13$). Specimen approximately 35 mm in diameter.

Psammechinus miliaris (Müller):

- 2, 4. Views of ambulacrum and interambulacrum at ambitus of Recent specimen USNM 174456 collected by Mary Kier from intertidal zone on eastern coast of Isle of Arran near Brodick, Scotland ($\times 13$). Specimen approximately 40 mm in diameter.

As can be seen in these photographs, one of the tubercles in *P. miliaris* is much larger than the others on the same plate, whereas there is much less differentiation in *P. philanthropus*. This difference is not present in young specimens of these two species as illustrated on Plate 4.

PLATE 6

Mellita acclinensis Kier:

1. Adapical view of USNM 174457 from Blow's locality 3 ($\times 1$). (An adoral view of this specimen is on Plate 7: figure 1.)
2. Adapical view of USNM 174458 from Blow's locality 3 ($\times \frac{1}{2}$) collected by Warren C. Blow and Barbara Gorcys.
3. Adapical view of fragment of USNM 174459 from the late Miocene Tamiami Formation from spoil banks from group of pits (sec. 29, T. 41 S, R. 23 E) about 1 mile SW of Ac-line, Charlotte County, Florida ($\times 1$).

PLATE 7

Mellita aclinensis Kier:

1. Adoral view of USNM 174457 from Blow's locality 3 ($\times 1$). (An adapical view of this specimen is on Plate 6: figure 1.)

Echinocardium marylandiense, new species:

- 2, 3. Adapical, adoral views of the holotype USNM 174460 from the middle Miocene Choptank Formation, Scientists' Cliffs, Calvert County, Maryland ($\times 2$). (For detailed locality data, see description of species; rear and side views of this specimen are on Plate 8: figures 1, 2.)

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PLATE 8

Echinocardium marylandiense, new species:

- 1, 2. Rear and side views of holotype USNM 174460 from the middle Miocene Choptank Formation, Scientists' Cliffs, Calvert County, Maryland ($\times 2$) (for detailed locality data, see description of species; adapical and adoral views are on Plate 7: figures 2 and 3), collected by W. F. Foshag and J. Benn.

Echinocardium orthonotum (Conrad):

3. Adapical view of USNM 174461 from spoil from the north and south side of the Intra-coastal canal SW of Little River, just E of Vereen Marina, Horry County, South Carolina ($\times 1$), collected by Druid Wilson.
- 4-7. Adapical, adoral, rear, right side views of USNM 174462 from Blow's locality 4 ($\times 1$).

1

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PLATE 9

Echinocardium orthonotum (Conrad):

- 1, 2. Adapical, adoral views of holotype, Academy of Natural Sciences of Philadelphia 1097, from the Yorktown Formation near Coggins Point, James River, Virginia ($\times 1.5$).
3. Slab, USNM 174463, from Blow's locality 1, showing the jumbled positions of the specimens, indicating that they were not presented in living position ($\times 0.5$).

1

2

3

PLATE 10

Spatangus glenni Cooke:

1–4. Adapical, adoral, rear, right side views of USNM 174464 from Blow's locality 2 ($\times 1$).

1

4

2

3

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