PROCEEDINGS OF THE 10TH SYMPOSIUM ON THE GEOLOGY OF THE BAHAMAS AND OTHER CARBONATE REGIONS

Edited by
Benjamin J. Greenstein and Cindy K. Carney

Production Editor:
Dana Bishop

Gerace Research Center
San Salvador, Bahamas
2001

Front Cover: The reef crest indicator species, *Acropora palmata*, on Gaulin's Reef, San Salvador Island. Gaulin's Reef is a classic bank-barrier reef that has shown remarkable resilience following two significant disturbances: El Niño-induced warming of the sea surface in 1998 and Hurricane Floyd in September, 1999 (see Peckol et al., this volume). Photo by Janet Lauroesch.

Back Cover: The oolite shoals of Joulter's Cay, north of Andros Island, Bahamas, site of the pre-meeting field trip. Photo by Ben Greenstein.

ISBN 0-935909-69-9

THE RELATIONSHIP BETWEEN LIVING ECHINOID POPULATIONS AND THEIR SKELETAL REMAINS IN THE SEA-FLOOR SEDIMENT, SAN SALVADOR, BAHAMAS

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ABSTRACT

Most previous investigations of the relationship between living echinoid populations and their skeletal remains in the sea-floor sediment have been limited to coarse size fractions. The present study examines this relationship based on sea-floor sediment samples that are composed largely of sand-sized particles.

Populations of five echinoid species common throughout the Caribbean were located at San Salvador, Bahamas, in June 1999, and a 1-meter square PVC frame was used at each site to record the population density in areas ranging from 6 to 24 square meters. Populations of *Tripneustes ventricosus* and *Meoma ventricosa* were found in the marine grass beds of Graham's Harbor north of the Bahamian Field Station. Populations of the rock urchin *Echinometra lucunter* and the long-spined *Diadema antillarum* were examined near the shore at Bamboo Point, Fernandez Bay; and the sand dollar *Leodia sexiesperforata* was surveyed at 200 meters off Bamboo Point. Multiple sediment samples were taken at each site using 1-pint plastic containers. Complete specimens of each of the five species, as well as all other echinoid taxa known to be native to San Salvador, were collected as reference specimens to ensure accurate identifications of individual ossicles. Sediment samples were sieved and picked for all echinoderm remains using size fractions down to and including 2 Ø (0.25mm). Each echinoid ossicle was identified as precisely as possible: to species in most cases.

Preliminary results of the analysis indicate that, in general, echinoid remains in the sand-dominated, sea-floor sediment match the corresponding live populations. Sediment samples from the *Meoma ventricosa* population are dominated by the spines of *Meoma,* with minor amounts of *Leodia.* Samples taken at the *Tripneustes* site reflect the living population with lesser amounts of *Diadema, Leodia,* and *Meoma.* The near-shore samples at Bamboo Point reflect the relative abundance of the two most abundant urchins: at both the *Echinometra* and *Diadema* sites, *Echinometra lucunter* ranks first, followed by *Diadema,* with *Leodia* third. *Leodia* samples are more diverse and are dominated by *Diadema* remains, with *Leodia* second and with significant amounts of *Meoma* and *Tripneustes.*

INTRODUCTION

Kier (1977) proposed that the relatively poor fossil record of regular echinoids (epifaunal) compared to irregular echinoids (infaunal) in Tertiary deposits could be explained by differences in preservation potential: regular echinoids were more susceptible to post-mortem skeletal disarticulation. Partly in response to this hypothesis, taphonomists have compared living populations of echinoids to echinoid skeletal remains in the sediment of the sea floor. Greenstein (1992, 1993) did such a study at San Salvador and Lee Stocking Islands and concluded that Kier was essentially correct because the skeletal remains of regular echinoids did not reflect the standing populations as well as those of irregular echinoids. However, Nebelsick (1992), in a study of the distribution of echinoid skeletal material in the Northern Bay of Safaga, Red Sea, found both regular and irregular remains to be highly correlated with facies types. He considered the distribution to reflect the standing populations, modified by taphonomic processes.

The contrasting results can probably be explained by differences in methodology. Whereas Greenstein's data consisted primarily of whole and partial tests encountered while SCUBA diving, Nebelsick based his work on sieved sediment samples using 2 mm as the finest screen. In a related study, Greenstein (1991) defended this 2 mm cut-off value on the assumptions that (1) smaller ossicles could not be identified at low taxonomic levels and (2) paleontologists would probably not detect fossils this small in outcrop work. In terms of the data sets used, the number of test remains associated with live individuals is small unless very large areas of the sea floor are surveyed (Greenstein, 1993). Although laboriously processing sediment in the field yielded high numbers of skeletal remains for Nebelsick, data on living populations were only qualitative to semi-quantitative (Nebelsick, 1992).

The approach used in the present study is to map a relatively densely populated area with a given population and to process small samples of the natural sea-floor sediment, including the sand-sized fractions in the analysis. This is the method used by Sadler (Sadler and Lewis, 1996; Sadler, 1997), who mapped live populations of *Meoma ventricosa* (irregular) and *Tripneustes ventricosus* (regular) in Graham's Harbor, San Salvador, and included the very-coarse-sand fraction (1-2 mm) in the sediment analysis. At both the *Meoma* and the *Tripneustes* sites, echinoid remains were dominated by the resident species. Sadler postulated that the presence of marine grasses and the relatively low water energy in Graham's Harbor allowed small test fragments and spines to accumulate (Sadler, 1997). The objectives of the current investigation are (1) to identify and document morphologic features that can be used to distinguish individual test plates and spines at the genus and species level for San Salvador's common echinoid species, and (2) to see if natural sea-floor sediment samples, which are mostly sand-sized particles, accurately reflect the living populations. This second objective is addressed using size fractions previously considered too small for such analysis, and sediment samples taken from some relatively high-energy environments. This paper accomplishes the first objective; the second is still in progress, but preliminary results are reported here.

MATERIALS AND METHODS

Populations of five echinoid species common throughout the Caribbean were located and mapped at San Salvador, Bahamas, in June 1999. The precise location of each population was recorded using a GPS unit. Two populations were found in Graham's Harbor and three at Bamboo Point in Fernandez Bay (Figure 1). The Graham's Harbor sites were sampled in order to replicate Sadler's study (Sadler, 1997). The *Tripneustes ventricosus* population was situated in a Turtle Grass bed in Graham's Harbor at N24°07.412"- W74°27.968" in 2.8 m of water. The sea biscuit *Meoma ventricosa* was located further offshore in Graham's Harbor at N24°07.896"- W74°28.528" and occupied a sand and Manatee Grass bed in 6.1 m of water.

Echinometra lucunter, the common rock urchin, was located in the intertidal zone at Bamboo Point, Fernandez Bay, at N24°02.9"- W74°31.86". This population inhabited a rocky area in 0.0 to 0.1 m of water. *Diadema antillarum*, the long-spined urchin, was located 2-3 m offshore from the *Echinometra*

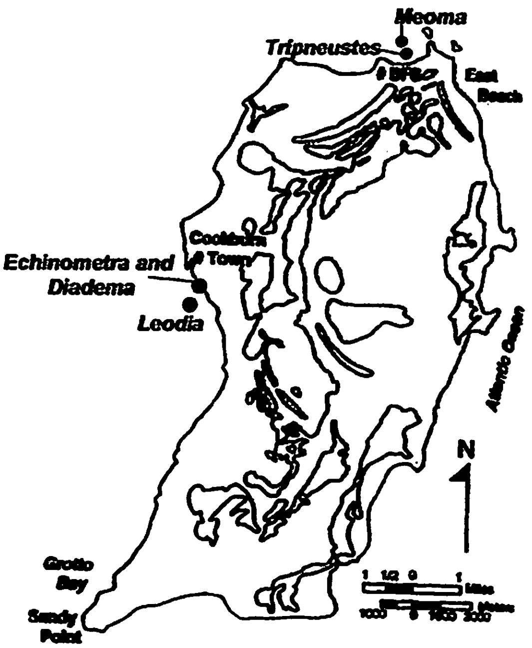

Figure 1. Location map indicating study sites in Graham's Harbor and at Bamboo Point.

population, also in a very rocky environment in water depth of approximately 1m. The sand dollar *Leodia sexiesperforata* was examined on a barren sand flat in 5 m of water approximately 200 m from Bamboo Point, Fernandez Bay, on a bearing of 250°.

Using SCUBA equipment and a 1 x 1 m PVC grid at each offshore site, the location of each living and dead echinoid was mapped within a prescribed area. The areas surveyed ranged from 6 m^2 to 24 m^2, depending upon the density of the echinoid populations. Six one-pint sediment samples were taken from each surveyed site. Live individuals of each of the five species were also collected as reference specimens.

Reference specimens were bleached in a 1:3 solution of Clorox and water, repeatedly in some cases, to disarticulate the skeleton. Other echinoid species present, but relatively rare, at San Salvador were available in our collections and were processed in the same way: *Eucidaris tribuloides, Lytechinus variegatus, Clypeaster rosaceus,* and *Plagiobrissus grandis* (test only). Skeletal remains of these reference specimens were then examined using a light microscope (Olympus VMZ with a doubling lens) to study the morphologic characteristics of each species. In addition, a Zeiss DSM 940 Scanning Electron Microscope (SEM) with digital imaging capabilities was used to examine the skeletal elements in detail in order to refine our methods of fragment identification.

Two sediment samples from each site were bleached in a 1:3 Clorox and water solution to eliminate the organic material. The samples were then wet sieved using standard mesh screens of –2 Ø to 3 Ø, in 1 Ø intervals. Sediment from the –2 Ø (4 mm) to the 2 Ø (0.25 mm) size fractions was scrutinized under a light microscope. Each echinoid fragment was picked, identified as precisely as possible, and recorded.

RESULTS

The spines and test plates of sea urchins display a number of detailed morphologic characters (Figure 2). By closely examining the separate ossicles of the reference specimens, it was possible to use certain of these features to identify echinoid ossicles and fragments to specific taxa. Between 82% and 95% of the echinoid grains found in each sediment sample were identifiable to the genus and species level. The diagnostic characters used in identification are described below for each species studied. Although illustrated here by SEM images, the morphologic features can also be recognized by using a binocular light microscope. The microscope we used provided a maximum magnification of 80x.

Echinometra lucunter
(Figure 3)

The test fragments of the rock urchin are thicker than those of any other echinoid taxon

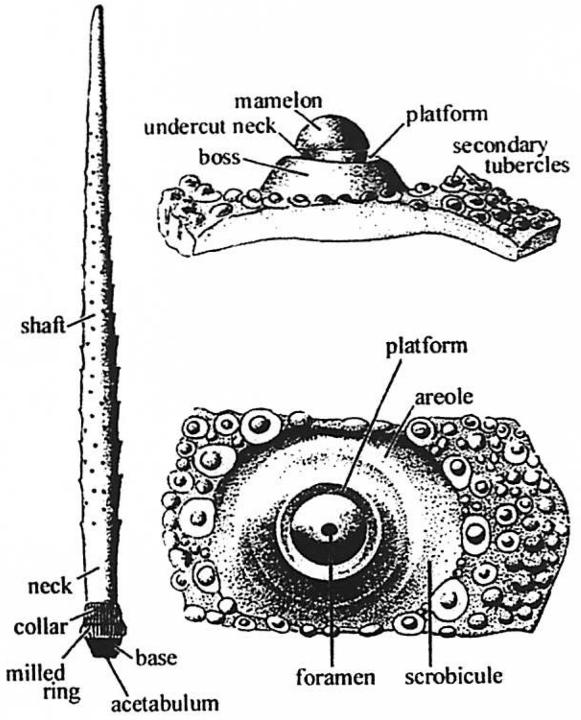

Figure 2. Diagram showing echinoid morphologic features used in this study. After Fell, 1966.

studied. They are often distinguishable from similar fragments *of Tripneustes ventricosus* because the former typically are more equilateral (Figure 3B), whereas those of *T. ventricosus* are more rectangular. The tubercles of *E. lucunter* are characterized by a smooth, solid mamelon with no foramen (hole), and an undercut neck. They also exhibit a smooth platform (site of spine attachment surrounding the mamelon) and a featureless boss (the sloping part of the tubercle between the plate and the mamelon). They have a mildly depressed areole (Figure 3B, C).

The spines of *E. lucunter* exhibit the highest degree of tapering of any of the species studied. Primary ornamentation consists of prominent longitudinal ridges extending the length of the spine, with short horizontal ridges (Figure 3E) as secondary ornamentation, giving the appearance of a spine constructed of small rectangular blocks. The base of the spine is distinctive with a prominent milled ring and a featureless, subrectangular basal section. The acetabulum (socket structure at the base of the spine) is smooth (Figure 3E). In cross section, the spine is highly organized and very dense, more so than that of any other taxon examined (Figure 3F).

Diadema antillarum
(Figure 4)

Test fragments of the long-spined urchin are very thin and fragile. The tubercles have a mamelon with a circular foramen, a symmetrically crenulated platform, smooth boss, and a shallow areole (Figure 4B).

The spines taper very slowly and fragments often retain their original alternating red and white color to some degree. They also have a very distinctive pattern of overlapping leaf-like barbs pointing outward, away from the spine (Figure 4C). The spine shaft is hollow (Figure 4E).

The milled ring is crenulated and canted to one side; the spine base is with a crenulated acetabulum (Figure 4D).

Tripneustes ventricosus
(Figure 5)

The plate fragments of *T. ventricosus* are thick and more rectangular than equilateral. The mamelon is smooth and solid with a slightly undercut neck. The tubercles have a smooth platform and a featureless boss; there is no conspicuous scrobicule (Figure 5C), the deep outer portion of the areole (Figure 2). *Tripneustes* can be distinguished from *Lytechinus* because its ambulacral pores

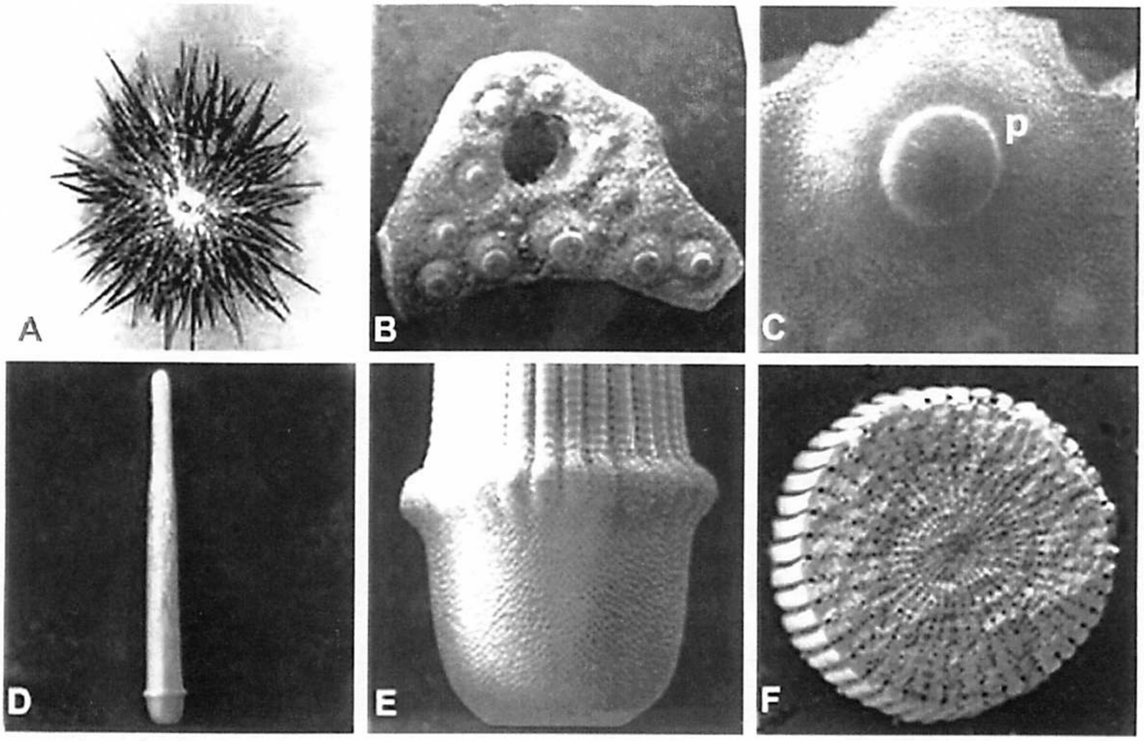

Figure 3. ***Echinometra lucunter.*** *A) Whole specimen, aboral view. Scale is 1 cm. B) Subtriangular test plate. Photographed at x34. C) Tubercle with solid mamelon and smooth platform (p). Photographed at x100. D) Spine showing rapid tapering. Photographed at x13. E) Prominent milled ring and subrectangular spine base, photographed at x90. F) Cross section of spine showing dense, regularly arranged stereom. Photographed at x45.*

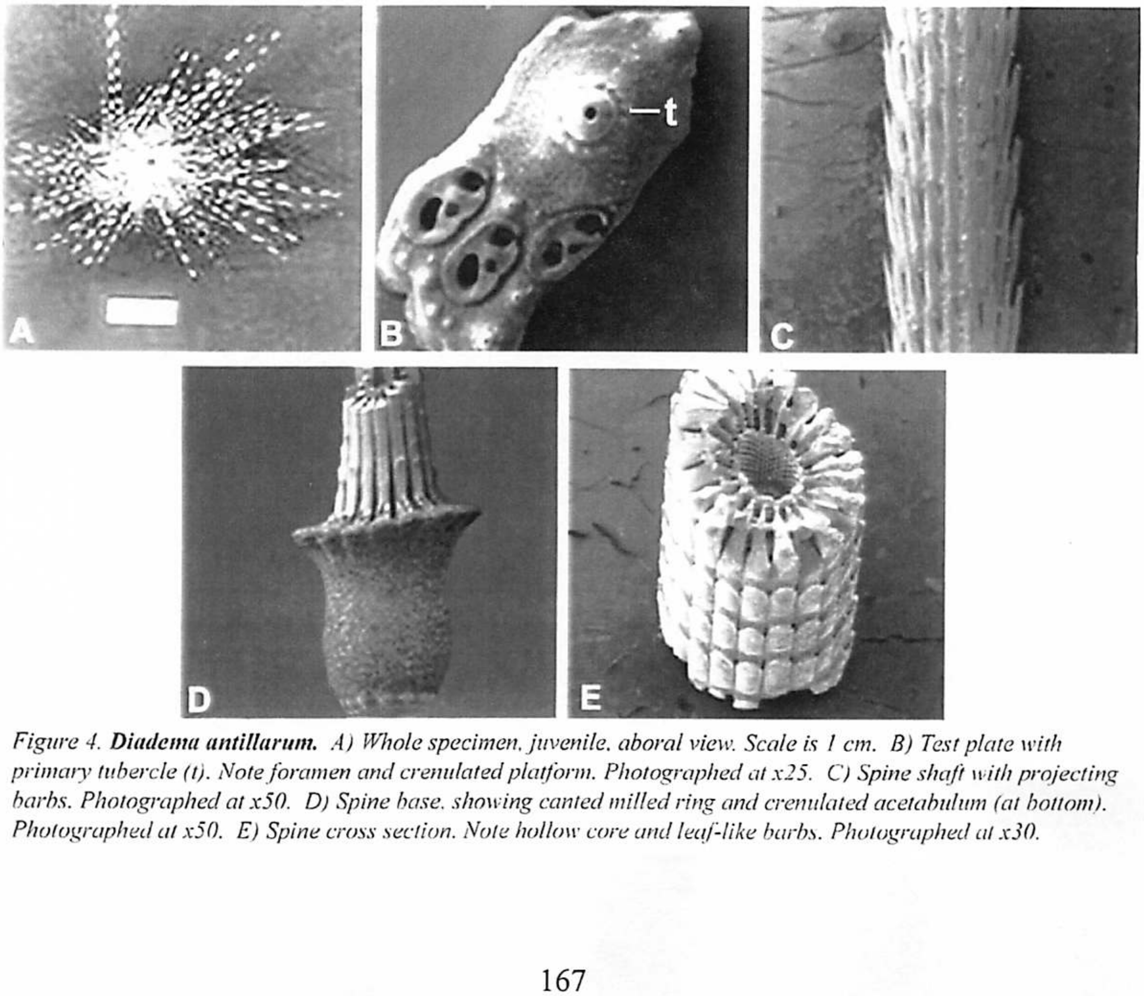

Figure 4. ***Diadema antillarum.*** *A) Whole specimen, juvenile, aboral view. Scale is 1 cm. B) Test plate with primary tubercle (t). Note foramen and crenulated platform. Photographed at x25. C) Spine shaft with projecting barbs. Photographed at x50. D) Spine base, showing canted milled ring and crenulated acetabulum (at bottom). Photographed at x50. E) Spine cross section. Note hollow core and leaf-like barbs. Photographed at x30.*

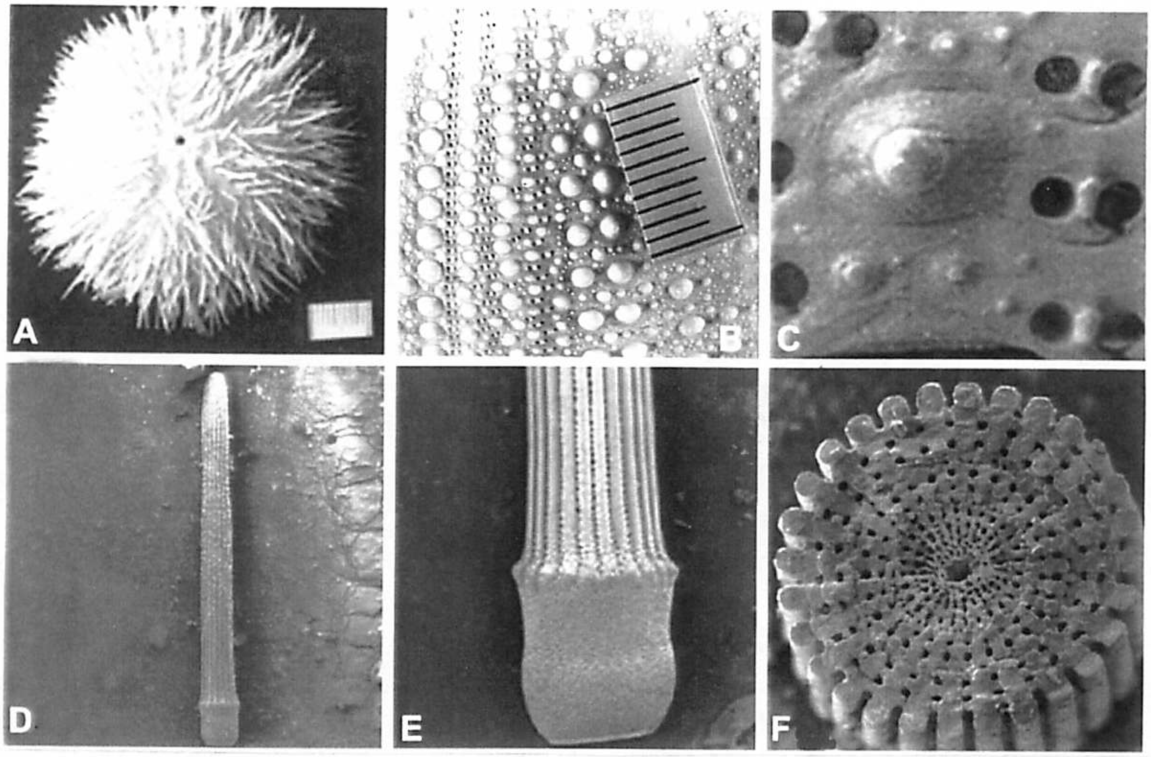

Figure 5. ***Tripnuestes ventricosus.*** *A) Whole specimen, aboral view. Scale is 1 cm. B) One-half of ambulacral area, showing three vertical rows of pores. Scale in mm. C) Tubercle with solid mamelon and smooth platform. Photographed at x25. D) Entire spine. Photographed at x29. E) Spine base, with small milled ring and tumid base. Photographed at x50. F) Spine cross section showing well-organized, dense stereom. Photographed at x100.*

are arranged in three vertical series (Figure 5B), as opposed to one row in *Lytechinus* (Figure 6B).

The spines of *T. ventricosus* taper to a lesser degree than those of *Echinometra lucunter.* They have similar longitudinal ridges to those of *E. lucunter*, but lack the secondary ornamentation (Figure 5D). The milled ring is symmetrical and crenulated, but does not protrude as far as that of *E. lucunter*. The base is tumid and has a smooth acetabulum (Figure 5E). In cross-section, the spines are relatively dense, but slightly less dense than those of the rock urchin (Figure 3F), and have a narrow axial canal (Figure 5F).

Lytechinus variegatus
(Figure 6)

L. variegatus test fragments are very similar to those of *T. ventricosus*, except that the ambulacral pores of *L. variegatus* are not arranged in three series (Figure 6B, C). The spines too are very similar to those of *T. ventricosus*, except that the milled ring is slightly canted (Figure 6D) and, in cross-section, the interior structure of the *L. variegatus* spines are less dense and more poorly organized (Figure 6E).

Meoma ventricosa
(Figure 7)

Meoma ventricosa test plates are of medium thickness relative to those of the other taxa studied. The distinctive tubercles have a mamelon with a large circular to oval foramen, and an asymmetrically crenulated platform, with crenulations more closely spaced together on one side than the other (Figure 7B). The boss is featureless; the areole is asymmetrical (Figure 7B).

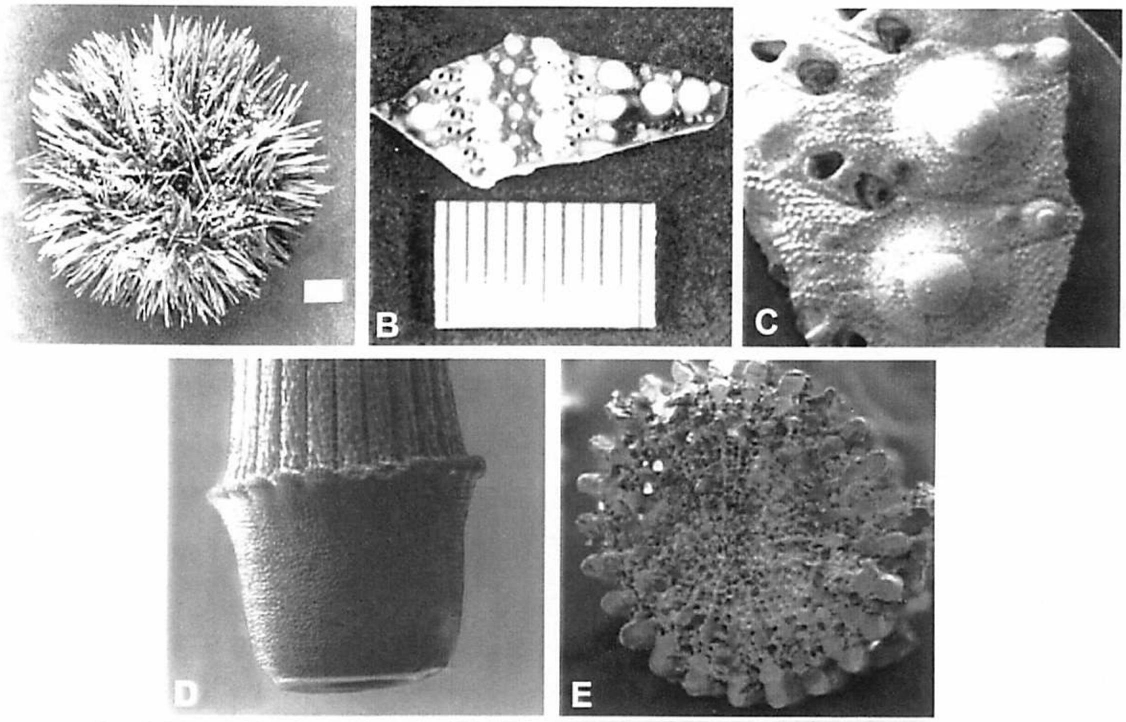

Figure 6. ***Lytechinus variegatus.*** *A) Whole specimen, aboral view. Scale is 1 cm. B) Ambulacral area with a single series of pores on each side. Scale is in mm. C) Tubercle with solid mamelon. Photographed at x20. D) Spine base. Note slightly canted milled ring. Photographed at x60. E) Spine cross section. Photographed at x80.*

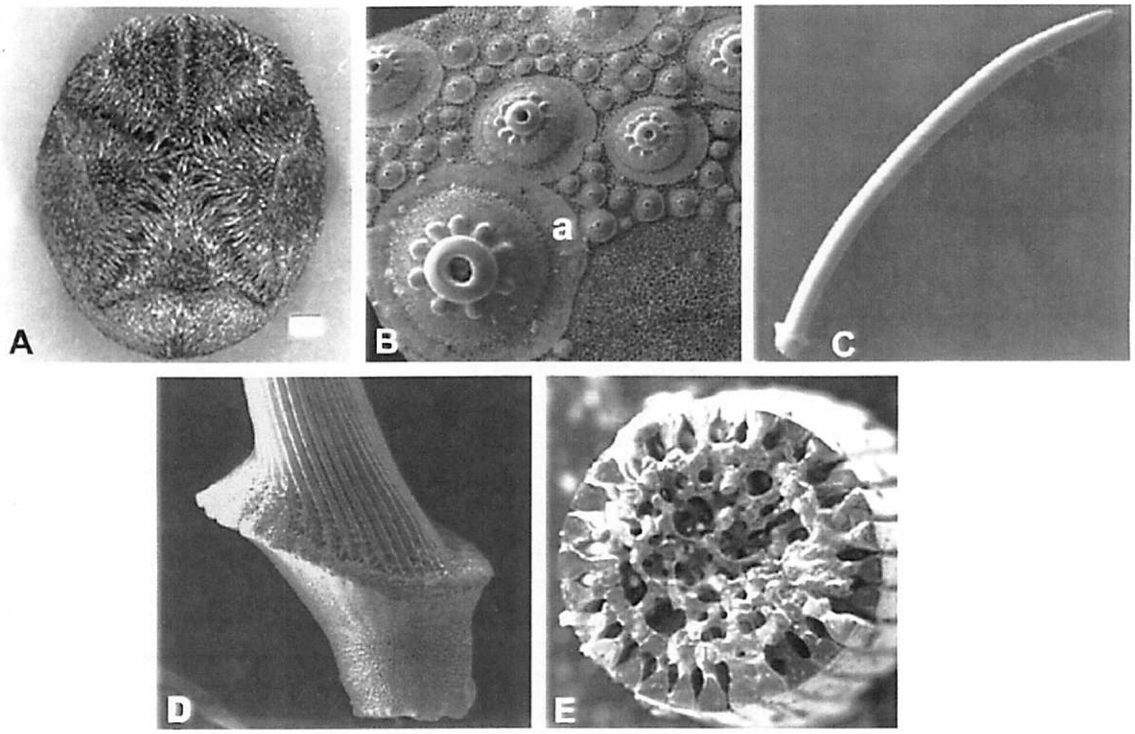

Figure 7. ***Meoma ventricosa.*** *A) Whole specimen, aboral view. Scale is 1 cm. B) Tubercles, each showing a distinct areole (a), foramen, and asymmetrical, crenulated platform. Photographed at x36. C) Entire spine, with characteristic curvature. Photographed at x19. D) Spine base, with canted and asymmetrical milled ring. Photographed at x50. E) Spine cross section showing irregular internal zone. Photographed at x230.*

The spines of the *M. ventricosa* show a great deal of specialization in the different regions of the test, but almost all show a degree of curvature. The majority of spines are characterized by a conspicuous bend in the shaft approximately 1/4 the length of the shaft from the base. Others have a continuous, gradual curve (Figure 7C). The spines originating from the oral side of the test culminate in a cupped point. Except for those from the fascioles and ambulaca, all spines of *M. ventricosa* display a dramatically canted and crenulated milled ring and an asymmetrically crenulated acetabulum (Figure 7D). In cross-section, the spines of *M. ventricosa* are more dense than those of *L. sexiesporforata*, but similar to the sand dollar in the disorganization of the internal zone (Figure 7E).

Leodia sexiesperforata
(Figure 8)

Test fragments of the sand dollar do not normally disassociate into individual plates. Test fragments have irregular internal struts and a highly porous stereom. The tubercles are located in a depression within the test. Tubercles have an oval foramen and an asymmetrically crenulated platform similar to that of *Meoma ventricosa* (Figure 8B).

The aboral spines of *Leodia sexiesperforata* are significantly smaller most *Meoma ventricosa* spines. Typically the shaft expands distally to its maximum thickness at approximately 1/3 of its length. Two slight bends in the shaft produce a subtle S-shape. The spine base has a pronounced milled ring and a crenulated acetabulum. The peripheral spines are the largest and straightest, though they are rarely completely straight (Figure 9C).

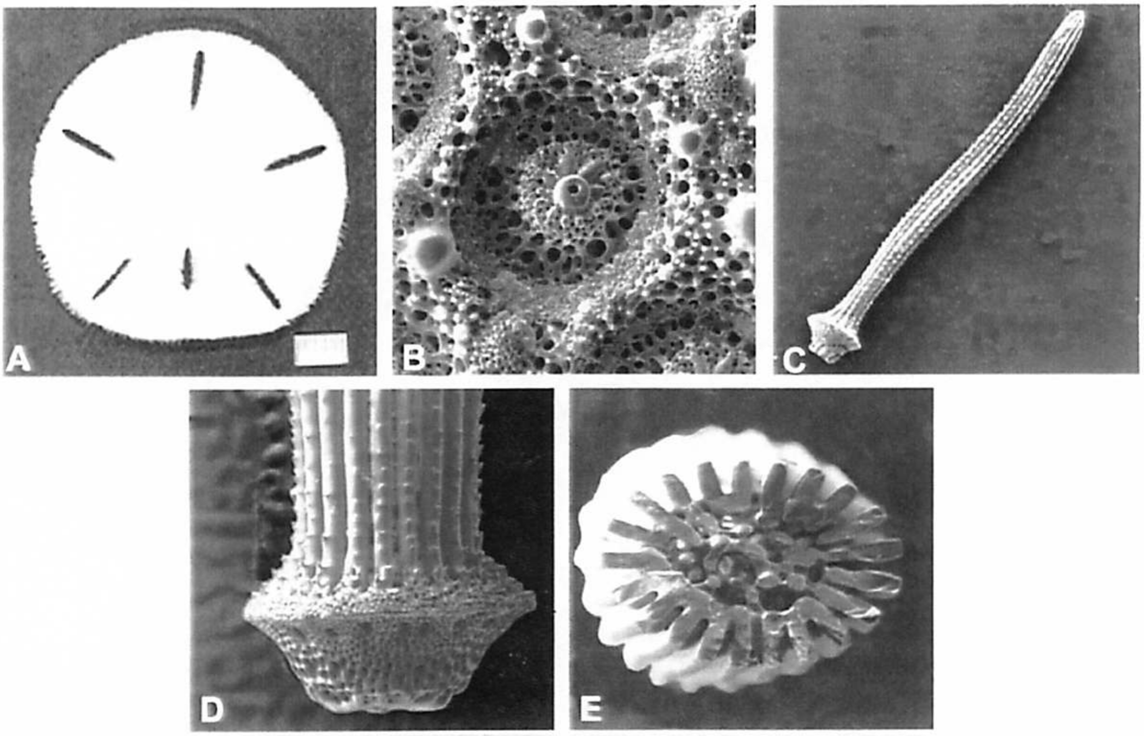

Figure 8. ***Leodia sexiesperforata.*** *A) Whole specimen, aboral view. Scale is 1 cm. B) Primary tubercle located within a depression. Photographed at x200. C) Peripheral spine showing two slight bends. Photographed at x100. D) Peripheral spine base, with smooth milled ring, short base, and slightly crenulated acetabulum. Photographed at x250. E) Peripheral spine cross section showing porous and unorganized internal stereom. Photographed at x350.*

The short base has a small, symmetrical, uncrenulated milled ring and a slightly crenulated acetabulum (Figure 8D). The cross section of the peripheral spines shows them to be very unorganized in their internal construction and to be relatively porous (Figure 8E).

Eucidaris tribuloides
(Figure 9)

The test plates of *Eucidaris tribuloides* are the thickest individual plates of the echinoids studied. The tubercles have a globular mamelon with a circular foramen, smooth platform, and a featureless boss (Figure 9B).

The pencil urchin has 3 types of spines; primary, secondary, and ambulacral. The primary and secondary spines differ only in size, and they have a maximum thickness at less than 1/2 their length (Figure 9D). The milled ring is ornamented with small, narrow crenulations, and a collar above the milled ring is distinguished by finer vertical ridges; the base is very short with a featureless acetabulum (Figure 8F). The ambulacral spines, which flank the ambulacral grooves, are short, laterally compressed, and lack a distinct base (Figure 9E).

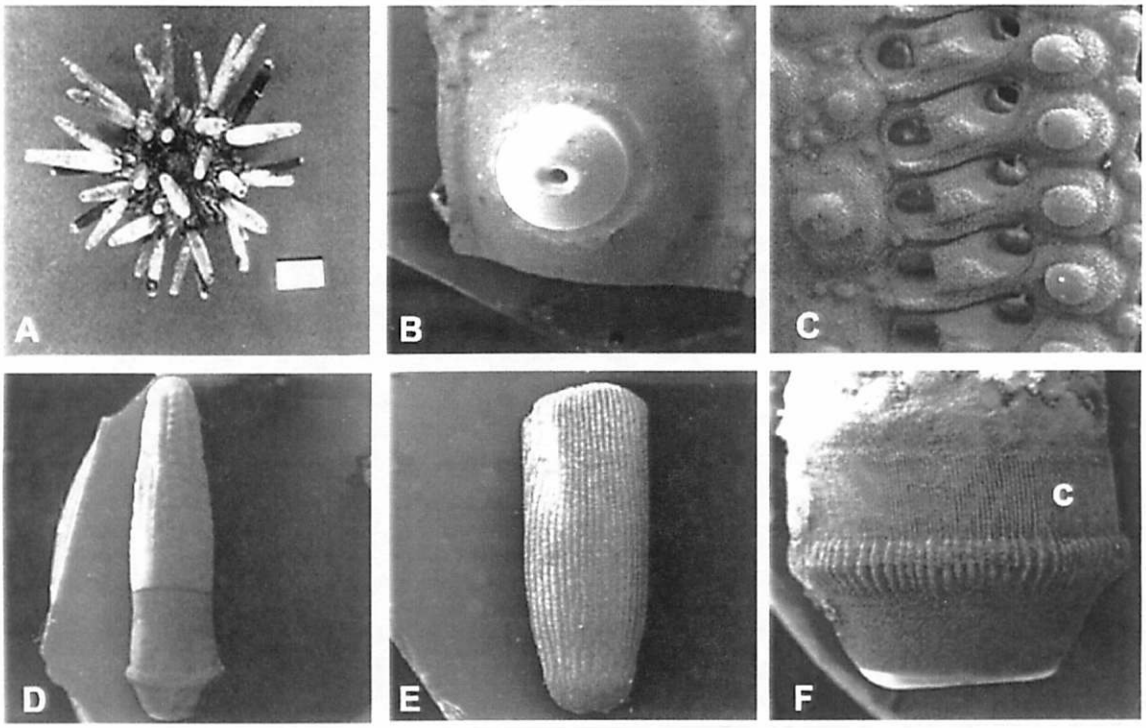

Figure 9. ***Eucidaris tribuloides.*** *A) Whole specimen, aboral view. Scale is 1 cm. B) Primary tubercle with globular mamelon and circular foramen. Photographed at x25. C) Ambulacral area with ambulacral-spine tubercles. Photographed at x40. D) Secondary spine. Note irregular tapering. Photographed at x15. E) Complete ambulacral spine, with indistinct spine base. Photographed at x30. F) Spine base, with milled ring and collar (c). Photographed at x28.*

Clypeaster rosaceus
(Figure 10)

C. rosaceus is very similar *to Leodia sexiesperforata* in many ways. For example, the tests of both are not found as individual plates. The test is extremely thick and the internal construction includes numerous irregular struts. Also like *L. sexiesperforata*, the tubercles are set in depressions in the test. The mamelon has a circular foramen and a crenulated platform (Figure 10B).

The spines of *C. rosaceus* are straight and taper evenly toward the tip from a maximum thickness near the base. Spines show specialization according to the area on the test. The oral spine base is subrectangular with an inconspicuous milled ring (Figure 10D). In aboral spines, the base is asymmetrical and has an incomplete acetabulum (Figure 10E). In cross-section, the spines of *C. rosacea* have a more organized internal zone than those of *L. sexiesperforata*, and are slightly more dense (Figure 10F).

Sediment Sample Analyses

In Graham's Harbor, the sediment samples from the *Tripneustes ventricosus* population (Figure 11A) are heavily dominated by the remains (mostly spines) of that echinoid, with much lesser contributions by the remains of *Diadema, Meoma*, and *Leodia.* A similar dominance is exhibited by the remains of *Meoma ventricosa* in the samples from its population, with *Leodia* ranking second and with small amounts of *Tripneustes* remains (Figure 11B). These

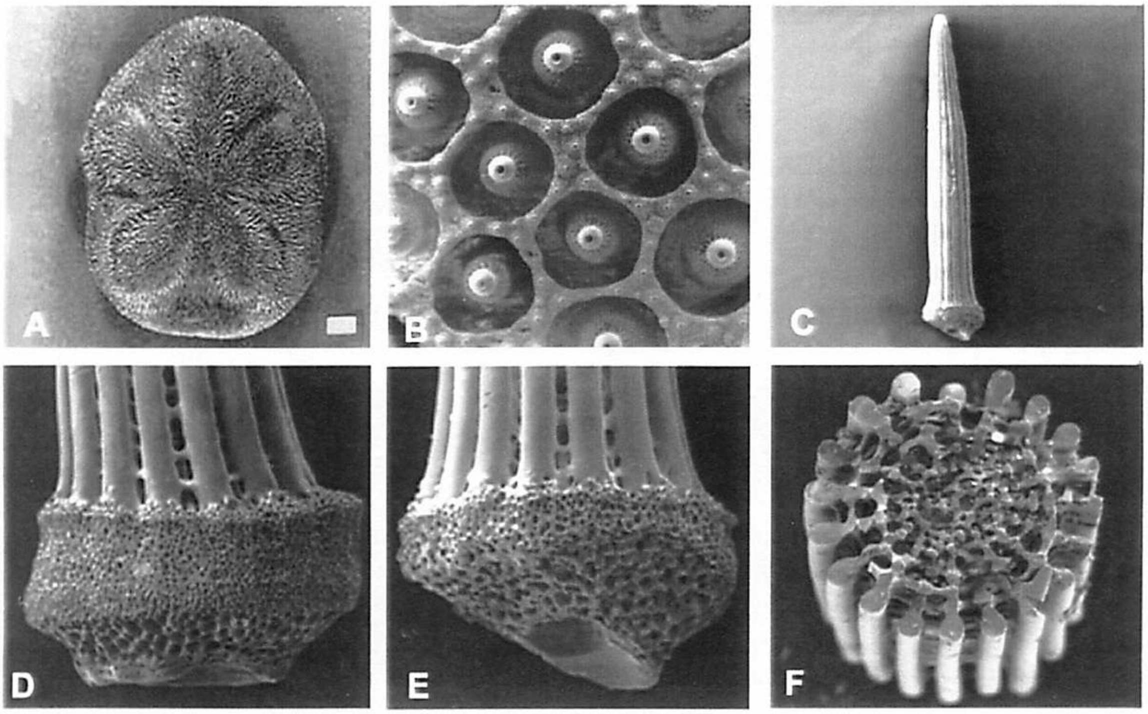

Figure 10. ***Clypeaster rosaceus.*** *A) Whole specimen, aboral view. Scale is 1 cm. B) Primary tubercles set in depressions, each with a central foramen and crenulated platform. Photographed at x30. C) Complete spine, x40. D) Box-like base of oral spine, with indistinct milled ring, x200. E) Asymmetrical base of aboral spine with incomplete acetabulum, x200. F) Spine cross section showing porous stereom.*

results are consistent with Sadler's (1988) findings.

In the higher-energy environments at Bamboo Point, the *Echinometra* sediment samples follow the same pattern of being conspicuously dominated by the resident species (Figure 11C), with lesser amounts of *Diadama* remains. Samples from the *Diadema antillarum* site (Figure 11D) are very similar to the *Echinometra* samples: *Echinometra* ranks first, followed by *Diadema*. The sediment samples taken from the *Leodia sexiesperforata* site (Figure 11E) are more diverse. Skeletal remains of *Diadema antillarum* are most abundant, followed by *Leodia*, with significant contributions from *Tripneustes* and *Meoma*.

DISCUSSION

The morphologic features presented above allow identification of more than 80 percent of the echinoid grains to genus and species using a binocular light microscope. This includes one combined category because *Leodia sexiesperforata* and *Meoma ventricosa* spines cannot be distinguished in all cases. Unidentifiable grains include some so taphonomically altered as to be identifiable only as echinoid remains as well as some that could only be recognized as some kind of echinoderm. (We recognize that environments with higher species diversity could result in more difficulty in recognizing specific taxa, resulting in a higher percentage of unknowns; compare Nebelsick, 1992).

Results of the sediment analysis from the *Tripneustes* and *Meoma* sites studied in Graham's Harbor corroborate the findings of Sadler (1997). The presence of *Leodia* skeletal remains in the *Meoma* samples is explained by the fact that both of these species were found living at the site. The abundance of *Echinomentra* remains at the *Diadema* site is also easily explained because the *Echinomentra* site was only a few meters away and its population density was very high. The unexpected dominance by the remains of *Diadema* within the sediments of the *Leodia* site is somewhat more difficult to explain. The *Diadema antillarum* fragments could have originated from nearby offshore reefs or from other populations along the shore, such as near the Cockburn Town dock, and may have been transported to the site by wave- and tide-generated currents. The construction of *D. antillarum* spines, especially the hollow spine shaft and overlapping barbs (Figure 4), may make them conducive to transportation. Furthermore, we found that many of the very small spines of *Leodia* pass through the 20 screen. Therefore *Leodia* is underrepresented in the portion of the sediment samples picked.

With regard to the difference in preservation potential between regular and irregular urchins, the outcome depends upon the size of the skeletal remains studied. Regular echinoids have a poorer preservation potential than irregulars (Kier, 1977) when whole or partial tests are concerned (e.g., Greenstein, 1993), however inclusion of separate ossicles and fragments (e.g., Nebelsick, 1992) allows the recognition of both groups from sea-floor remains, with direct implications for paleoecologists (Gordon and Donovan, 1992). This study demonstrates the practicality of making use of the vast amount of data available in sand-sized material both in terms of making actualistic studies more efficient and supplementing the limited areas of outcrop available to paleontologists.

CONCLUSIONS

At the San Salvador sites we examined, the vast majority of echinoid fragments found within samples of the sea-floor sediment as fine as medium-grained sand can be identified at the genus and species level. These echinoid remains accurately reflect living populations, although samples may be influenced to some degree by neighboring echinoid populations, especially those of close proximity and high population density. Sand-sized fractions can be included profitably in taphonomic and paleoecologic studies of echinoids.

FUTURE RESEARCH

In the present study, survey sites were chosen because of a concentration of a given species. However, distances of several tens of meters of sea floor, uninhabited by echinoids, commonly separated one population from the next. Future work will include sediment samples taken from outside known populations along transects. This will make it possible to compare the skeletal remains at standing populations to those of (presently) barren areas. Taphonomic states of echinoid remains will also be assessed in an attempt to determine the effects of time averaging.

ACKNOWLEDGMENTS

We would like to thank Dr. Donald T. Gerace, Chief Executive Officer of the Bahamian Field Station, and Mr. Kenneth Buchan, Executive Director, for their logistical support. We thank the staff of the Bahamian Field Station for their friendliness and assistance. We would also like to thank Amy Jones for her assistance in collecting field data, and Dr. Michael Miller, Botany and Microbiology Department, Auburn University, for his guidance and expertise in the SEM laboratory. J.P.S. would like to dedicate this paper to the memory of his father, Dr. Lonnie G. Schein.

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