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**An integrated study of echinoid taphonomy: Predictions for the
fossil record of four echinoid families**

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University of Cincinnati, 1990

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AN INTEGRATED STUDY OF ECHINOID TAPHONOMY:
PREDICTIONS FOR THE FOSSIL RECORD OF FOUR ECHINOID FAMILIES

A Dissertation submitted to the
Division of Graduate Studies and Research
of the University of Cincinnati

in partial fulfillment of the
requirements of the degree of

DOCTOR OF PHILOSOPHY

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1990

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UNIVERSITY OF CINCINNATI

May 29 **19** 90

*I hereby recommend that the thesis prepared under
my supervision by* Benjamin J. Greenstein
entitled An Integrated Study of Echinoid Taphonomy:
Predictions for the Fossil Record of Four Echinoid
Families
*be accepted as fulfilling this part of the requirements for
the degree of* Doctor of Philosophy

Approved by:

~~David L. Meyer~~
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~~Wayne A. Lynn~~

ABSTRACT

The nature of taphonomic overprint affecting the fossil records of the regular echinoid Families Cidaridae, Diadematidae, Toxopneustidae and Echinometridae is investigated using a synthesis of actualistic and literature-derived data. The actualistic portion of this study focuses on the following extant members of the four families: *Eucidaris tribuloides*, *Diadema antillarum*, *Tripneustes ventricosus* and *Echinometra lucunter*. Population censuses of these animals in tropical reef and near-reef environments demonstrate that the distribution of macro- and microscopic skeletal material does not reflect the distribution of the living fauna. Field experiments with freshly-killed carcasses of *Eucidaris*, *Diadema* and *Echinometra* indicate that loss of all organic tissue occurs within six days after death suggesting that fossil specimens of these echinoids will be rare in facies analogous to the environments studied. Moreover, the loss of organic connective tissue within six days' exposure in normal marine conditions suggests that recognition of fossil material depends on A) taxonomic differences in coronal rigidity related to sutural interlocking, and B) identifiability of isolated skeletal elements. Thus the condition of fossil specimens will vary between taxa. The prediction of rarity of occurrence of fossil echinoids is supported by examination of an exposure of Pleistocene reef and near-reef facies. However, the scarcity of fossil material makes more specific tests of the above predictions impossible.

Decay experiments with specimens of *Diadema*, *Echinometra* and *Eucidaris* indicate that a similar sequence of disarticulation oc-

curs as a result of the decay of connective tissues. The spines detach, followed by the loss of the peristomial and apical plates, and Aristotle's Lantern. Finally the corona disarticulates along ambulacral plate sutures. The timing of disarticulation differs for each species: spines of *Diadema* begin to detach after one day of decay whereas those of *Echinometra* detach after three days and those of *Eucidaris* detach after periods exceeding five days. Coronas of *Diadema* and *Eucidaris* were observed to disarticulate within seven and ten days of decay, respectively. Coronas of *Echinometra* did not disarticulate after ten days of decay.

Tumbling experiments using bleached carcasses of the four echinoids under study reveal that the amount of skeletal material contributed to >2 mm, 1-2 mm, $500\ \mu$ - 1 mm, $125\ \mu$ - $500\ \mu$, and $<125\ \mu$ size fractions does not differ significantly between tumbling periods of one, ten and 100 hours. However, significant ($\alpha = .05$) differences between species exist in the composition of the >2 mm size fraction after tumbling. Carcasses of *Diadema* and *Eucidaris* contribute primarily spines. Carcasses of *Echinometra* and *Tripneustes* contribute primarily coronal material. For all echinoids, the relative amounts of spine, lantern and coronal material contributed to the >2 mm fraction do not differ significantly between tumbling periods of one, ten and 100 hours. For each echinoid, the amount of coronal breakage inflicted by tumbling does not vary significantly between tumbling periods of one, ten and 100 hours. However, the amount of breakage does vary significantly ($\alpha = .05$) between species. *Diadema* suffer the most breakage, with an average breakage coefficient of 173.47. *Echinometra* suffer the least break-

age, exhibiting an average coefficient value of 4.65. Specimens of *Eucidaris* and *Tripneustes* fall within this range, with values of 89.36 and 34.31, respectively.

The results of the actualistic experiments are synthesized into predictions of the condition of fossil material expected to represent each group in the stratigraphic record. Members of the Family Diadematidae are predicted to occur primarily as skeletal fragments, mostly spines. Members of the Family Echinometridae are predicted to occur as intact coronas without spines, lantern elements, or apical and peristomial plates. Members of the Family Cidaridae are predicted to occur primarily as isolated spines, large coronal fragments, and as intact coronas devoid of spines, lantern elements, or apical and peristomial plates. Finally, members of the Family Toxopneustidae are predicted to occur primarily as intact, partial or fragmented coronas only.

Predictions of taphonomic bias predicted to affect the type species described in the Families Cidaridae, Echinometridae and Toxopneustidae are supported by literature data on their preservational styles. Moreover, for the Family Cidaridae, the distribution of preservational styles within subfamilies does not generally differ from that of the family: a bimodal distribution exists between spines and intact, denuded coronas. The prediction that members of the Family Diadematidae will be represented primarily by skeletal fragments is not supported by the literature data. This is because the extreme fragility of the diadematoid corona dictates extraordinary circumstances of preservation that are not accounted for in the experiments performed.

The evolutionary history of the Family Cidaridae has a characteristic taphonomic overprint that has changed systematically since the apparent origination of the family in the Middle Triassic. Early members of the group are described primarily on the basis of spines. An increase in the "diversity" of preservational styles (ranging from exceptionally well preserved forms to isolated skeletal fragments) coincides with an increase in generic diversity beginning in the Middle Jurassic. Few type specimens, composed primarily of spines and large coronal fragments, are described from the Neogene and Pleistocene. The number of described type species decreases from the Eocene through the Pleistocene, illustrating a "reversed Pull of the Recent" stemming from the taxonomic utility of extant forms.

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Cincinnati, May, 1990

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CHAPTER 1: INTRODUCTION

The fossil record of a clade is, in part, a consequence of taphonomic processes that may obscure or alter the underlying evolutionary signal(s). Taphonomic processes may also yield patterns of preservation that provide information on the organisms themselves as well as the environments in which they lived (Brett & Baird, 1986). Thus, the diversity history of a group as deduced from fossil data has a distinct taphonomic overprint. Clearly, to understand a group's evolutionary history, a thorough knowledge of taphonomic processes likely to affect it must be developed. Surprisingly, few such studies of echinoids exist.

The purpose of this dissertation is to use several avenues of research to assess the overprint of taphonomic bias on the fossil record of echinoid echinoderms. To achieve this objective, the general methodology comprises a synthesis of several analyses including:

1. Population censuses of selected echinoids in several reef and near-reef environments to determine their live and dead distributions.
2. Decay experiments in the field and laboratory to observe the timing of decay and disarticulation of the echinoids under study.
3. Tumbling experiments using bleached carcasses to determine whether differences in skeletal durability exist.
4. Synthesis of results of field and laboratory work into predictions of taphonomic overprint likely to affect fossil occurrences of the echinoids under study.

5. Test of the predictions, initially by determining the preservational style of echinoids preserved in Pleistocene reef and near-reef facies analogous to the Recent environments studied.

6. Further test of the predictions using literature-derived data on the preservational style of the type material of species comprising each family of echinoid studied.

General Background

The Class Echinoidea apparently originated in the Ordovician and has a long and abundant fossil record. Bambach (1985) has outlined the diversity history of the group using Sepkoski's (1981) data. The echinoids are an example of a group that diversified because of adaptations that enabled exploitation of additional previously unoccupied ecospace. The result is a clade diversity diagram with a thin Paleozoic stem that mushrooms in diversity in the Mesozoic and Cenozoic (Fig. 1). In general, the diversity history of the group since the Triassic is one of diversity maintenance with replacement in one subclass (Perischoechinoidea) and diversity expansion in a second, more recent subclass (Euechinoidea) (Bambach, 1985). Detailed analyses of the functional significance of the evolutionary trends thought to be responsible for the group's diversity history have been presented for Paleozoic and post-Paleozoic forms (Kier, 1965 and 1974, respectively).

Aside from general studies of echinoid preservation (Kier, 1977; Smith, 1984), specific research on echinoid taphonomy has been conducted along three distinct, yet interrelated venues: 1] Preservational style of fossil occurrences (e.g. Hawkins & Hampton,

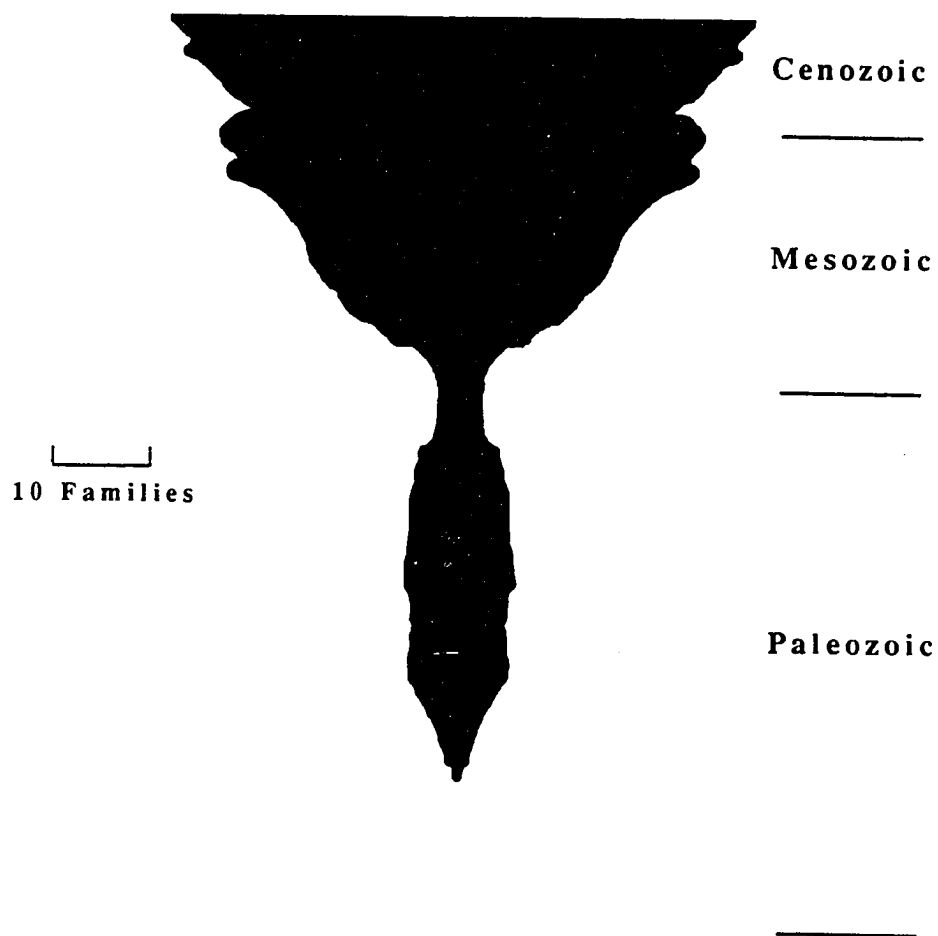


Figure 1 -- Family diversity of the Class Echinoidea (after Bambach, 1985).

1927; Spencer, 1938; Aslin, 1968; Bantz, 1969; Bloos, 1973); 2] Occurrences of exceptionally well-preserved fossils: Lagerstätten (Wright, 1855-1880; Richter, 1931; Kier, 1958, 1966, 1968; Rosenkranz, 1971; Seilacher, 1976), and 3] Field and laboratory experimentation with Recent specimens (Schäfer, 1972; Kidwell & Baumiller, 1989).

Work with Recent specimens, although valuable for providing information on the nature of taphonomic bias inherent in the fossil record, has been the most neglected area of echinoid taphonomic research to date. There are two reasons for the paucity of such data: 1] The nature of taphonomic processes makes field experiments extremely difficult. Specimens are hard to maintain and monitor in such a way that meaningful data can be obtained. Moreover, disturbance of specimens for examination imparts an unnatural taphonomic element. Thus, beyond Schäfer's (1972) study, field observations remain largely anecdotal. 2] Taphonomic research on many vertebrate and invertebrate groups in Recent environments has experienced a renaissance in the last six years. Within this limited time context, the scarcity of field research on a single group is less remarkable.

The actualistic portion of this study focuses on four species of regular echinoids inhabiting shallow Caribbean and tropical Western Atlantic environments. Their epifaunal habit and distribution into distinct and accessible reef and near-reef environments make it relatively easy to study taphonomic processes affecting them in a variety of environments with different substrates and energy regimes.

Moreover, the echinoids chosen vary morphologically in ways that could affect their preservation potential.

The habitat preferences of the species under study have been outlined by Clark (1933) and Kier and Grant (1965). *Diadema antillarum* Philippi (Family Diadematidae), is primarily a cryptic inhabitant of high energy, shallow reef environments. However, prior to the pan-Caribbean demise of populations of *Diadema* (Lessios, 1984), the echinoid was ubiquitous in all near-reef environments except for clean sand, from the intertidal zone to over 40 m depth. At night this species grazes algae from reef surfaces and preys on live coral (Bak & van Eys, 1975; Carpenter, 1981). *Eucidaris tribuloides* Lamarck (Family Cidaridae) may be found under large sections of coral rubble (or inside vacant gastropod shells), on sandy or rocky substrates (but not clean sand) and in deeper forereef environments to at least 30 m depth.. *Echinometra lucunter* Linnaeus (Family Echinometridae) is very abundant in shallow water (maximum depth 3 m) near shore, along high energy intertidal and shallow subtidal rocky shorelines. *Echinometra* is also present on shallow rocky substrates created by reefs or shoals far from shore. This echinoid excavates holes in hard substrates while grazing on algae. *Tripneustes ventricosus* Lamarck (Family Toxopneustidae) live primarily in, or adjacent to, seagrass beds in low energy lagoonal environments. Its depth of habitation is restricted by the depth tolerance of seagrass, from 1 - 12 m.

The species studied represent families with different geologic ranges and diversity histories. The Cidaridae have undergone diversity maintenance with replacement since the middle Triassic as

•

members of the Subclass Perischoechinoidea. The Echinometridae and Toxopneustidae have undergone diversity expansion (since the Late Cretaceous and Eocene, respectively) as members of the Subclass Euechinoidea. The Diadematidae, members of the Subclass Euechinoidea, have undergone diversity maintenance with replacement. Thus, the echinoids chosen represent a range of habitats and evolutionary histories that can be used as a backdrop for the studies of taphonomic processes affecting them.

To convey best the multifaceted nature of this research, Chapter Two describes the methodology used in the field, in the laboratory and for collecting the literature-derived data. Chapter Three presents the results of field and laboratory work and a discussion of their taphonomic implications. Predictions of taphonomic overprint are presented in Chapter Four, along with tests of those predictions using field- and literature-derived data. Finally, Chapter Five applies the conclusions reached concerning taphonomic overprint to the actual diversity patterns of one of the groups selected for study.

Historical Background

Works by Buckland (1836), d'Orbigny (1849) and d'Archiac (1869) indicate that the concept of differential fossilization has been known to paleontologists for at least 150 years. More recently, Efremov (1940) introduced the term taphonomy as the study of "...the transition (in all details) of animal remains from the biosphere into the lithosphere..." (Efremov, 1940 p. 85). The study of taphonomy may be divided into two subdisciplines: 1) biostratinomy -- the study of processes (generally mechanical and physical) affecting an

organism between its death and final burial (Weigelt, 1919); and 2) diagenesis -- processes affecting organismal remains between their final burial and discovery as fossils. Diagenetic processes are generally chemical in nature (see Müller, 1979; Wilson, 1988 for reviews of both subdisciplines).

Efremov's definition of taphonomy (1940) as well as an extended work towards establishing "laws" of taphonomy (1950) were predated by taphonomic research conducted by two separate groups in Germany that comprised several researchers. The "Halle School" (Seilacher, 1973) included Johannes Weigelt who introduced the term biostratinomy (1919) and applied the concept to vertebrates (1927) and plants (1928b). A. H. Müller expanded the study of biostratinomy to include invertebrates (1951b, 1963).

The "Frankfurt School" can be traced to Rudolf Richter, who founded the Wilhelmshaven Marine Station on the North Sea in 1928 to conduct "Aktuopaläontologie" (actualistic paleontology), the study of the paleontology of living organisms. Richter's work on fossil orientation (1922, 1937, 1942) expanded biostratinomic research to the interpretation of depositional regimes. Wilhelm Schäfer, also from Frankfurt, produced a survey of biostratinomic processes affecting a wide range of marine animals (1962). The translated edition (1972) continues to serve as a taphonomic reference for current researchers in the United States.

The legacy of the "Frankfurt School" is currently maintained at the University of Tübingen. Taphonomic research at Tübingen is characterized by Adolph Seilacher's work with Fossil-Lagerstätten (Seilacher, 1970; Seilacher & Westphal, 1971; Seilacher *et al.*, 1985),

fossil orientation (Seilacher, 1973) and applications of taphonomy to paleoecological research (A. & E. Seilacher, 1976).

In the United States, the study of taphonomy developed independently among vertebrate and invertebrate workers (Olson, 1980). Study of invertebrate taphonomy was slow to develop but can be traced to Boucot's comparison of size frequency distributions of living and fossil populations (1953) as well as R.G. Johnson's research on shell burial (1957) and conceptual work on the formation of fossil assemblages (1960). Subsequent taphonomic research emphasized the role of taphonomy in cautioning paleontologists about the biases inherent in the fossil record (e.g. Fagerstrom, 1964; Lawrence, 1971; MacDonald, 1976; Peterson, 1976; Stanton, 1976; Kier, 1977; Schopf, 1978). This negative aspect of taphonomy is perhaps best illustrated by the title of a 1968 paper by D. R. Lawrence "Taphonomy and Information Losses in Fossil Communities."

D. L. Meyer and C. E. Brett organized a symposium, held at a 1984 section meeting of the Geological Society of America, entitled "The Positive Aspects of Taphonomy." The symposium became a catalyst for vigorous research that has extended the range of applications and subtlety of taphonomic analysis. The renewed research activity of the last six years has resulted in an avalanche of taphonomic literature, theme issues of two major journals (*Palaios*, 1(3), 1986 and *Palaeogeography, Palaeoclimatology, Palaeogeography* 63(1-3), 1988), theme sessions on taphonomy at national scientific meetings and has perhaps reached its zenith with a three-session taphonomy symposium convened at the 28th International Geological Congress by S. M. Kidwell and F. T. Fürsich. It is against this

background of energetic taphonomic research that this study is presented.

CHAPTER 2: METHODS

Field Methods

All fieldwork was based at the Bahamian Field Station, San Salvador, Bahamas, and the West Indies Laboratory, St. Croix, U.S. Virgin Islands. Both localities were selected on the basis of their diverse and abundant populations of regular echinoids and the accessibility of reef and near-reef environments. In addition, San Salvador was selected because excellent exposures of well-preserved Pleistocene reef and near-reef facies are present. Three types of fieldwork were performed: 1] censuses of live and dead populations of echinoids, to determine the amount of taphonomic bias affecting the subfossil assemblages; 2] burial experiments, to assess the timing of disarticulation of skeletal remains; 3] examination of Pleistocene reef and near-reef facies to determine the amount and nature of fossil echinoid material present.

Population Censuses

Censuses of echinoid populations were conducted along transects constructed in three areas: Graham's Harbour in San Salvador, and Smuggler's Cove and Rod Bay in St. Croix (Figs. 2 & 3). Graham's Harbor has been described as a high-energy lagoon by Colby and Boardman (1989) and contains abundant populations of the echinoid *Tripneustes ventricosus* in the seagrass beds and sand patches that comprise the floor of the lagoon. A 700 m transect line was established bearing 350 degrees from the Bahamian Field Station boat ramp in Graham's Harbour (Fig. 2). Maximum water depth along the

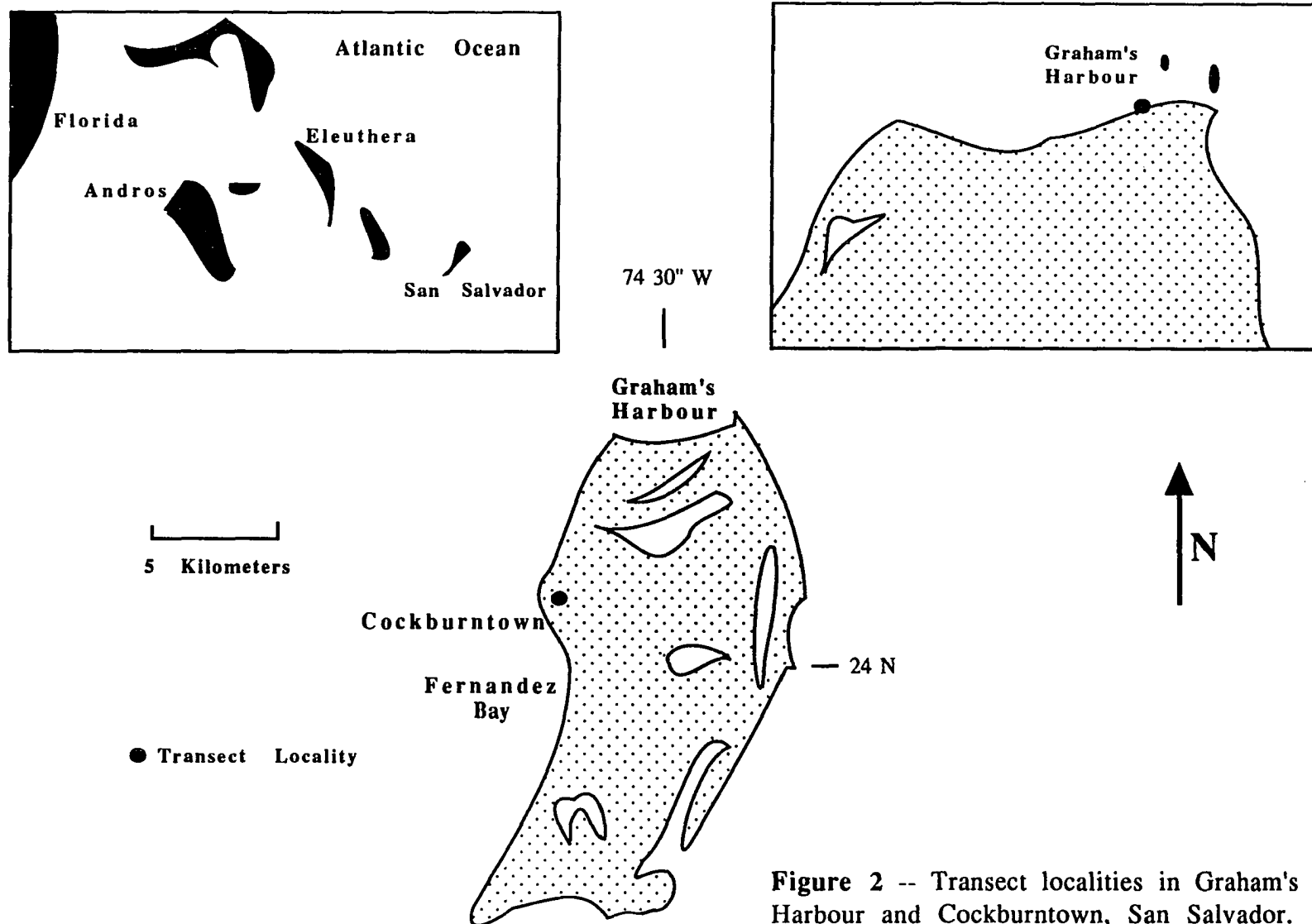
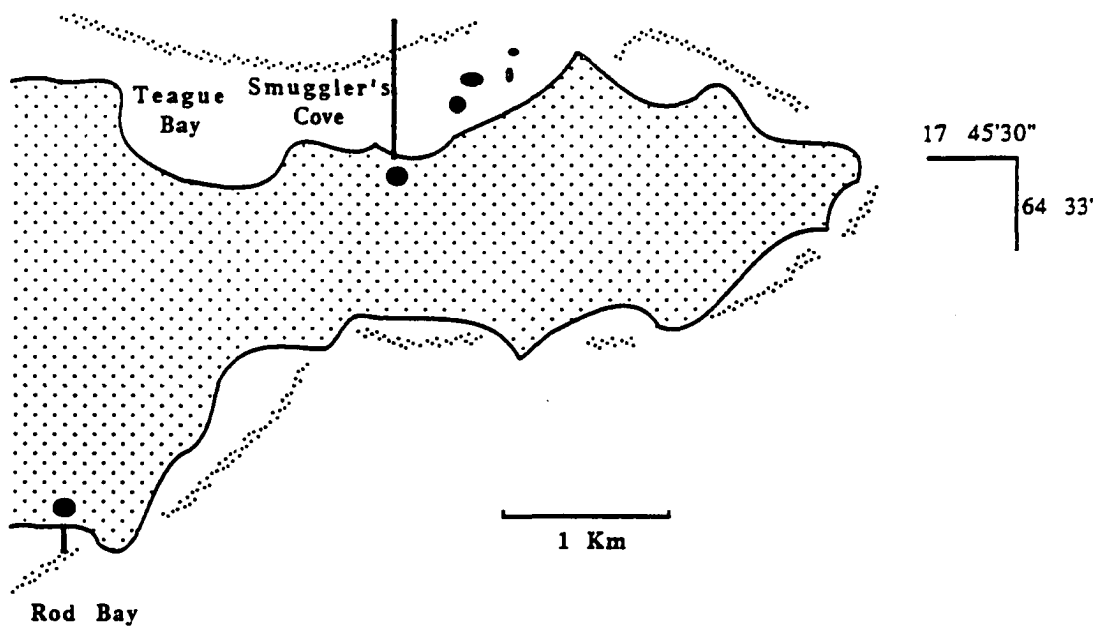
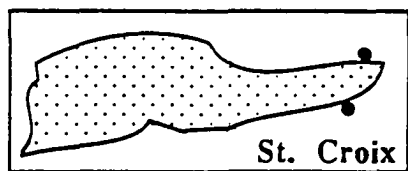


Figure 2 -- Transect localities in Graham's Harbour and Cockburntown, San Salvador.

transect was 4 m. At stations 100 m apart, a 1 m² quadrat was placed adjacent to the transect line; live and dead echinoids within the quadrat were counted and the condition of the dead material was recorded (Fig. 4). The quadrat was then flipped over and another square meter was studied. This process was repeated ten times at each station resulting in a census of a 1 x 10 m² "column" situated perpendicular to the transect line and occurring every 100 m. Surficial sediment samples were collected from the first quadrat analyzed at each station for later analyses to determine the contribution of echinoderm skeletal elements.

The Smuggler's Cove site was selected because several reef and near-reef environments are present within a relatively short distance. A 720 m transect line was constructed heading due North from the Smuggler's Cove dock (Fig. 3). Echinoids were counted in a rocky shoreline zone, *Callianassa*-dominated sandy areas, *Thalassia*-dominated grassbeds, patch reef, reef tract and shallow (water depth 1.5 m) and deep (water depth 12 m) forereef environments. Water depth from shore to the reef tract in Smuggler's Cove reached a maximum of 6 m. The echinoid population census was conducted in the same manner as in Graham's Harbour except that sampling stations were 60 m rather than 100 m apart.

Populations of regular echinoids were observed to be particularly diverse and abundant at Rod Bay, the third census locality (Fig. 3). A 50 m transect was constructed and a population census was conducted using the methodology outlined above at stations 10 m apart. Within the transect, rocky shoreline, *Thalassia*-dominated seagrass beds, a zone of coral-algal rubble and an environment of



- Bank Barrier Reef
- ● ● Patch Reefs
- Transect Line

Figure 3 -- Transect localities in Smuggler's Cove and Rod Bay, St. Croix, U.S.V.I.



Figure 4 -- Square meter quadrat made of PVC pipe used for gathering census data from each transect constructed. For the four echi-
noid groups under study, all live and dead material present within
the quadrat was recorded. The condition of the dead material was
also recorded.

very small patch reefs were encountered. Maximum water depth along the transect was 1 m.

Sediments obtained from stations along all three transects were dried, impregnated with epoxy and ground into standard thin sections. Thus, all size fractions were represented in thin section to mitigate the possibility that different echinoids would break down into different size fractions. The thin sections were point counted on a 1 mm² grid following the method of Ginsburg (1956). Echinoderm skeletal elements were counted by taking advantage of the unit extinction they exhibit in cross-polarized light, and their percent contribution to the sediment was calculated. This method did not allow for the differentiation of echinoid skeletal elements from those of other echinoderms.

Burial Experiments

The purpose of the burial experiments was to determine the timing of decay of organic tissues and consequent disarticulation of the echinoid corona in natural surroundings. The backreef environment occurring along the transect in Smuggler's Cove was selected because the occurrence of live individuals in the backreef and adjacent reef tract suggested that dead material might also be present. Specimens of *Diadema antillarum*, *Eucidaris tribuloides* and *Echinometra lucunter* were killed by placing them in a freezer overnight. Although frozen solid upon removal from the freezer, the specimens thawed completely during the interval between removal from the freezer and placement on the backreef in Smuggler's Cove. The echinoids were placed in cages with open tops, sides with mesh

sizes of 2 cm² and floors of standard window screening material (Fig. 5). These "open" cages were used to allow scavenging and yet contain the specimens for monitoring over a period of several days. They were placed at 5, 10 and 20 cm depth below the sediment-water interface in a wave-rippled, sandy substrate immediately behind the reef tract in 4 m of water. The specimens were periodically observed for 12 days before being removed for study.

Cockburntown Reef

The purpose of studying the Pleistocene reef and near-reef facies exposed in Cockburntown, San Salvador, was to assess the nature of the echinoid fauna preserved in depositional environments analogous to those Recent environments in which the population censuses were conducted. The methodology for studying the outcrops was therefore similar to that employed for the population censuses conducted in the Recent environments.

The Cockburntown reef, exposed in a quarry just north of Cockburntown, San Salvador, has been interpreted by White *et al.* (1984) to represent an *in situ* coral reef and adjacent facies. Because the strata are dipping slightly to the west (i.e. into the sea) excellent bedding plane exposures of units interpreted to represent shallow subtidal sands and backreef environments are present (Fig. 6). The unit interpreted to represent the reef tract proper occurs at the shoreline; it exhibits the black and deeply pitted appearance of a phytokarst surface. Except for large, *in situ* coral heads, fossils are difficult to study (Fig. 7).

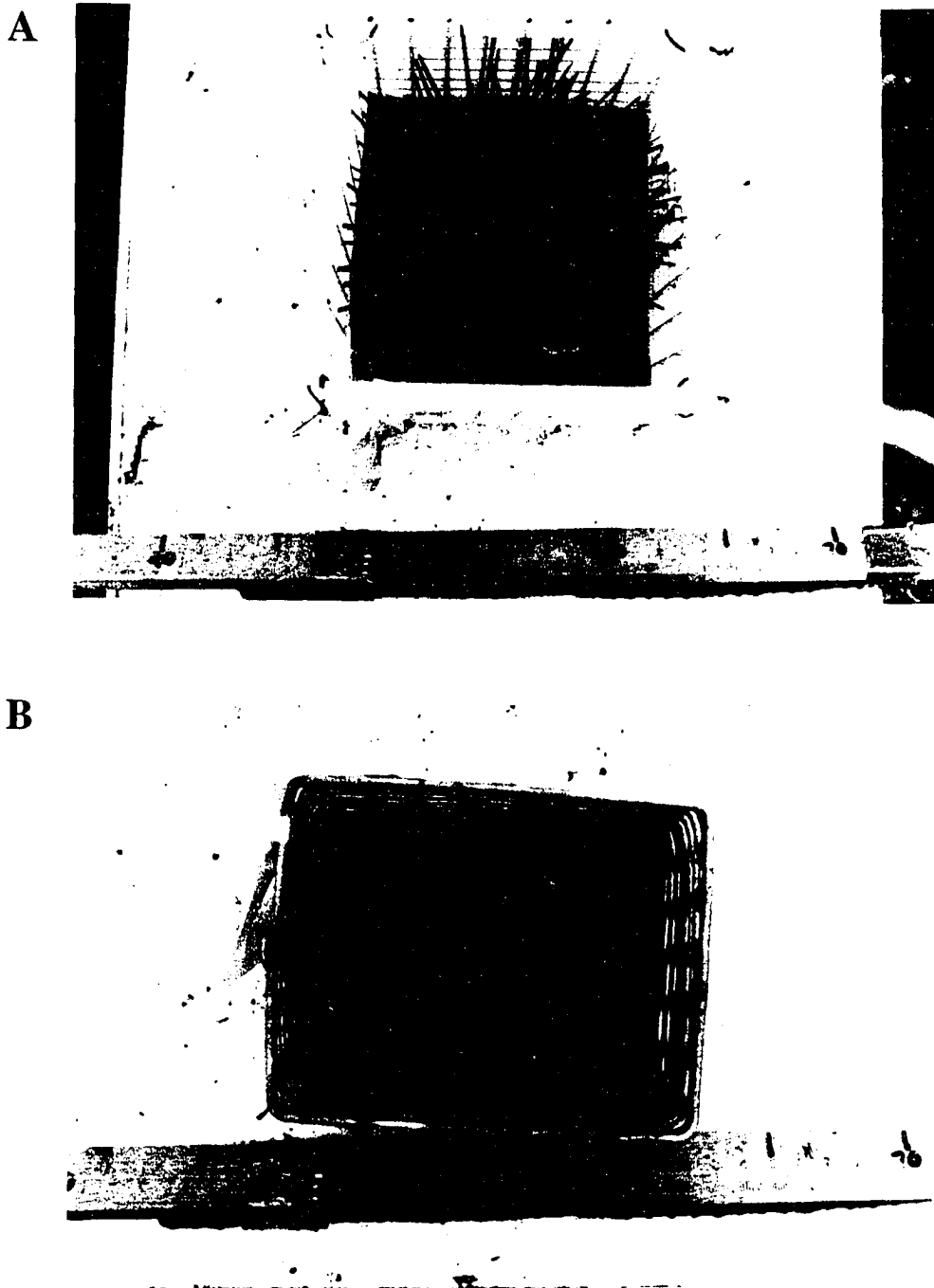


Figure 5 -- Echinoid specimens prior to burial in the backreef of Smuggler's Cove. A) *Diadema antillarum*. B) *Echinometra lucunter* and *Eucidaris tribuloides*. Specimens were killed by freezing overnight.

A



B



Figure 6 -- Pleistocene reef and near-reef facies exposed near Cockburntown, San Salvador and described by White *et al.* (1984). A) *A. palmata*-dominated coralstone overlying *A. cervicornis*-dominated rubblestone that represent reef tract and backreef environments, respectively. B) Calcarenite interpreted as a shallow subtidal sand (note trough cross-bedding).

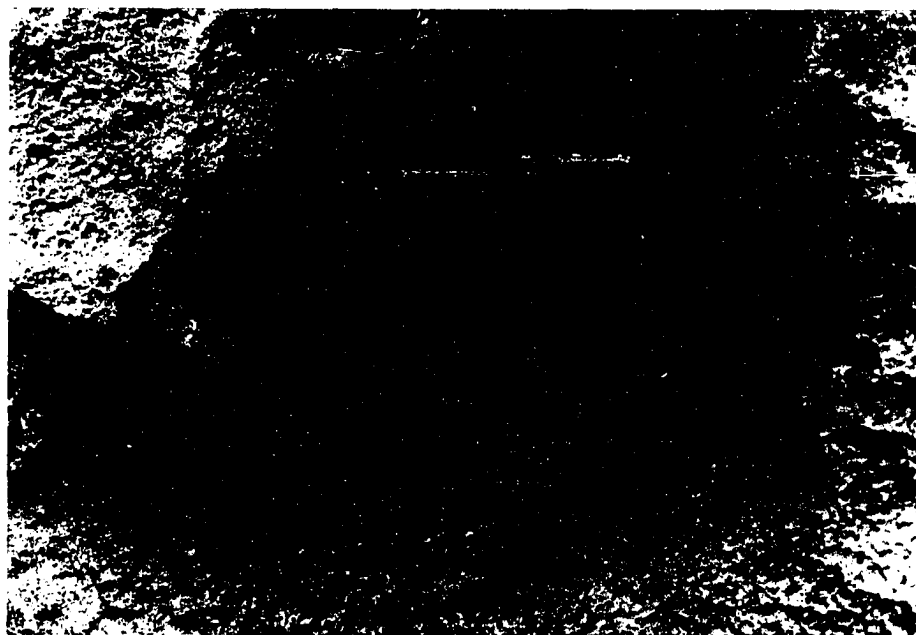
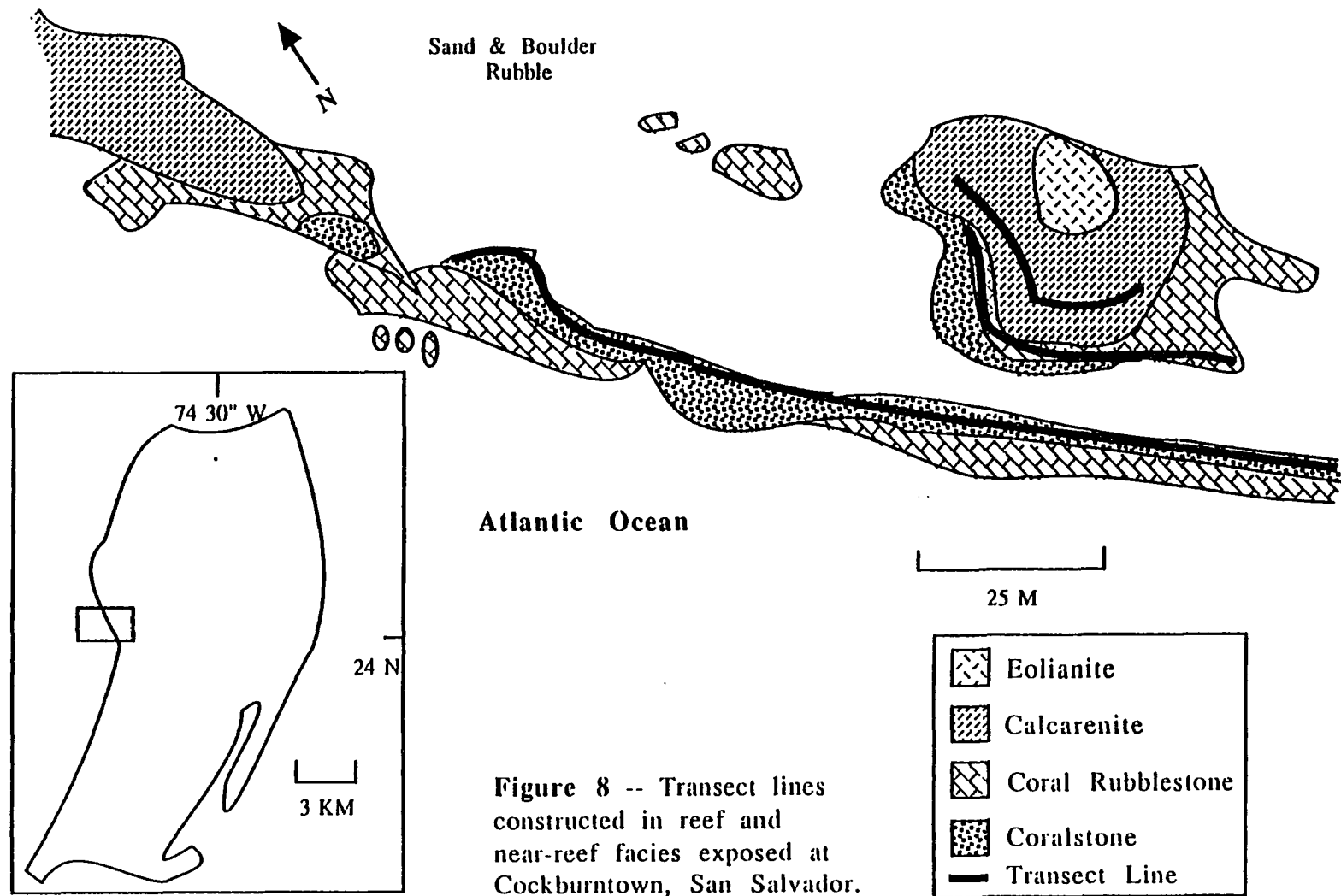


Figure 7 -- View of a bedding plane surface of the Pleistocene reef tract facies exposed near Cockburntown, San Salvador. Note the development of an extensive phytokarst. Aside from large *in situ* coral heads, individual macrofossils are extremely difficult to identify.



A total of three transects were constructed in the Cockburntown Quarry (Fig. 8). Two were constructed along separate exposures of the coral-rubblestone facies interpreted to represent a reef/back reef environment (White *et al.*, 1984). The first of these followed the west wall of the quarry for 120 m. A square meter quadrat was placed over the bedding plane exposure at 30 m intervals and the type of echinoid and preservational style were recorded for all fossil occurrences. The coral-rubblestone facies was also the target of the second transect, which was constructed along a knoll directly opposite the quarry's west wall (Fig. 8). Along this transect, the quadrat was placed every 10 m until the unit pinched out 50 m around the knoll. Data on fossil echinoid occurrences were again recorded. The third transect was constructed along a bedding plane exposure of a calcarenite interpreted by White *et al.* (1984) to represent a shallow subtidal sand. Because only nine meters of this unit were exposed, fossil echinoid data were collected from the quadrat every meter along the transect line.

Rock samples were obtained from the different facies exposed at Cockburntown. Samples were cut to standard blanks and vacuum-impregnated with epoxy before being ground into standard thin sections. As with the surficial sediment samples collected in tandem with the population censuses, the thin sections were point counted on a 1 mm² grid to determine the contribution of echinoderm skeletal elements.

Laboratory Methods

Laboratory experiments were performed at the West Indies Laboratory, St. Croix and at the University of Cincinnati. They were intended to assess the relative timing of decay and skeletal disarticulation of the echinoids under study. Three different experiments were performed: 1] Tumbling experiments, to assess whether any taxonomically-controlled differences in skeletal durability and size distribution of skeletal material exist; 2] Decay experiments in sealed and open containers, to observe the effect that organic deterioration had on the integrity of the skeleton; 3] Time-lapse cinematography, to monitor the decay process continuously over a period of several days.

Tumbling Experiments

Specimens of *D. antillarum*, *E. lucunter*, *E. tribuloides* and *T. ventricosus* were preserved in 95% ethanol for transport back to Cincinnati. Each specimen was placed in a 4:1 solution of water and household bleach to oxidize all of the organic tissue contained within its skeleton. The denuded skeleton was then dried for several days under a laboratory hood. Dried skeletons were weighed and then placed in room temperature (22° C) synthetic seawater (Instant Ocean) in a baffled plastic tumbler attached to a variable speed motor (Fig. 9). The baffle ensured that the contents would tumble once with each rotation rather than slide around the outer wall. Five trials of 1, 10 and 100 hours each were run at 25 rpm. for each echinoid. At the end of each trial, the contents of the tumbler were wet-

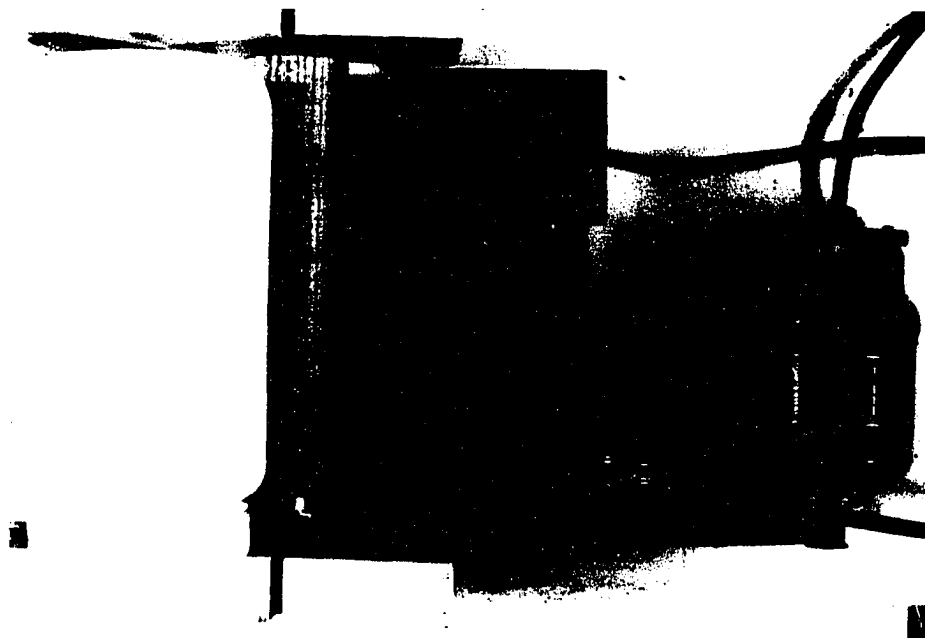


Figure 9 -- Apparatus used for all tumbling experiments. Container was filled with 1/2 gallon of seawater (Instant Ocean) and variable-speed motor was set at 25 r.p.m. A ruler 1.5" wide was epoxied to the inside of the container to make the echinoids fall through the water with every rotation.

sieved through a stack of nested sieves, and the stack was dried for several days under a laboratory hood. Once dry, the >2 mm, 1-2 mm, 500 μ -1 mm and 125 μ -500 μ size fractions were isolated for analysis. Spines, coronal material and lantern elements in the three larger size fractions were counted and weighed. Because of the minute grain size, the 125 μ -500 μ size fraction was weighed without identifying different skeletal elements.

Decay Experiments

Frozen specimens of *Diadema*, *Eucidaris* and *Echinometra* were placed in glass containers with fresh seawater and allowed to decay for ten days at room temperature (22° C). Aerobic (open containers) and anaerobic (sealed containers) trials were performed for each echinoid. Specimens were placed in the containers with either no sediment, sediment from the fore-reef in Smuggler's Cove or sediment from the backreef in Smuggler's Cove. Thus, for each echinoid, three aerobic and three anaerobic trials were conducted. All were carried out under darkened conditions except when removed for photographs. Open containers were kept under a darkened hood while sealed containers were kept in a closet. Both sealed and open containers were removed as carefully as possible for observations and photographs of the decay process every two days. Although this added disturbance could possibly have promoted disarticulation, no appreciable destruction of carcasses was observed to occur.

Time-lapse Cinematography

Frozen specimens of *Diadema*, *Echinometra* and *Eucidaris* were placed in a flowing seawater aquarium to ensure the presence of bacteria. Water temperature in the aquarium was 30° C. The specimens were photographed with a super-8 movie camera (Sankyo Model EM60XL) loaded with 50 ft. cassettes of Kodak Ektachrome, and the built-in timing mechanism of the camera was set on one frame per minute. Thus set, the camera would expose one cassette of film over two day-night cycles. Illumination at night was provided by a 75 watt bulb in a lamp suspended over the aquarium. A total of three cassettes of film were used to photograph the specimens over a one week period.

Construction of the Literature Database

The purpose of assembling data on the preservational style of fossil echinoids is to provide a test of the taphonomic predictions derived from the field and laboratory work. Moreover, the data can be used to explore patterns of preservation with respect to taxonomic, stratigraphic and lithologic factors.

Lambert and Thiery (1909-1925) produced a monograph listing all fossil and living echinoid species known through 1924 and a reference to an adequate description of each. All of the references given for species in the four families under study that are described using fossil material are type descriptions. I have reconciled the taxonomy of the Lambert and Thiery monograph with that of the Treatise. Kier and Lawson (1978) compiled an update to Lambert

and Thiery's list that included fossil and living species described between 1924 and 1970 and followed the taxonomy given in the Treatise. I have updated the list of fossil species to include those described between 1970 and 1988 by checking citations in the Zoological Record. The result is a list of all species known in the Families Diadematidae, Echinometridae, Cidaridae and Toxopneustidae that have been described on the basis of fossil material, and a reference to the description of the type material.

Each primary echinoid literature reference was obtained to study the taphonomic condition of the type material on the basis of the photographic plates included in the reference. A taphonomic code ranging from 1 (whole corona with spines attached) to 7 (skeletal fragments) was assigned to each specimen based on the relative completeness of the test (Figs. 10A, 10B). A description of each code follows.

Code 1 -- Whole corona, intact with spines attached, little to no abrasion of the corona (Fig. 10A).

Code 2 -- Whole corona, intact, no spines attached. Corona may be abraded to unabraded (Fig. 10A).

Code 3 -- Whole corona, compressed and/or fractured, spines attached, little to no abrasion (Fig. 10A).

Code 4 -- Whole corona, compressed and/or fractured, no spines attached. May be abraded to unabraded (Fig. 10B).

Code 5 -- Partial corona, ranging in completeness between a complete interambulacrum and a corona intact with the exception of a few adapical or adoral plates. Spines attached, little to no abrasion (Fig. 10B).

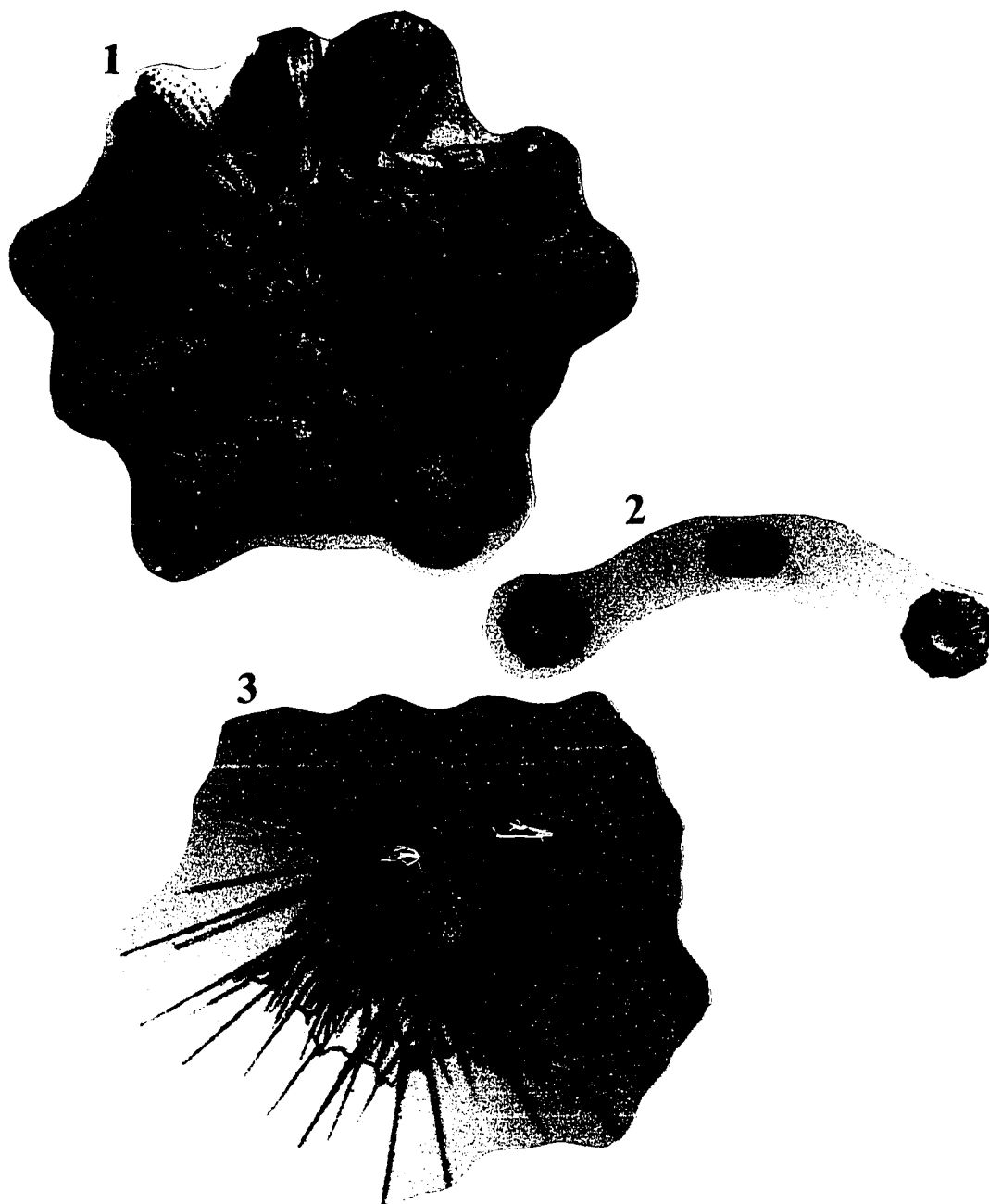


Figure 10A -- Examples of the taphonomic codes discriminated for assignment to the literature-derived data. All of these specimens were photographed from Wright's monographs of British fossil Echinodermata (1855-1860). Code 1) intact corona with spines attached; Code 2) intact denuded corona; Code 3) complete corona either compressed or fractured, spines attached.

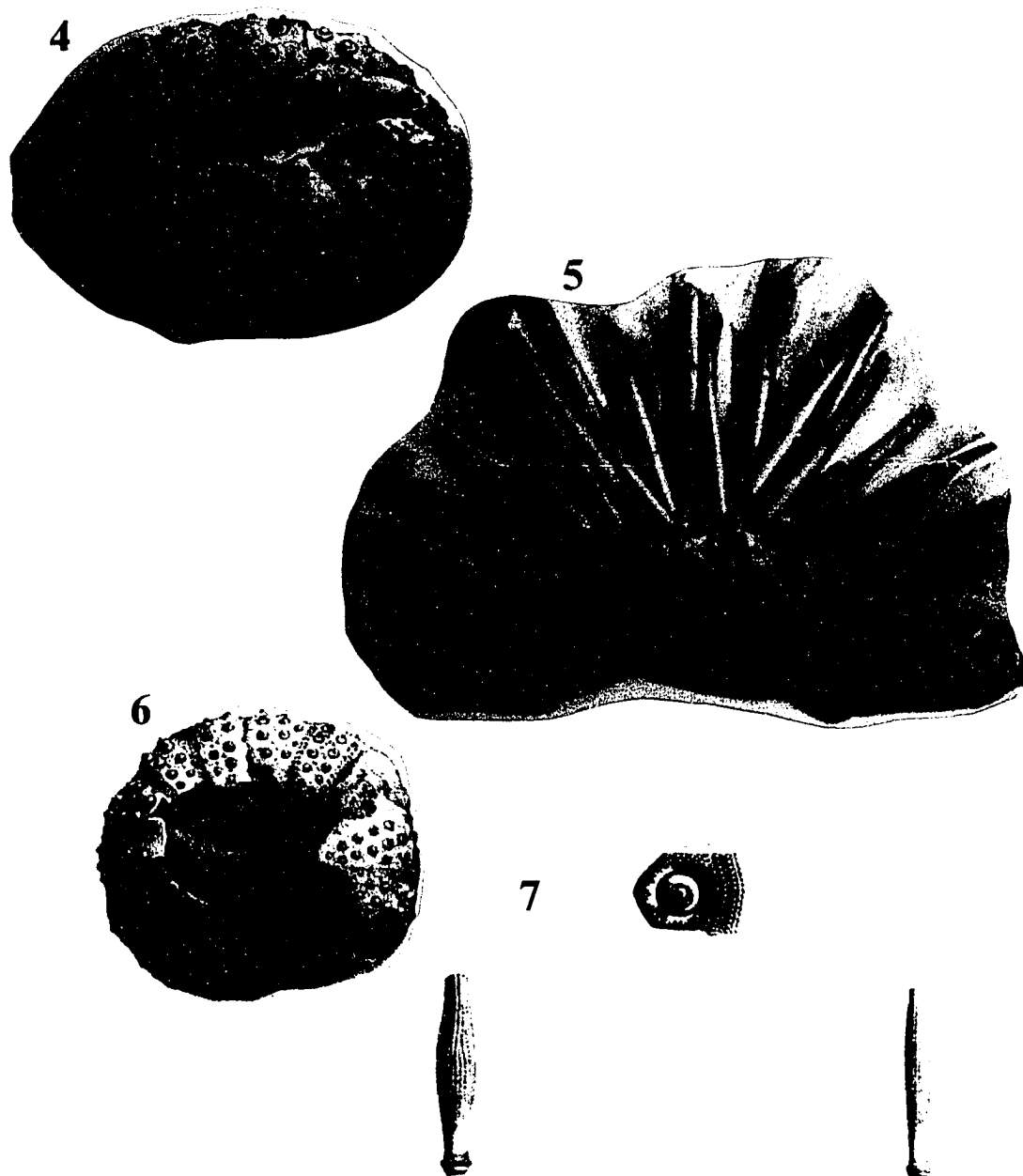


Figure 10B -- Examples of the taphonomic codes discriminated for assignment to the literature-derived data, continued. Code 4) complete denuded corona either compressed or fractured; Code 5) Coronal fragment larger than an interambulacrum, spines attached; Code 6) Coronal fragments larger than an interambulacrum; Code 7) Fragments smaller than an interambulacrum.

Code 6 -- Partial corona, distinguished as for Code 5, no spines attached. May be abraded to unabraded (Fig. 10B).

Code 7 -- Coronal fragments, ranging in size between a single plate and an incomplete interambulacrum (Plate Fig. 10B).

Presence/absence data on spines, test, Aristotle's lantern, apical plates and peristomial plates were collected. For example, if a lantern was described to occur associated with an intact corona, and no spines were attached to the corona, the fossil would be assigned to taphonomic code 2 and the "present" category contained in the "lantern" field of the appropriate record would be selected. Finally, additional information on stratigraphic horizon, enclosing lithology and locality was recorded when the information was contained in the reference.

CHAPTER 3: RESULTS & DISCUSSION

Field Results

Population Censuses

Although the echinoids under study are generally recognized as ubiquitous in shallow reef and near-reef environments (Kier & Grant, 1965), their distribution at all three localities is patchy. A total of 130 m² in Smuggler's Cove, 60 m² in Rod Bay and 800 m² in Graham's Harbor were analyzed for the presence of live and dead echinoids. Raw data are presented in Appendix III.

Few living echinoids, and no dead echinoids, were present in Smuggler's Cove and live echinoid occurrences were concentrated at three of the 13 transect stations. *Echinometra lucunter* were observed in low numbers (average of 2.6 per square meter) in five of the ten quadrats analyzed at transect Station 0 (Fig. 11) along the rocky shoreline. No additional echinoids were observed until the reef tract was reached at Station 540, where live individuals of *E. lucunter* were again observed, in slightly higher numbers (average of 6 per square meter) in eight of the ten quadrats counted. One live *Tripneustes ventricosus* was also present. Highest echinoid diversity, but at low abundance, occurred at Station 600, in the shallow forereef environment; *D. antillarum*, *E. lucunter* and *E. tribuloides* were all present. No intact or partial coronal material was observed anywhere along the transect.

Sediment samples were obtained from all the transect stations in Smuggler's Cove except Stations 360 and 600. Because the first quadrat of each of these stations was located directly on a coral head,

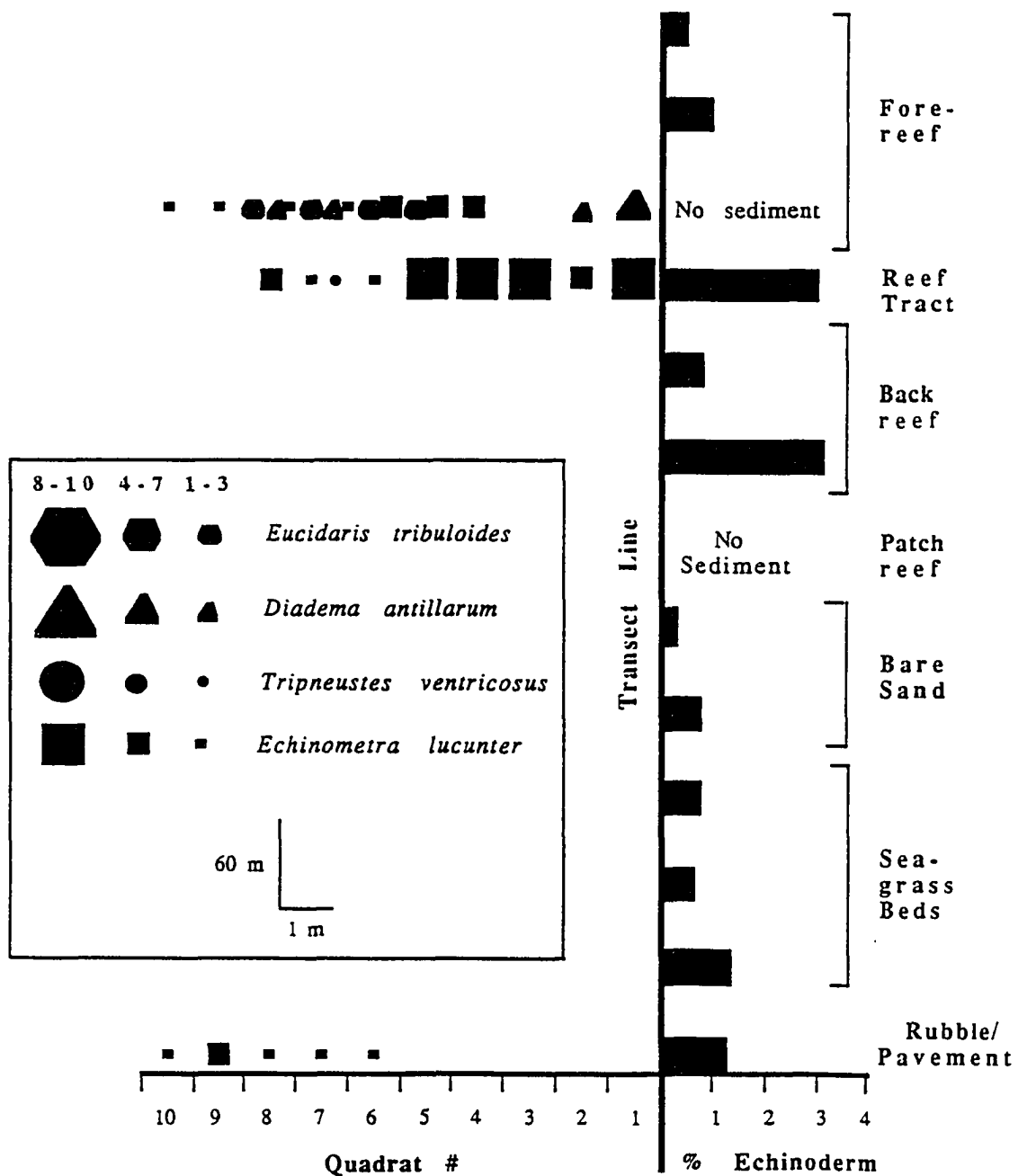


Figure 11 -- Schematic representation of the Smuggler's Cove transect. Symbols to the left of the transect line indicate live echinoid abundance. Histogram to the right of the transect line shows the percent echinoderm grains point-counted in sediment samples.

associated with a small patch reef at Station 360 and in the forereef at Station 600, no sediment was available.

Constituent particle analysis of the sediments reveals that echinoderms are minor contributors to the sediments in all of the environments encountered in Smuggler's Cove, averaging 1.2% of the total constituents. The two highest concentrations of echinoderm material, 3.2% at station 420 and 3.0% at Station 540, are outside the 95% confidence interval computed for the mean value for all stations.

Examination of the echinoid fauna in Rod Bay yielded comparable results (Fig 12): no dead material was associated with living individuals. Live echinoids were present at three of the six transect stations analyzed. Relatively high numbers of live *Echinometra* were present in all 10 of the quadrats analyzed at Station 0, averaging 28.1 per square meter. One *Tripneustes* was also present. Individuals of *Echinometra* occurred, in low abundance (average of 3.8 per square meter), in five of the ten quadrats studied at Station 40; two *Tripneustes* were present in one quadrat. Finally, echinoids were present on a small patch reef encountered at Station 50. Low numbers of *Echinometra* (average of 3.4 per square meter) were counted in five of the ten quadrats, while two *Eucidaris* were observed in each of two quadrats.

The coral rubble-pavement that predominantly comprises the substrate in Rod Bay made sediment sampling difficult. As a result, samples were obtained from only two of the six stations. The results of constituent particle analysis are comparable to those obtained at Smuggler's Cove: echinoderms are minor contributors to the sedi-

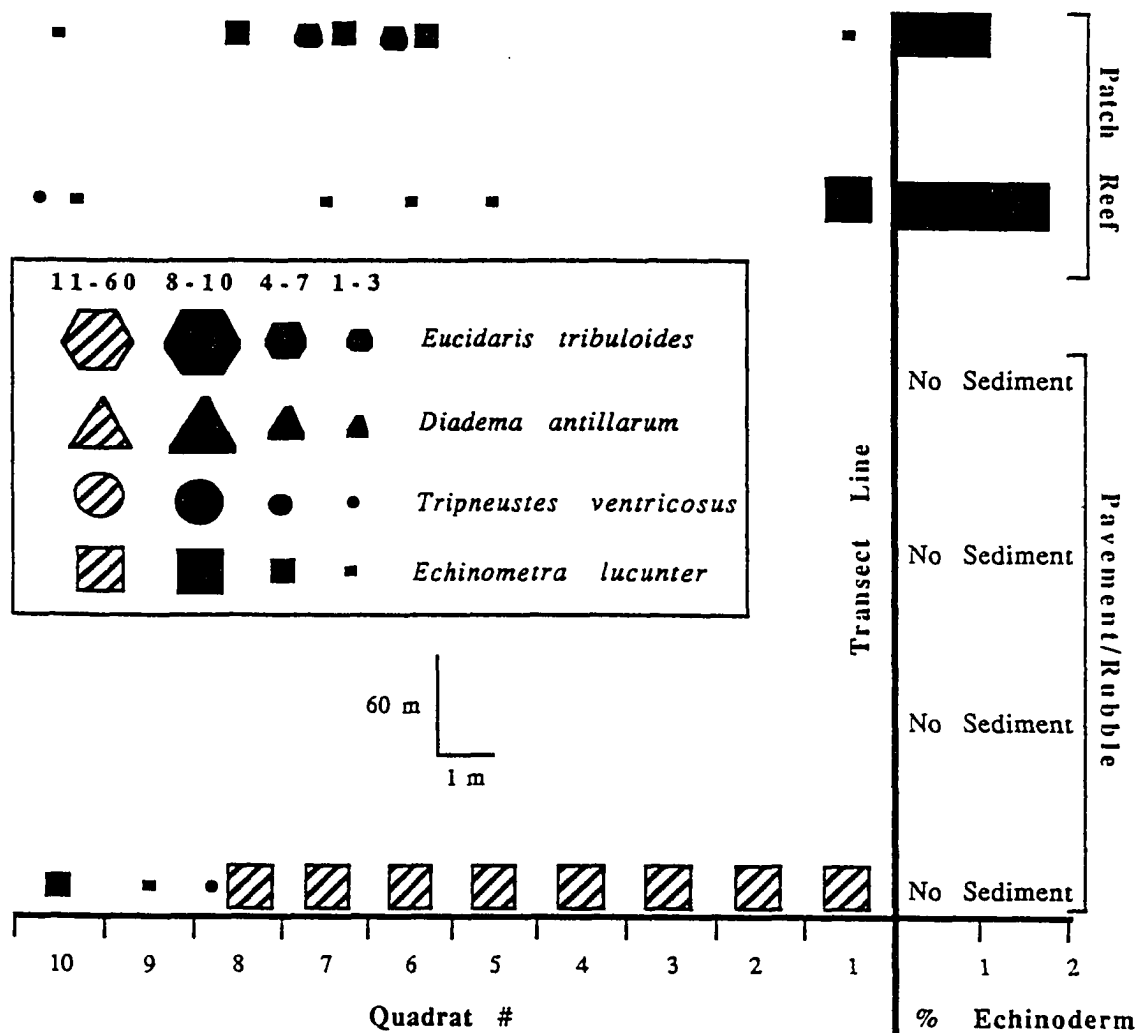


Figure 12 -- Schematic representation of the Rod Bay transect. Symbols to the left of the transect line indicate live echinoid abundance. Histogram to the right of the transect line shows the percent echinoderm grains point-counted in sediment samples.

ment, comprising 1.7% and 1.1% of the constituents in samples obtained from Stations 40 and 50, respectively.

Tripneustes ventricosus was the only regular echinoid found in the census of Graham's Harbour. Although only one live individual was counted (at Station 400), eight dead individuals, in various states of degradation, were observed distributed along the transect at Stations 300, 400, 500 and 700 (Fig. 13). Condition of the dead material ranged from freshly killed with organic tissue still present, to isolated fragments of interambulacrum encrusted with algae (Fig. 14). Except in the case of the freshly-killed individual, spines, apical system and elements of the Aristotle's Lantern were not associated with coronal material. Without exception, all relatively intact coronas observed along the transect (and in Graham's Harbor in general) exhibited bore holes.

Constituent particle analysis of sediment samples obtained at each station revealed that the contribution of echinoderm material is lower in Graham's Harbor than either Smuggler's Cove or Rod Bay. At all stations where sediment was available to sample, echinoderm grains comprise less than 1% of the sediment.

Burial Experiments

Specimens of *D. antillarum*, *E. lucunter* and *E. tribuloides* buried to 5 and 10 cm sediment depths were observed after exposure on the backreef for one, six and twelve days. Specimens buried to 20 cm were observed after one and twelve days only. Results are illustrated in Figures 15- 16.

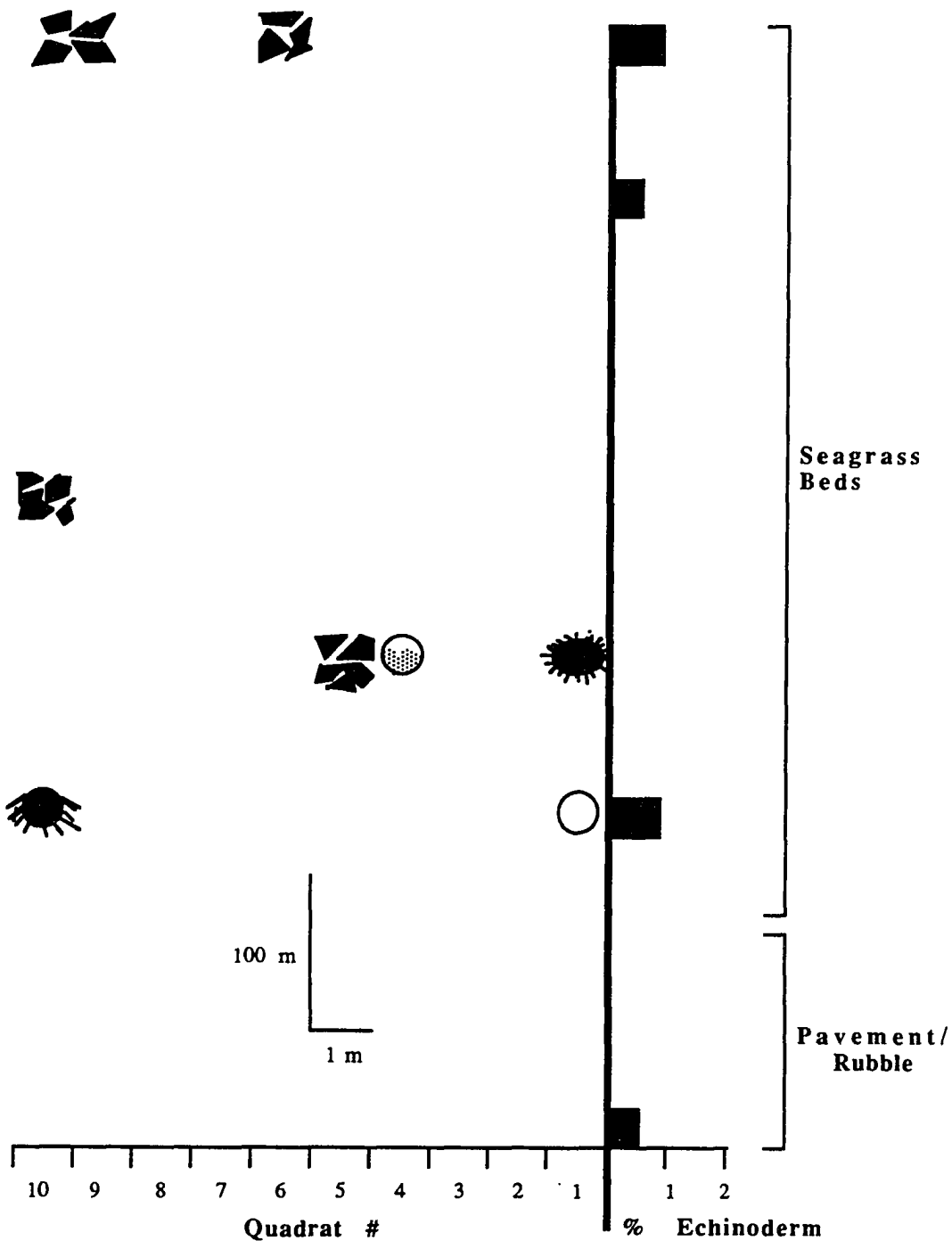


Figure 13 -- Results of population census in Graham's Harbour. *Tripleneustes venticosus* was the only echinoid present. Echinoids were found alive (☼), freshly killed (☼), as an intact bleached corona (○), as an encrusted corona (⊙), as fragments of interambulacra (☼), and as smaller coronal fragments (☼).

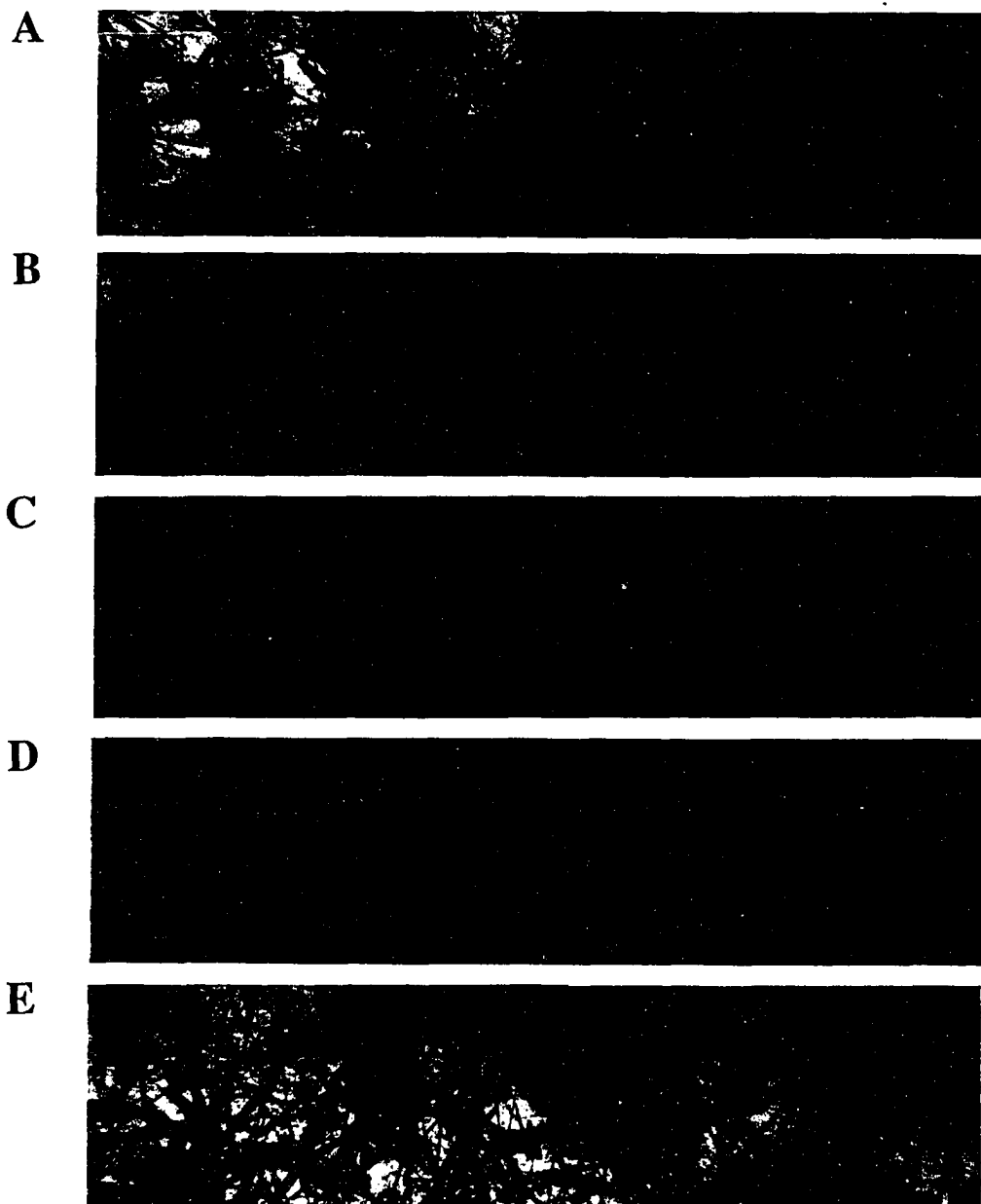


Figure 14 -- Dead *Tripneustes ventricosus* observed in various states of degradation in Graham's Harbour, San Salvador. A) Fresh kill, the spines were still moving on this specimen; B) Intact bare corona (note probable gastropod bore hole); C) Relatively intact and heavily encrusted corona. Arrow points to the alga *Acetabularia* growing from the corona. Presence of this alga as well as the degree of encrustation suggests that the corona remained intact for a relatively prolonged period on the sea floor; D) Large coronal fragments encrusted with algae; E) Small encrusted coronal fragments.

Although all three *Diadema* specimens were intact after one day of exposure, cassid gastropods were present on the specimens buried to 5 and 10 cm depth (Fig. 15). After six days, the *Diadema* specimen at 5 cm was denuded of spines, apical system and Aristotle's Lantern. The corona, although intact, was full of sediment and was starting to separate along its ambulacral plate sutures. No organic tissue remained. Although the connective tissues of the *Diadema* specimen buried to 10 cm had undergone some decay, it was not sufficient to cause loss of spines; the corona was still intact. After 12 days, the corona of *Diadema* at 5 cm had been reduced to large fragments of interambulacra. Spines and lantern elements were not present. The coronas of specimens buried to 10 and 20 cm depth remained intact. Decay of organic material resulted in the detachment of spines (which were present in the cage), apical system and Aristotle's Lantern (which were not present).

When compared to one another, all three specimens of *Echinometra* exhibited essentially the same pattern of disarticulation (Fig. 16). After one day, specimens buried to 5 and 10 cm were intact whereas the specimen buried to 20 cm had lost approximately 50% of its spines as a result of organic decay. After six days, coronas of specimens buried to 5 and 10 cm were intact and devoid of organic matter. Spines, lantern elements and apical plates were not present in the cage, although numerous echinoid spines were present in the sediment of the backreef. After 12 days, all three specimens had been reduced to intact empty coronas.

All specimens of *Eucidaris* remained intact after one day of exposure (Fig. 16). After six days, decay had proceeded sufficiently so

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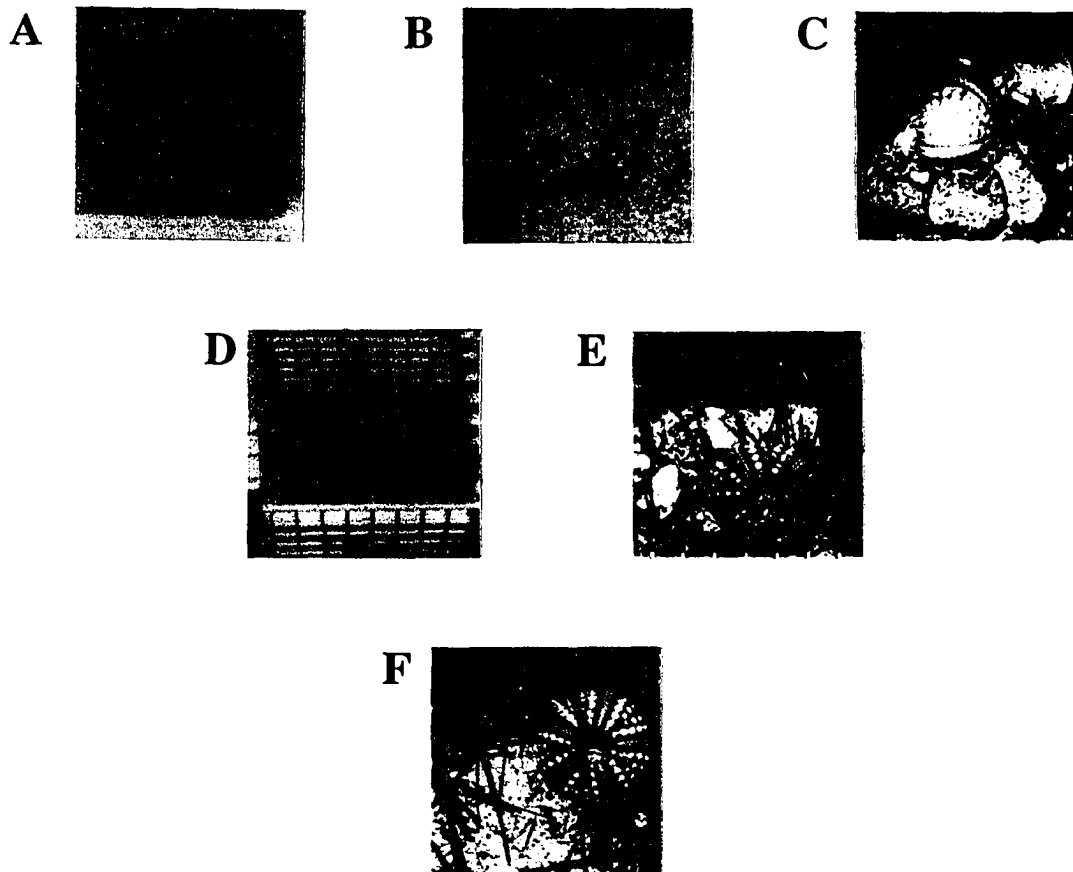


Figure 15 -- The sequence of decay of *Diadema antillarum* placed in the backreef in Smuggler's Cove. A-C) Specimen buried to 5 cm after one, six and twelve days; D-E) Specimen buried to 10 cm after one and twelve days; F) Specimen buried to 20 cm after twelve days. Specimen buried to 10 cm was not disturbed for observation after six days. Specimen buried to 20 cm was not disturbed for observation until the conclusion of the experiment.

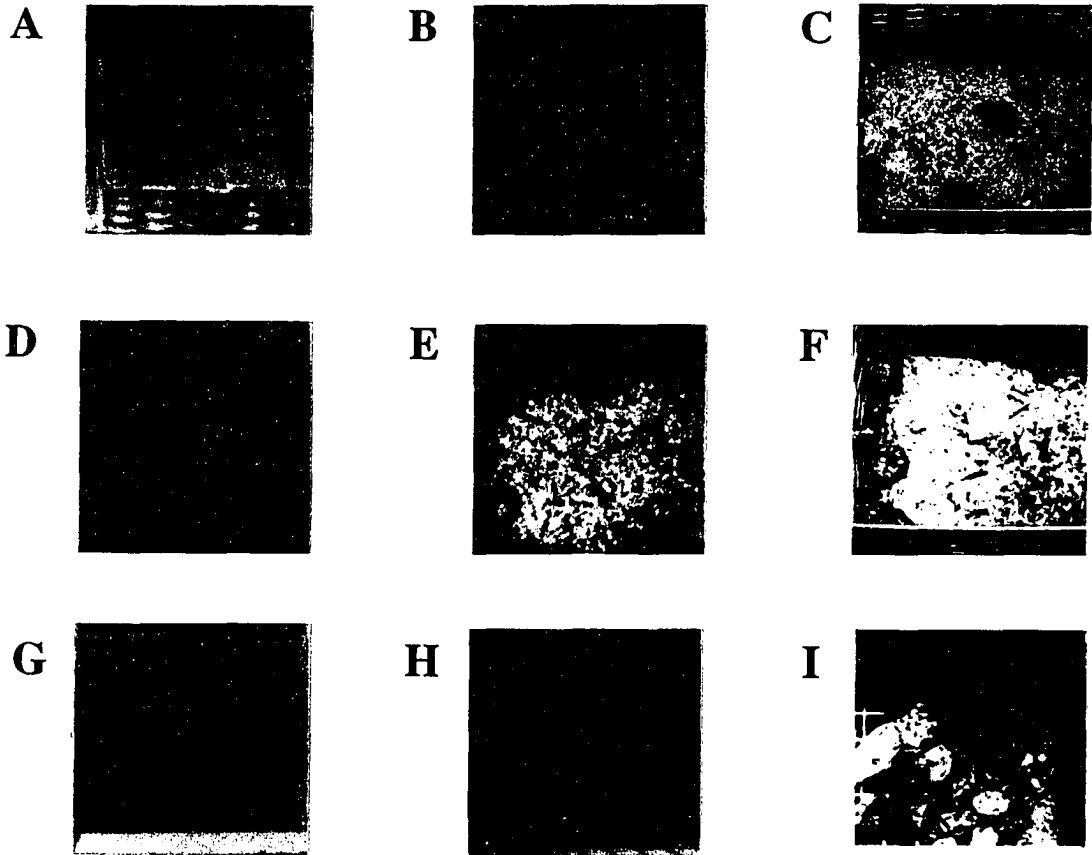


Figure 16 -- The sequence of decay of *Echinometra lucunter* and *Eucidaris tribuloides* placed in the backreef in Smuggler's Cove after one, six and twelve days. A-C) Specimens buried to 5 cm; D-F) Specimens buried to 10 cm; G-I) Specimens buried to 20 cm. Two specimens of *Echinometra* and one specimen of *Eucidaris* were placed in each cage.

that the spines, lantern and apical system had disarticulated from the corona. Spines were present adjacent to the specimens at all depths. Apical plates were absent from all three cages while demipyramids of the Aristotle's Lantern were absent from the cage buried to 5 cm and present immediately adjacent to the test of the specimen buried to 10 cm. After 12 days, only coronal material and disarticulated spines remained of all three specimens. The coronas buried to 5 and 20 cm were intact, whereas the corona buried to 10 cm consisted of fragments of interambulacra.

Taphonomic Predictions based on Field Work

The absence of recognizable echinoid remains in Smuggler's Cove and Rod Bay suggests that, in the environments studied, echinoids are rapidly acted on by biostratinomic processes. This has been previously demonstrated for *Diadema* by Greenstein and Meyer (1985a, b) and Greenstein (1989). The presence of recognizable remains in Graham's Harbor indicates that post-mortem degradation may not be as rapid in that lagoon. The ubiquitous presence of bore holes in dead *Tripneustes* implies that predation is an important source of mortality. Cassid gastropods are present in Graham's Harbor and have been shown to prey, with few exceptions, exclusively on echinoids (Hughes & Hughes, 1981). Once preyed upon, tests of *Tripneustes* lose their spines, apical system and Aristotle's Lantern. Although loss of these elements results primarily from decay of organic tissues, spine loss can also result from the feeding technique of cassids (Hughes & Hughes, 1981). The observation of *Tripneustes* tests encrusted with algae (see Fig. 14) indicates that,

once denuded, tests of *Tripneustes* can remain intact long enough to become encrusted with algae. Large segments of interambulacra can also survive further degradation long enough for encrustation to occur.

Constituent particle analyses reveal that sediment composition is an unreliable indicator of the distribution of the living fauna at all three localities. The low percentages of echinoderm material in the sediment would make changes in live echinoid abundance statistically difficult to recognize in the sedimentary record. Moreover, results from Smuggler's Cove suggest that even statistically significant deviations from normal levels of echinoderm material do not accurately reflect the distribution of the living fauna. This conclusion extends my earlier finding (Greenstein, 1989) that a pulse of exceptional amounts of echinoid material were not preserved in the sediments of the fringing reefs of Bonaire, Netherlands Antilles.

Burial experiments indicate that, under normal marine conditions, six days is sufficient time to "bleach" an echinoid of its organic material. This process, as well as the method of predation of *Tripneustes*, results in rapid loss of organic connective tissues and consequent breakdown of the echinoid skeleton into essentially two parts: a corona lacking connective tissues and disarticulated skeletal elements (spines, lantern and apical system). It is this material that will be further acted upon by biostratinomic and diagenetic processes; the fate of this material determines the condition of preserved recognizable remains of the echinoids under study.

Once organic connective tissue has decayed, the rigidity of an echinoid corona is determined by taxonomically-controlled variations

in the interlocking of stereom across plate sutures (Smith, 1984). Extensive interlocking of stereom occurs in echinaceans such as *Echinometra* and *Tripneustes* (Régis, 1977), while very little is present in cidarids (*Eucidaris*) and diademataceans (*Diadema*) (Smith, 1980; 1984). The contrast between degraded coronas of *Diadema* and *Eucidaris* buried to 5 and 10 cm, respectively, and intact coronas of *Echinometra* in burial experiments as well as the presence of intact coronas of *Tripneustes* in Graham's Harbour corroborates this fact. The lack of disarticulation of *Diadema* tests buried to 10 and 20 cm may be the result of burial, but no definitive statement can be made on the basis of one experimental trial. The fragile tests (because of a lack of sutural interlocking) and low abundances of *Diadema* and *Eucidaris* in the environments studied are responsible for the lack of recognizable coronal remains.

Echinometra and *Tripneustes* represent the other end of the "durability spectrum" for the echinoids studied. No intact coronas of *Echinometra* were found associated with the living fauna. Because these echinoids live in high energy environments (rocky shoreline and reef tract) in Smuggler's Cove and Rod Bay, a high degree of sutural interlocking and relatively high abundance do not necessarily make their preservation any more likely than preservation of *Diadema* or *Eucidaris*.

In Graham's Harbor, the association of relatively low numbers of living *Tripneustes* with several occurrences of skeletal remains may be related to their source of mortality, as well as to the degree of sutural interlocking: predation by boring gastropods results in a relatively intact corona. In the lagoon, coronas can remain intact

long enough to become encrusted, which may further enhance their chances of preservation. Thus, for these echinacean skeletons, possessing a relatively high degree of sutural interlocking, physical and ecological differences in the two environments may play a role in determining their preservation potential.

The patchy distribution of echinoids at all three localities can be expected to produce a scattered distribution of disarticulated skeletal elements that, even though time-averaged, comprise a small portion of the sediment. If these elements possess characteristics useful for taxonomic classification, they may become the only fossil data upon which the presence of echinoids may be inferred. Although this would be particularly true for cidarids and diademataceans, echinaceans living epifaunally in high energy environments (i.e. *Echinometra*), may also be preserved in this manner.

On the basis of field results and in the absence of unusual circumstances of preservation, the following taphonomic predictions can be made for echinoids preserved in analogous facies:

1. In general, fossil specimens of the echinoids under study will be rare.

2. The loss of organic connective tissue after six days' exposure in normal marine conditions suggests that the recognition of fossil material depends on A] taxonomic differences in coronal rigidity related to sutural interlocking, and B] identifiability of isolated skeletal elements. As a result, the condition of fossil specimens will vary between taxa.

3. Fossil occurrences of *Diadema* and *Eucidaris* are likely to be as disarticulated spines, lantern elements, apical plates or coronal

fragments. Although *Echinometra* possesses a relatively robust corona, in facies analogous to the environments studied, fossil occurrences will also be as disarticulated skeletal elements. Fossil *Tripneustes* are likely to be present in lagoonal facies as intact tests or segments of interambulacra; coronal material may be encrusted and bored. Although not attached to intact coronal material, additional skeletal elements will be distributed in low abundances in the sediment.

4. In rocky shoreline, reef and near-reef facies, the distribution of fossil material will not represent that of the living populations, and echinoderm material will represent a small proportion of the constituents forming the rock.

Laboratory Results

Decay Experiments

As noted earlier, the initial set-up for decay experimentation constituted a 6-way test for oxygenation (sealed vs. open containers) and sediment conditions (no sediment, backreef sediment and fore-reef sediment) for each of the three echinoids used in the decay experiments. However, other than an obvious difference in grain size, no further characteristics of the sediments obtained from the back-reef and fore-reef were noted. Moreover, Allison (1988) demonstrated stoichiometrically that decaying carcasses have a tremendous oxygen demand which cannot be compensated for by diffusion alone. Kidwell & Baumiller (in press) found that the oxygen demand of a single 6.5 g echinoid carcass in a 4 liter container was so great that tap water (initially 3.75 ml/l O₂) was reduced to an anoxic state in

less than 24 hours. Using ophiuroids, Jones (1987) also determined that decay experiments performed in open containers proceeded under anaerobic conditions. Thus for each echinoid, the decay experiments were reduced to a test of two sediment conditions (presence/absence) under conditions of anaerobic decay.

Six semi-quantitative states of decay, ranging from intact, freshly-killed specimens (State 1) to disarticulated fragments with varying amounts of organic tissue (State 6), were discriminated on the basis of experimental observations (Fig. 17). The pattern of decay of specimens placed in containers with no sediment mirrored that of specimens decaying in the presence of reefal sediments (Fig. 18). For specimens of *Diadema* and *Eucidaris*, the order of decay proceeded in much the same fashion as described for the regular echinoids *Echinus* by Schäfer (1972) and *Arbacia punctulata* by Kidwell & Baumiller (1989). After detachment of pedicellariae and spines, the peristomial and periproctal membranes disintegrate, the lantern disarticulates, the apical system collapses and finally the corona splits along plate sutures as a result of decay of connective tissues. Specimens of *Echinometra* also followed this pattern with the exception that they were not observed to disarticulate along plate sutures.

Spines of *Diadema* began to detach within one day of decay (Fig. 18A) with detachment continuing over the next five days. After seven days, specimens of *Diadema* were present in four of the six states of disarticulation, ranging from an intact corona missing <50 % spines to a corona split along ambulacral plate sutures. After 10 days, two additional coronas had disarticulated, and none retained

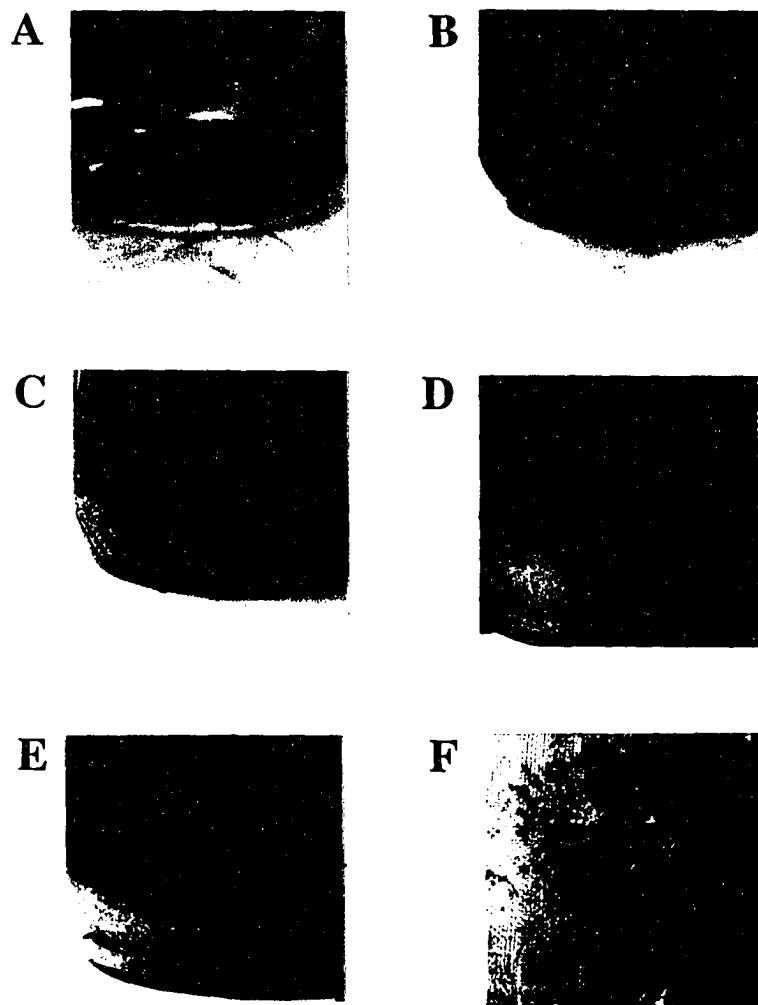


Figure 17 -- The six states of decay discriminated during the decay experiments performed in jars. A) intact corona with spines attached; B) intact corona with < 50 % spine loss; C) intact corona with > 50 % spine loss; D) intact corona denuded of spines, apical system and/or peristome attached; E) intact corona denuded of spines, apical system and peristome; F) coronal fragments. Examples A-D are specimens of *Echinometra lucunter*. Example E is a specimen of *Eucidaris tribuloides*. Example F is a specimen of *Diadema antillarum*.

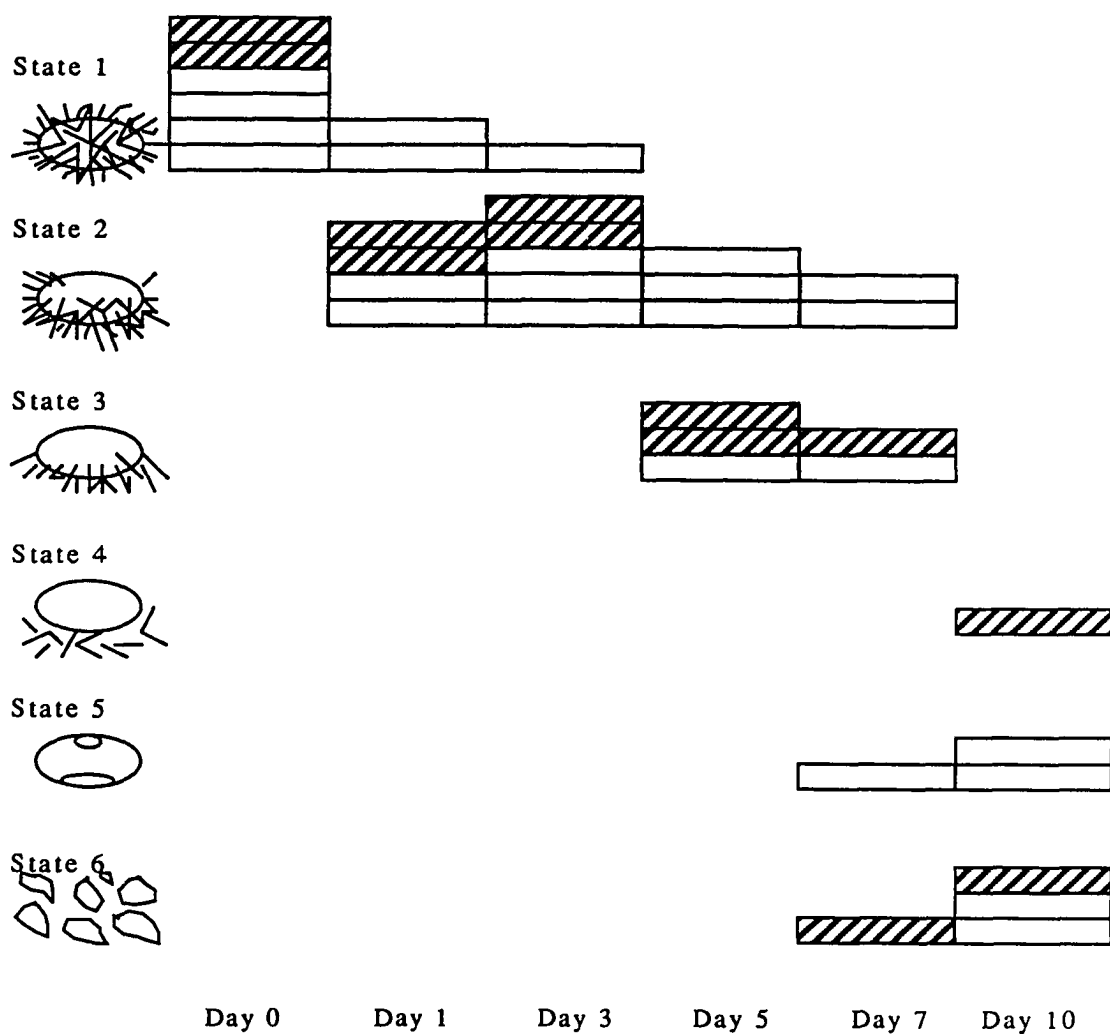


Figure 18A -- Decay of carcasses of *D. antillarum* in jar experiments. Presence in one state does not imply that the echinoid went through all preceding states. Each rectangle represents one echinoid specimen. Echinoids in jars with no sediment are represented by diagonal pattern.

any spines. All specimens but one were missing their lantern and apical system.

In contrast to *Diadema*, specimens of both *Echinometra* and *Eucidaris* retained their spines for longer periods. This is particularly true for *Eucidaris*, whose initial rate of disarticulation was the lowest of the three echinoids (Fig. 18B). Specimens of *Eucidaris* remained intact through three days of decay. After five days, one specimen had lost <50 % of its spines while the other five individuals continued to remain intact. Spine loss continued through seven days of decay, but no further disarticulation was observed until the tenth day, when four specimens had separated along ambulacral plate sutures.

Loss of spines from the coronas of specimens of *Echinometra* began after three days of decay (Fig. 18C), with continued loss through five days. After seven days, two specimens had lost all of their spines. The remaining specimens retained varying numbers of spines, although not to the degree that specimens of *Eucidaris* retained their spines after seven days. After ten days, all *Echinometra* coronas were intact, but devoid of spines. Two specimens still retained their lantern and apical system while these elements had disarticulated from the remaining specimens.

Time Lapse Cinematography

Difficulties with the camera equipment resulted in three extended intervals of continuous observation punctuated by two gaps in observation rather than continuous observation over a six day period. Of the total 148 hours during which the echinoids were allowed to decay, 115 hrs., 16 min. were observed. The first interval began

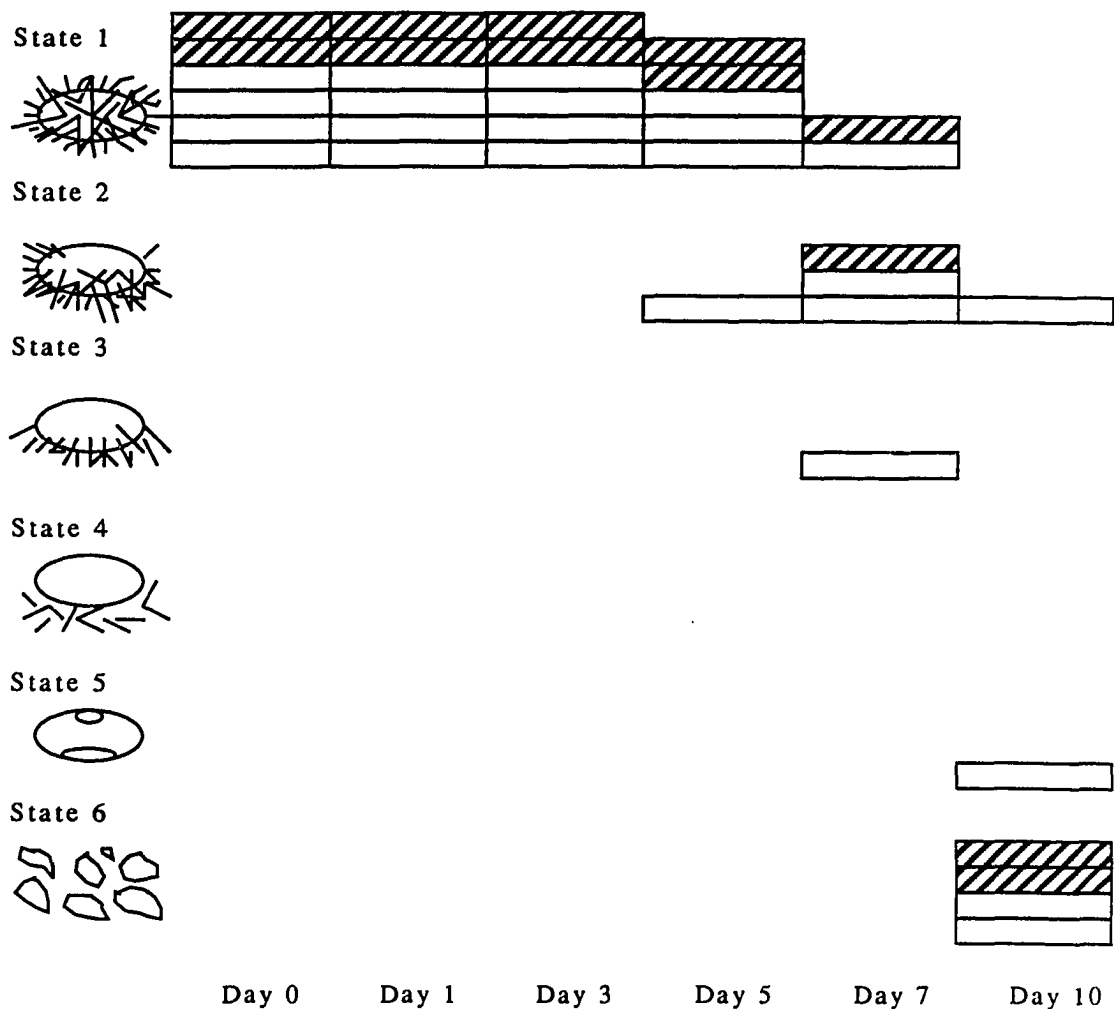


Figure 18B -- Decay of carcasses of *E. tribuloides* in jar experiments. Presence in one state does not imply that the echinoid went through all preceding states. Each rectangle represents one echinoid specimen. Echinoids in jars with no sediment are represented by diagonal pattern.

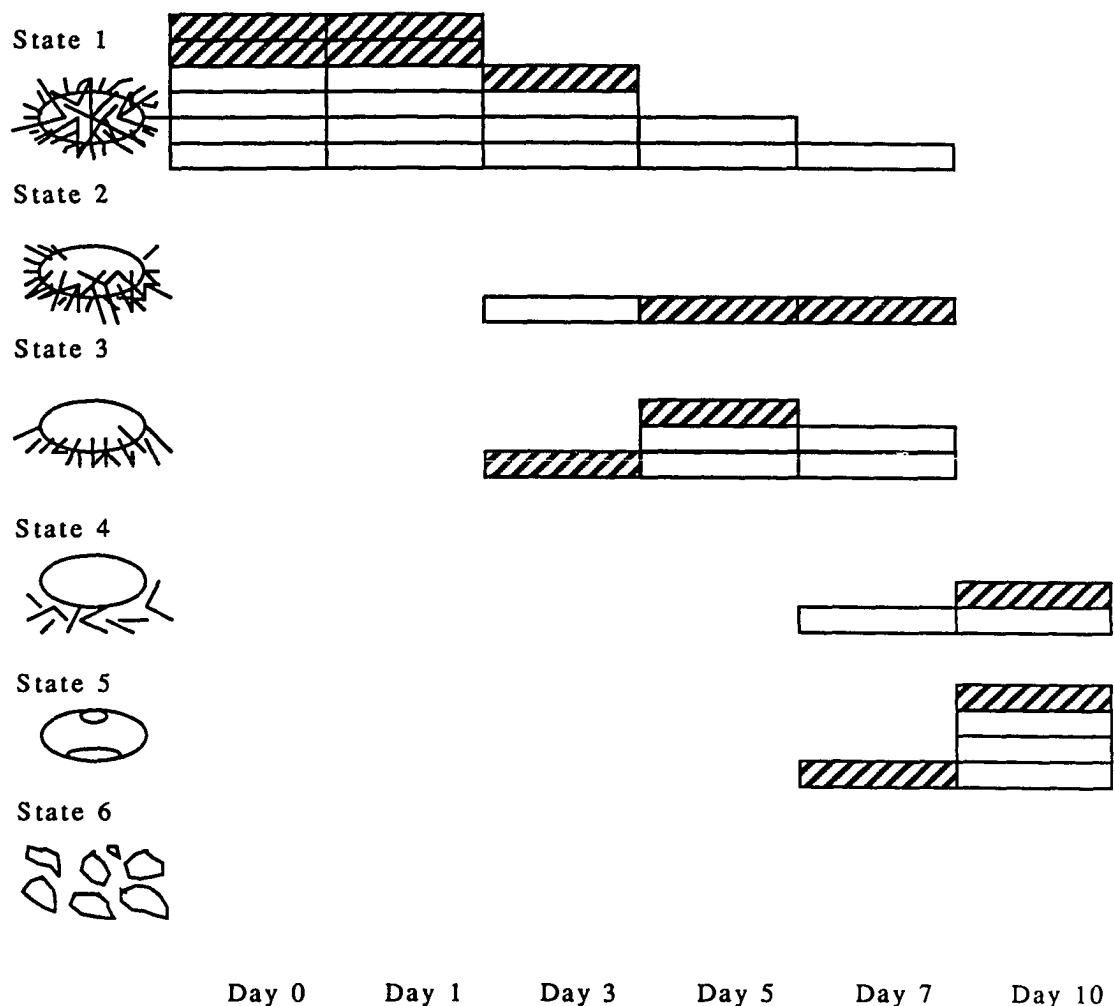


Figure 18C -- Decay of carcasses of *E. lucunter* in jar experiments. Presence in one state does not imply that the echinoid went through all preceding states. Each rectangle represents one echinoid specimen. Echinoids in jars with no sediment are represented by diagonal pattern

with the initial placement of the specimens in the flowing seawater aquarium and lasted 42 hr., 22 min. The second interval began after a 25 hr., 25 min. gap in observation, beginning 67 hr., 47 min. into the experiment and continuing for 14 hr., 36 min. until 82 hr., 23 min. into the experiment. The final interval began after a gap of 6 hr., 42 min., beginning at 89 hr., 5 min and continuing for 58 hr., 18 min. until the experiment was concluded. Observations were hampered during daylight by changes in film exposure, and facilitated at night by consistent exposure levels.

The development of algal (or possibly bacterial) "jackets" on all three specimens was first observed within 30 hours after placement in the aquarium. The algal coatings continued to thicken over all specimens forming a cap that appeared to bind the spines of the echinoids to the corona and interfere with disarticulation (Fig. 19). This observation was inadvertently shown to be correct when, upon removal of the echinoids after 168 hours, the specimen of *Echinometra* slipped out from underneath its "algal jacket" leaving its spines imbedded in the scum. The lantern and apical system consequently fell out of the corona (Fig. 20). Thus, decay had proceeded sufficiently to cause the disarticulation of skeletal elements. No buoyancy or movement of the corona as a result of bubbles produced by decay gases was observed.

Tumbling Experiments

Size Distribution of Skeletal Material -- When subjected to tumbling, skeletal material was distributed into the five delineated size fractions within one hour. For all echinoids, additional tumbling

19



20



Figure 19 -- *D. antillarum*, *E. lucunter* and *E. tribuloides* after six days of decay in a flowing seawater aquarium. Note extensive algal "jackets".

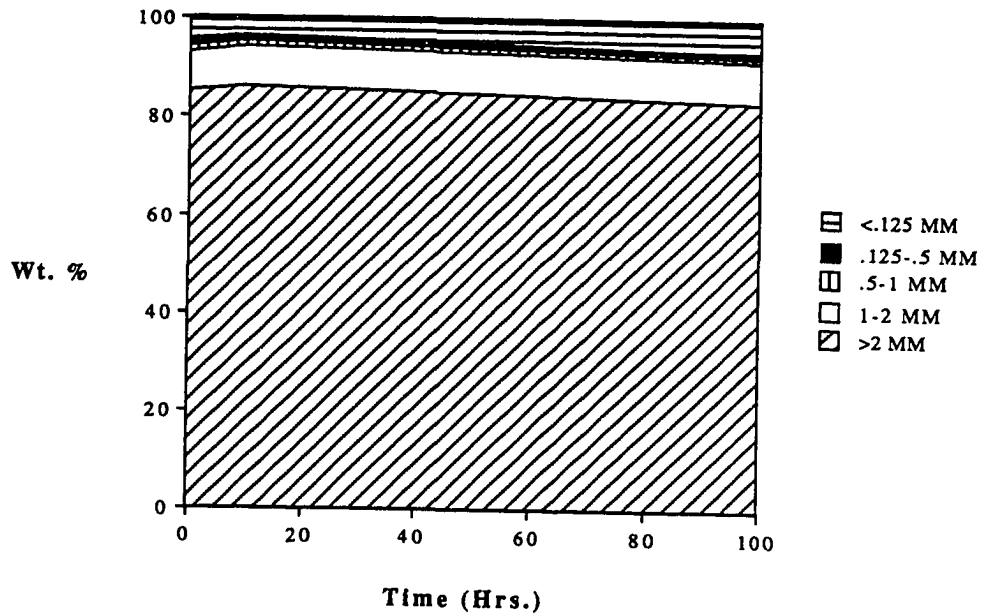
Figure 20 -- The same specimens after removal from the aquarium after six days of decay. When removed from the aquarium, the specimen of *Echinometra* lost its spines.

resulted in neither statistically significant ($\alpha = .05$) increases nor corresponding decreases in the size fractions when expressed as weight percent of the entire skeleton (Figs. 21 & 22). Eighty percent of the weight of skeletons of *Diadema* and *Echinometra* was present in the >2 mm size fraction after one, ten and 100 hour periods of tumbling (Fig. 21A, B). The same results were obtained for skeletons of *Eucidaris* (Fig. 22A): the >2 mm size fraction contained approximately 80% of their weight. Eighty percent of the weight of *Tripneustes* skeletons was divided between the >2 mm and 1-2 mm size fractions (Fig. 22B). These fractions contained approximately 60% and 20% of skeletal weight, respectively.

Composition of the >2 mm Size Fraction-- For all echinoids, the >2 mm size fraction was composed of spines, corona and elements of the Aristotle's Lantern. As might be predicted from Figures 21 and 22, the relative contributions of these skeletal elements to the fraction do not vary significantly with tumbling time. Significant ($\alpha = .05$) differences do exist, however, in the contributions of these elements when the different echinoids are compared (Figs. 23 & 24). For *Diadema*, spines comprise approximately 60%, corona 25% and lantern 15% of the weight of the fraction (Fig 23A). This contrasts with *Echinometra* (Fig. 23B) where the corona comprises approximately 50%, spines 35% and lantern 15% of the weight of the fraction. The results for *Eucidaris* resemble those for *Diadema*, with spines comprising approximately 65%, corona 25% and lantern 10% of the weight of the fraction (Fig. 24A). Finally, the >2 mm fraction of tumbled *Tripneustes* skeletons is, by weight, approximately 80% coronal material, 10% spines and 10% lantern elements (Fig. 24B). In

A

Diadema



B

Echinometra

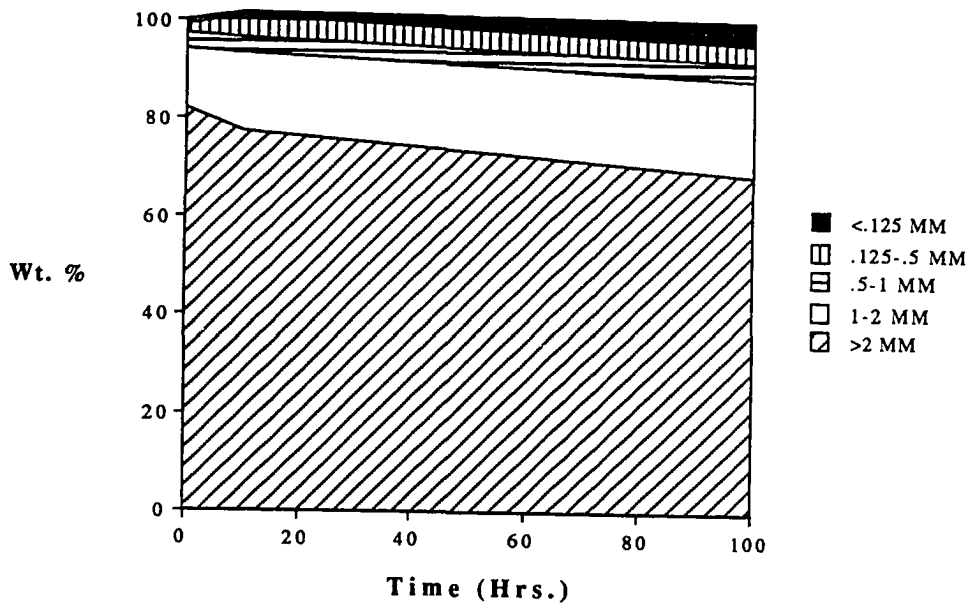
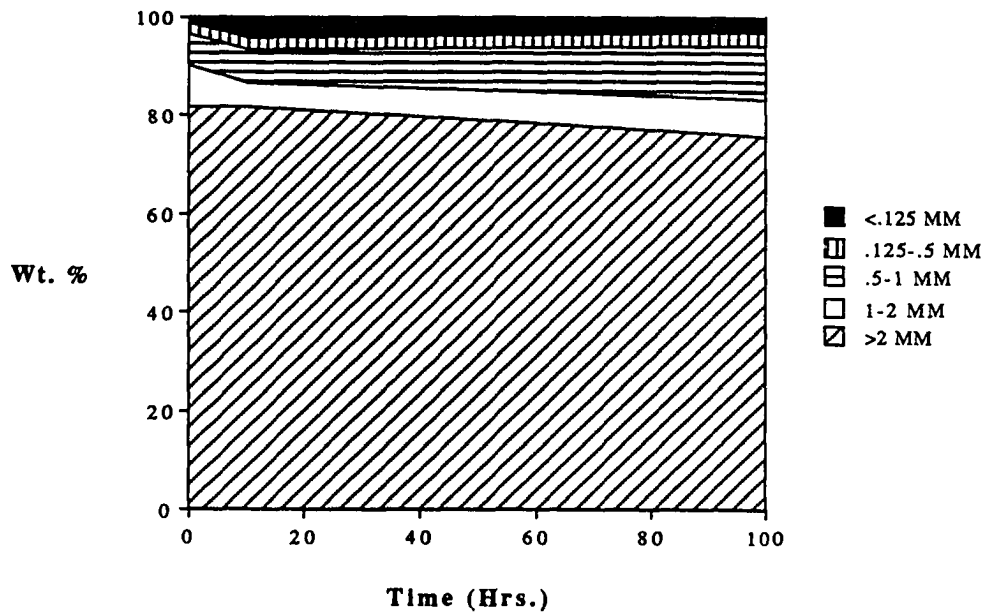


Figure 21-- The distribution of echinoid skeletal elements into the discriminated size fractions as a function of tumbling time. Values are means of five trials. A] *Diadema antillarum*; B] *Echinometra lucunter*.

A

Eucidaris



B

Tripneustes

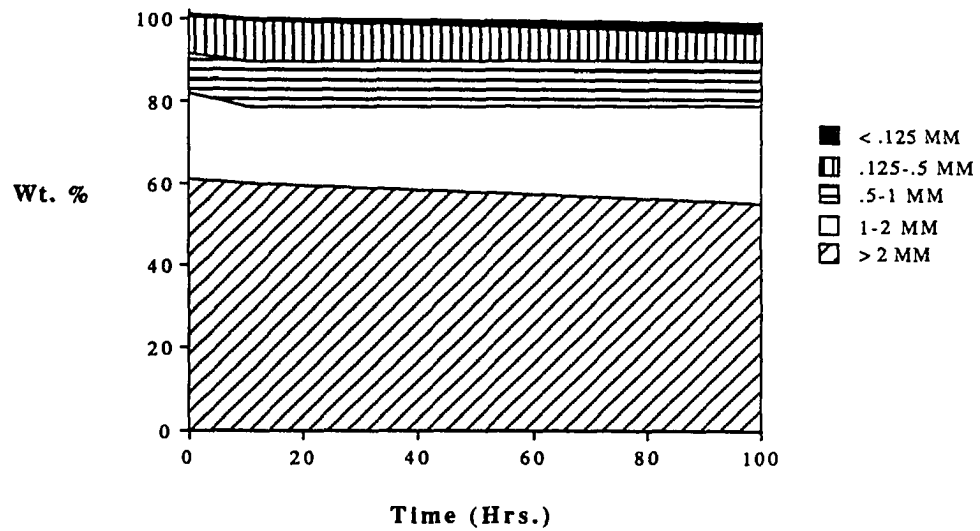


Figure 22--The distribution of echinoid skeletal elements into the discriminated size fractions as a function of tumbling time. Values are means of five trials. A] *Eucidaris tribuloides*; B] *Tripneustes ventricosus*.

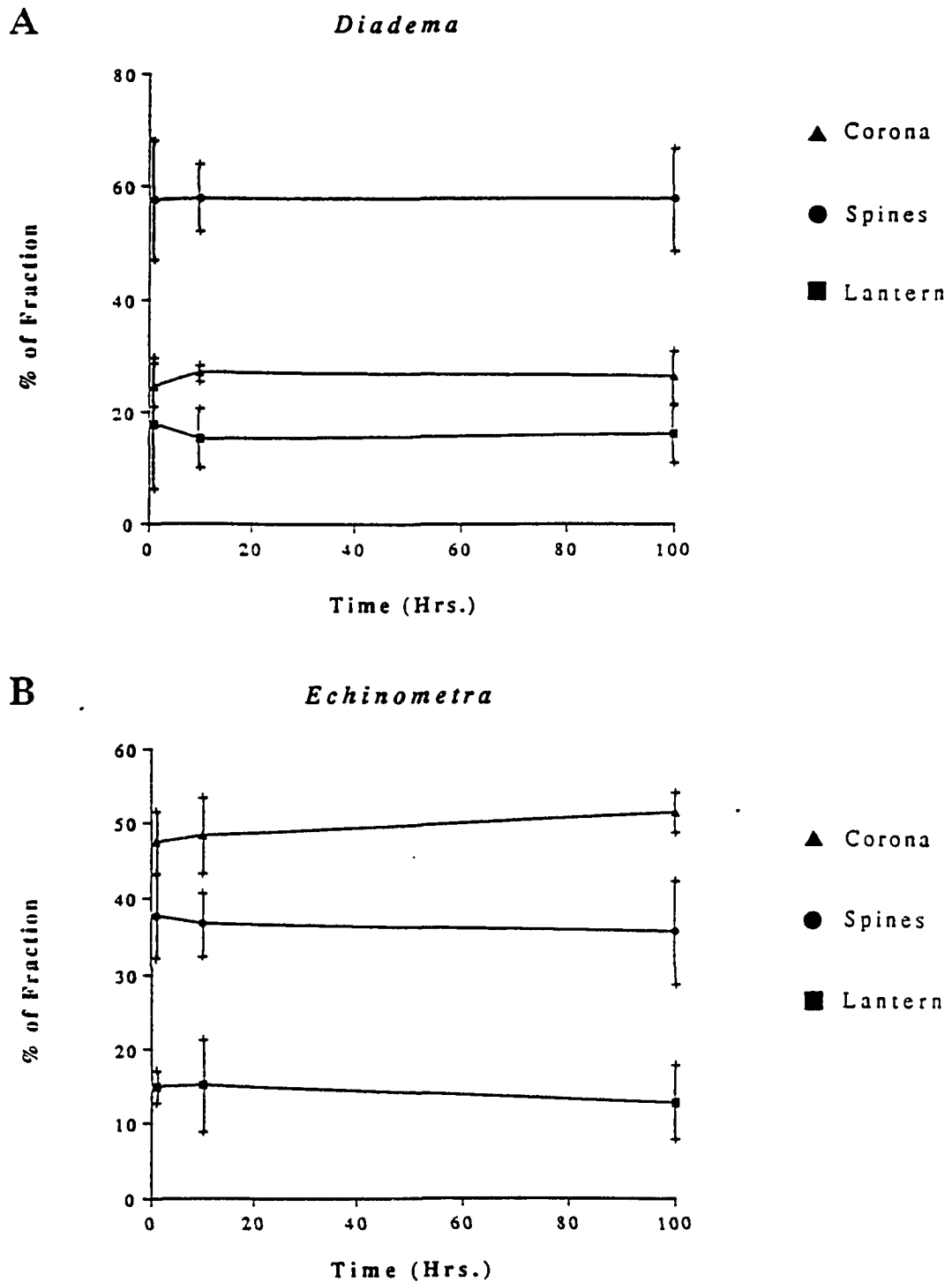


Figure 23 -- Composition of the >2 mm size fraction. Error bars represent 95% confidence intervals (N = 5) about the mean. A] *Diadema antillarum*; B] *Echinometra lucunter*.

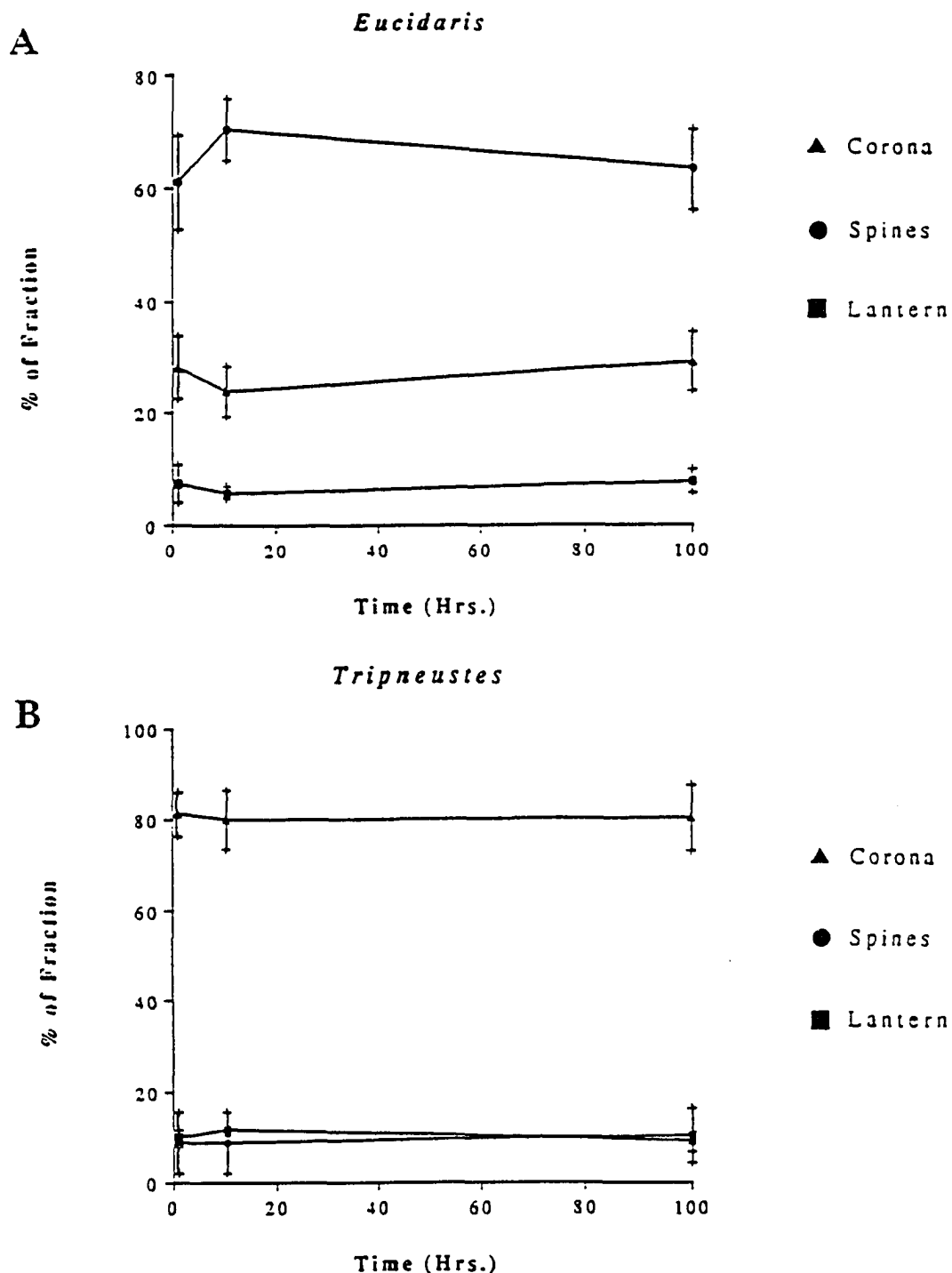


Figure 24 -- Composition of the >2 mm fraction. Shaded areas represent 95% confidence intervals (N = 5) about the mean. A] *Eucidaris tribuloides*; B] *Tripneustes ventricosus*.

the sense that coronal material predominates, the results for *Tripneustes* resemble *Echinometra*.

Degree of Breakage-- Differences in the degree of breakage incurred by the different echinoid species became apparent immediately as coronas of *Diadema* were observed to disarticulate within a few minutes of tumbling whereas other echinoid coronas exhibited variations in durability, some remaining intact for periods of 100 hours. Differences in the magnitude of disarticulation are qualitatively expressed in Figures 25 and 26. Quantitative assessment of breakage was obtained by calculating a coefficient of breakage for coronal material present in the >2 mm size fraction. The coefficient was calculated according to the formula:

$$CB = \frac{N}{W} * \frac{1}{WP}$$

where N = the number of pieces of corona in the >2 mm size fraction, W = the weight of those coronal pieces and WP = the weight percent of the coronal pieces in the >2 mm fraction relative to the entire echinoid skeleton. Higher coefficient values represent relatively more breakage. The inclusion of the second term ($\frac{1}{WP}$) normalizes the coefficient for differences in test size. For example, a small corona could conceivably break into many pieces that were less than 2 mm in size. In an extreme case, suppose only one coronal plate remained in the >2 mm size fraction. Calculating the coefficient simply by using

$$\frac{N}{W}$$

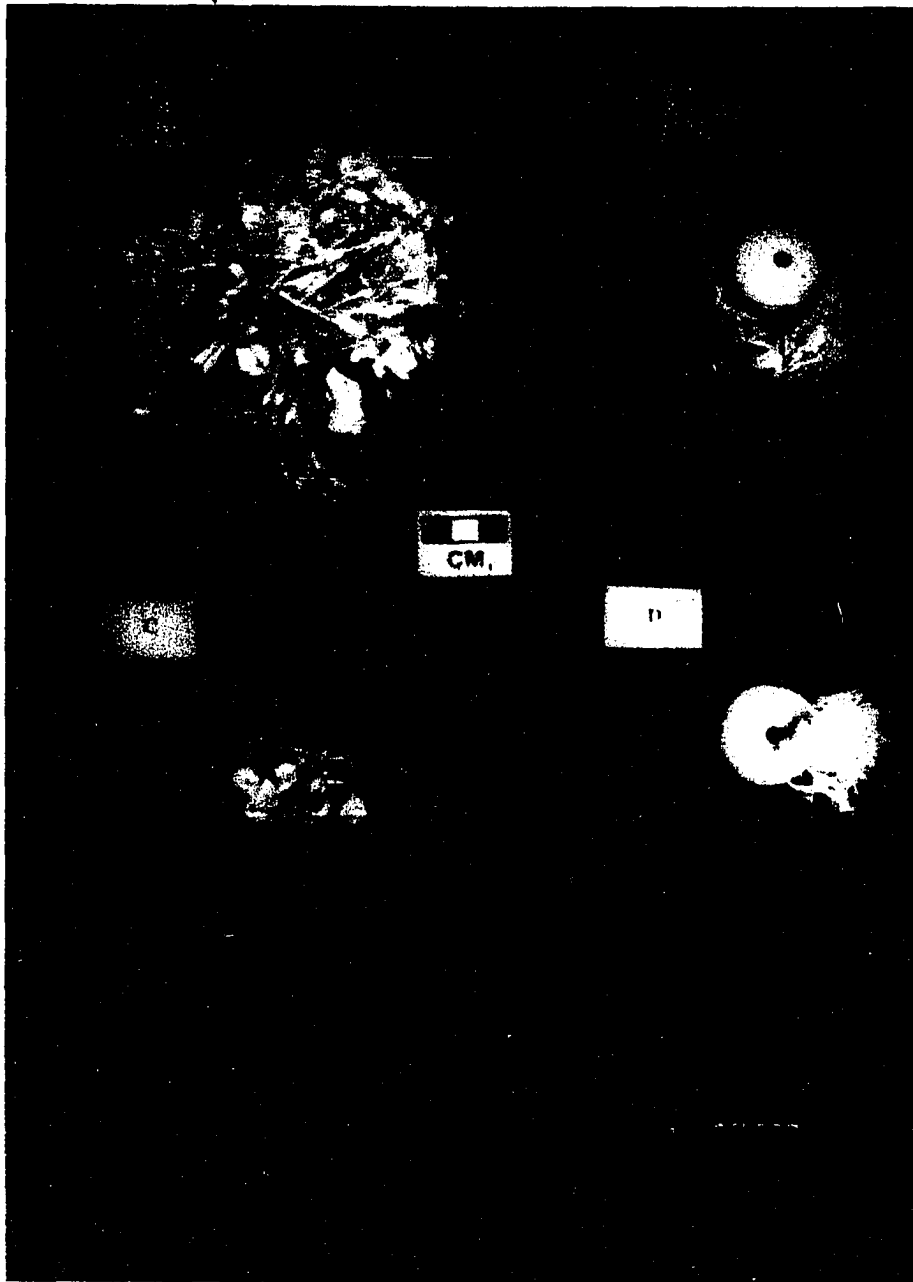


Figure 25 -- Echinoid specimens after 1 hour of tumbling. A) *Dia-*
dema antillarum; B) *Echinometra lucunter*; C) *Eucidaris tribuloides*; D)
Tripneustes ventricosus.

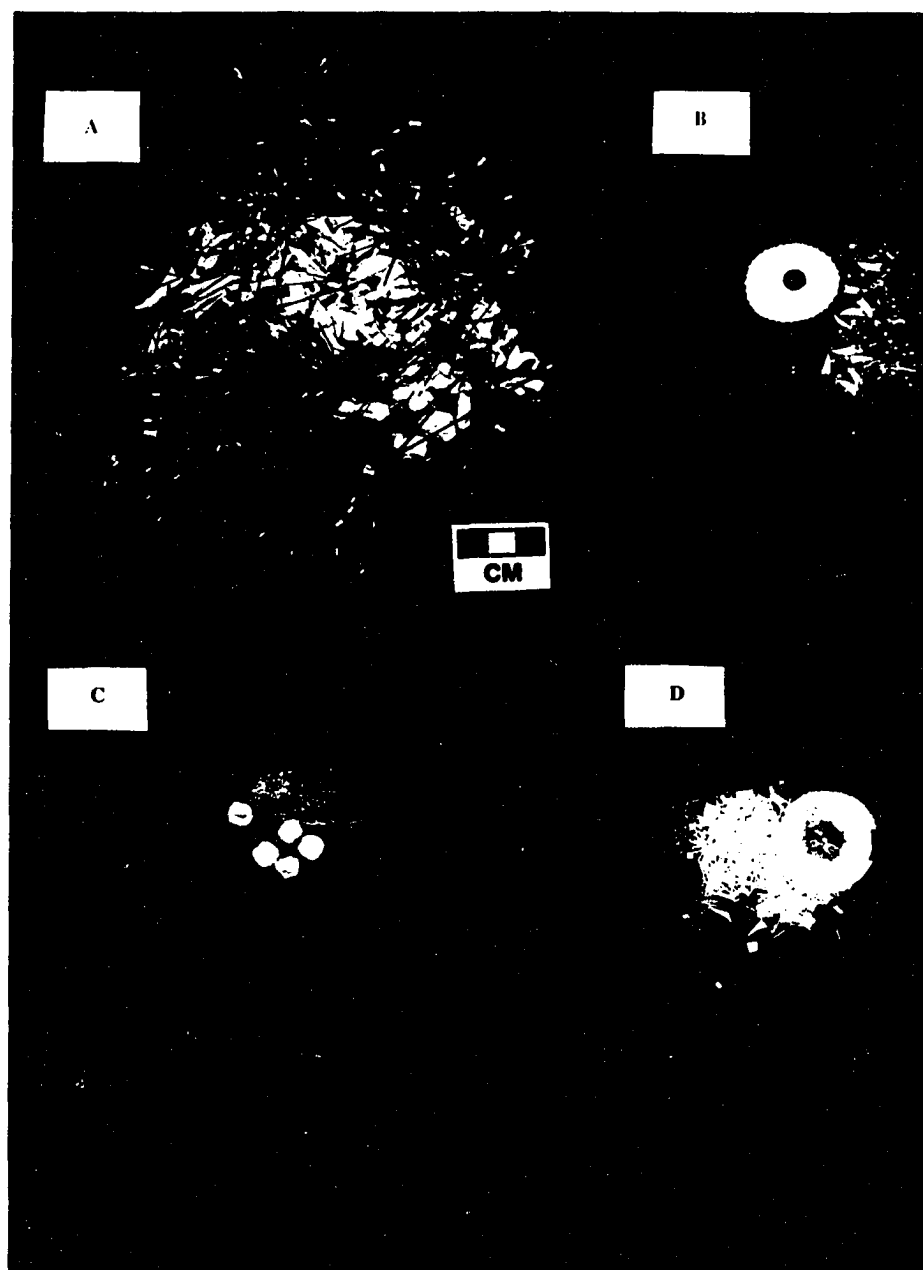


Figure 26 -- Echinoid specimens after 100 hours of tumbling. A) *Diadema antillarum*; B) *Echinometra lucunter*; C) *Eucidaris tribuloides*; D) *Tripneustes ventricosus*.

would yield a small value and an inaccurate representation of the amount of breakage. However, the weight percent of that coronal plate would be quite small. Thus, incorporating

$$\frac{1}{WP}$$

into the formula would increase the coefficient to represent the high degree of breakage.

Although there is no significant increase in coronal breakage with increased tumbling time (Fig. 27), significant ($\alpha=.05$) differences exist between the echinoid species in the amount of breakage incurred (Fig 28). *Diadema* coronas underwent the most breakage, with a mean coefficient value for all tumbling periods of 173.47 +/- 45.79. *Echinometra* underwent the least amount of coronal disarticulation, with a mean coefficient value of 4.65 +/- 2.31 for all tumbling intervals. *Eucidaris* and *Tripneustes* fell between these two extremes. *Eucidaris* exhibited relatively high amounts of breakage over all tumbling periods, with a mean coefficient value 89.36 +/- 26.25. Coronas of *Tripneustes* suffered less damage than *Eucidaris* and more damage than *Echinometra*. The mean coefficient obtained over all tumbling intervals for *Tripneustes* was 34.31 +/- 25.51.

Taphonomic Predictions based on Laboratory Work

Many (perhaps most) echinoids die from conditions that inflict little skeletal damage. These include senescence, desiccation, temperature fluctuations and disease (see Smith, 1984, for a review). Even death by predation, which normally accounts for a small proportion of deaths in a population (Himmelman & Steele, 1971;

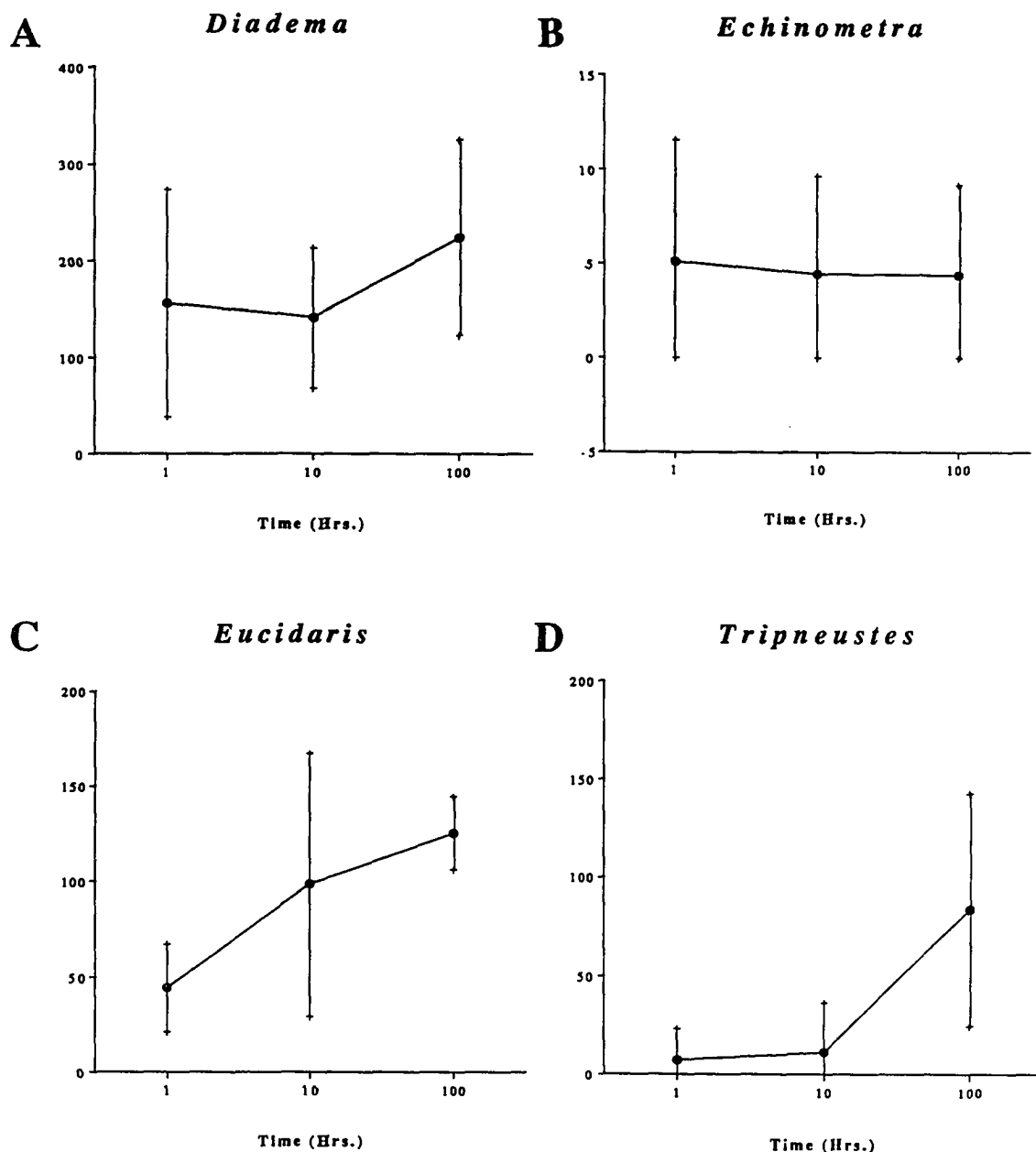


Figure 27 -- Breakage coefficients calculated for test material >2 mm in size plotted as a function of tumbling time. Error bars represent 95% confidence intervals about the mean. For all echinoids, N = 5. A] *Diadema antillarum*; B] *Echinometra lucunter*; C] *Eucidaris tribuloides*; D] *Tripneustes ventricosus*. Note the change in scale of the vertical axis for both *Diadema* and *Echinometra*.

Coefficients of Breakage: All Echinoids

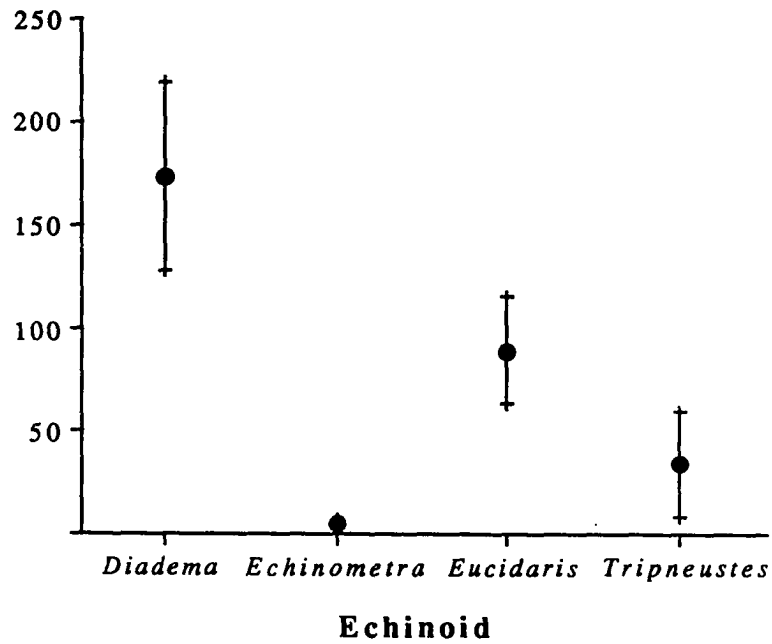


Figure 28 -- Breakage coefficients calculated for test material >2 mm in size for each echinoid over all tumbling trials. For each echinoid, N = 15. Error bars for *Echinometra* are subsumed by the size of the data point plotted.

Hendler, 1977; Smith, 1984), can produce relatively intact coronas, as attested to by the condition of dead *Tripneustes* in Graham's Harbor. In natural systems, therefore, intact dead carcasses are probably the rule at the start of the post-mortem interval.

The sequence of disarticulation observed during anaerobic decay is similar to that observed by Schäfer (1972) and Kidwell & Baumiller (1989) (for aerobic and both aerobic and anaerobic conditions, respectively) and suggests that, in the absence of physical and/or biological disturbance, regular echinoids disarticulate in a relatively predictable sequence in both oxygen regimes. Lack of disturbance, however, may be limited to quiet, anoxic environments, where biological activity is restricted or prohibited. The condition of fossil regular echinoids preserved in such environments may then reproduce the states of disarticulation observed under controlled circumstances. This hypothesis has been initially tested by Kidwell & Baumiller (in press) who identified all experimental states of carcass disintegration discriminated in the laboratory among the regular echinoids housed in the white chalk collections (Cretaceous) of the British Museum of Natural History.

More specifically, the results of the decay experiments suggest that although the pattern of resulting skeletal disarticulation is similar for a variety of regular echinoids, its timing is different for the three echinoids observed in this study. *Diadema* disarticulates rapidly, with noticeable spine loss within 24 hours and degradation into interambulacral fragments after seven days. However, *Eucidaris* exhibits a "disarticulation threshold" of seven days before which the skeletons remain fairly intact. Once the threshold is reached, how-

ever, spines are lost and the corona rapidly degrades into interambulacral fragments. Coronas of *Echinometra* never become fragmented, but the timing of skeletal disarticulation is intermediate to *Diadema* and *Eucidaris*: Specimens incurred noticeable spine loss after three days and further degradation to intact, empty coronas after seven days.

The use of the results of the decay experiments for making general taphonomic predictions (i.e. in aerobic environments) is justified because it has been suggested that the effects of aerobic and anaerobic decay are indistinguishable for macroinvertebrate carcasses (Plotnick, 1986; Kidwell & Baumiller, in press). Moreover, for proteinaceous skeletons, Allison (1988) found that anoxia in itself is ineffective as a conserving medium. The primary importance of anoxia was not in retarding decay, but in promoting early mineralization after initial decay.

Few of the observations made using time-lapse cinematography can be applied to predictions on the condition of fossil echinoid material. It should be noted, however, that the concept of suspension transport of echinoderms has received attention in the taphonomic literature. The idea was introduced with work on crinoidal facies (Müller, 1955; Ruhrmann, 1971a,b; Seilacher, 1973) and has been much debated in both the literature (e.g. Ruhrmann, 1971b; Blyth Cain, 1968; Meyer & Meyer, 1986) and in anecdotal observations. The structure of stroma is thought to facilitate the entrapment of gas bubbles produced by the decay of tissues within it (stroma). However, examination of the time-lapse films reveals that the echinoid coronas never become buoyant. Thus, buoyant trans-

port as a result of decay gases alone should not occur during the first 6 days of decay. The apparent "pinning" of the echinoids by the algal jackets probably did little to prevent floating since none of the 18 echinoid specimens used in the decay experiments developed algal jackets or floated.¹ Echinoids that die from desiccation have been observed, in nature, to float (Reyment, 1986), but this is a consequence of air entering the test rather than a result of the accumulation of gas bubbles in the stereom (Smith, 1984).

Results of transect work at all three localities and burial experiments conducted on the back reef in Smuggler's Cove indicate that intact dead echinoids do not decay slowly and undisturbed in the reef and near-reef environments under study, but instead rapidly become bleached carcasses. It is in this condition that they are exposed to subsequent biostratigraphic processes. Therefore, carcasses of echinoids in natural systems can be expected to disintegrate into various sizes in a manner similar to that observed during tumbling experiments, primarily as a function of coronal rigidity and the morphology of spines, test and lantern elements.

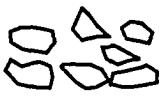
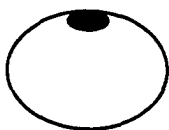
Results of the tumbling experiments indicate that after organic tissues have been removed, physical disturbance of the echinoids reduced the majority of the skeleton to elements >2 mm in size. In terms of recognizing echinoids in the fossil record, a size of 2 mm is a logical cut-off value, since fragments smaller than 2 mm would prob-

¹ Two specimens of *Diadema* were observed to float during the decay experiments, but they did so at the outset of the experiment (i.e. as a result of being frozen) before any organic decay had begun.

ably go undetected in outcrop and are unlikely to retain features that permit identification at lower taxonomic levels.

Coronal Material--Tumbling results indicate that the amount of coronal disarticulation varies significantly between the echinoids (Fig. 28). Style of disarticulation was evaluated semi-quantitatively using a scale developed on the basis of observations of all specimens; four states of disarticulation are discriminated (Table 1, Figure 29). Coronas of *Diadema* occur as fragments less than the size of an interambulacrum (State 4). Auricles are intact and connected to ambulacral plates. Coronas of *Echinometra* are usually whole (State 1) but are occasionally missing a few adapical test plates (State 2) and occur once as whole interambulacra separated along ambulacral sutures (State 3). *Eucidaris* are most commonly present in State 3 and occasionally present in State 4. Finally, coronas of *Tripneustes* are relatively evenly distributed among States 1, 2 and 4, as manifested in the wide range of values obtained for the breakage coefficient discussed earlier.

A quantitative test of the differences in the amount of coronal disarticulation suffered by each echinoid was performed using the Kolmogorov-Smirnov two-sample test on the frequency distributions of the states of disarticulation distinguished above. The test determines whether histograms generated by two frequency distributions represent samples from significantly different populations. Results of testing the distributions obtained for each echinoid corroborate the conclusions of Smith (1980, 1984) that differences in sutural interlocking occur at higher taxonomic levels. The echinoids may be divided into two groups, those with relatively extensive interlocking

4		15		4	5
3			1	11	4
2			3		
1			1 1		6

State	<i>Diadema</i>	<i>Echinometra</i>	<i>Eucidaris</i>	<i>Tripneustes</i>
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Table 1 -- Distribution of test material >2 mm in size into four states of disarticulation and the frequency with which these states occurred for each echinoid. N = 15.

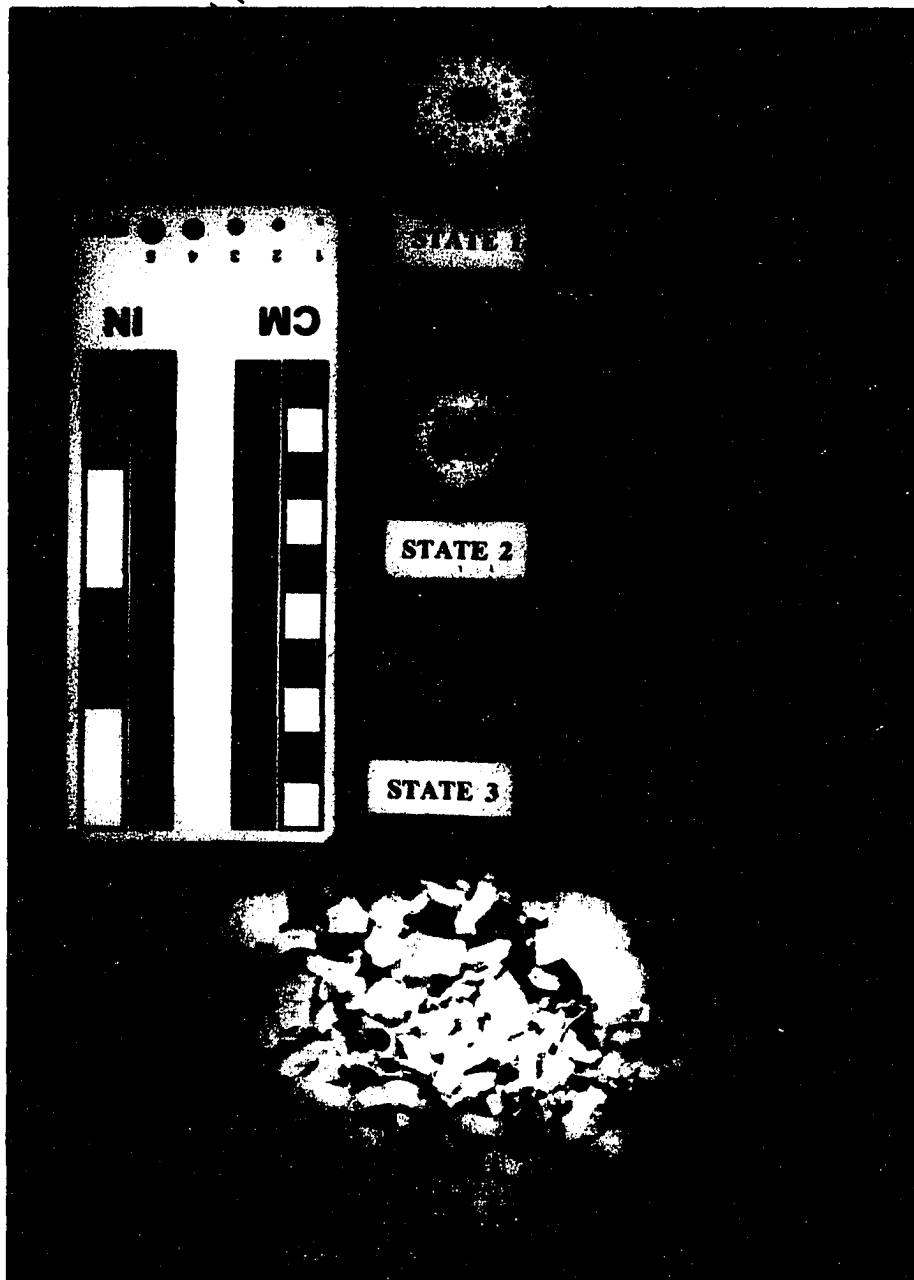


Figure 29 -- Four states of coronal breakage discriminated from the results of tumbling experiments. State 1) intact corona; State 2) coronal fragment larger than an interambulacrum; State 3) corona split along ambulacral plate sutures resulting in distinct interambulacral fragments; State 4) coronal fragments smaller than an interambulacrum. States 1, 2, 3 and 4 correspond to taphonomic codes 2, 6, 6 and 7, respectively. Thus only taphonomic codes 2, 6 and 7 were used for statistical comparison of tumbling results to literature-derived data.

of stereom across plate sutures (*Echinometra* and *Tripneustes*), and and those with little or no sutural interlocking (*Diadema* and *Eucidaris*). There are no significant ($\alpha = .05$) differences in the distribution of states of disarticulation exist within each group (Table 2). Significant differences do exist, however, between the frequency distribution obtained for *Diadema* and those obtained for both *Echinometra* and *Tripneustes*. Additionally, the distribution of states of disarticulation obtained for *Eucidaris* is significantly different than that obtained for *Echinometra*, but not for *Tripneustes* (however, the test of the null hypothesis was very close: comparison of histograms generated for *Eucidaris* and *Tripneustes* produced a value of $D = .400$ which was compared to $D(.05) = .496$ -- see Table 2). Characterization of the differences in coronal disarticulation in this fashion is useful in that it provides predictions of taphonomic overprint that can be tested quantitatively.

Additional Skeletal Material-- Spines of *Diadema* and *Eucidaris* are the primary contributors to the >2 mm size fraction. *Diadema* possesses large numbers of spines which contributed numerous (500-600) intact and broken pieces to the fraction. *Eucidaris* possesses fewer, more robust spines, which are commonly encrusted and contributed fewer (25-50) pieces to the fraction. Thus, spine abundance is responsible for the pattern observed for *Diadema*, whereas spine weight is responsible for producing that observed for *Eucidaris*. Spines of *Echinometra* are secondary contributors to the >2 mm fraction because they are relatively small and few in number. *Tripneustes* spines are exceedingly small; they were therefore minor contributors to the >2 mm size fraction.

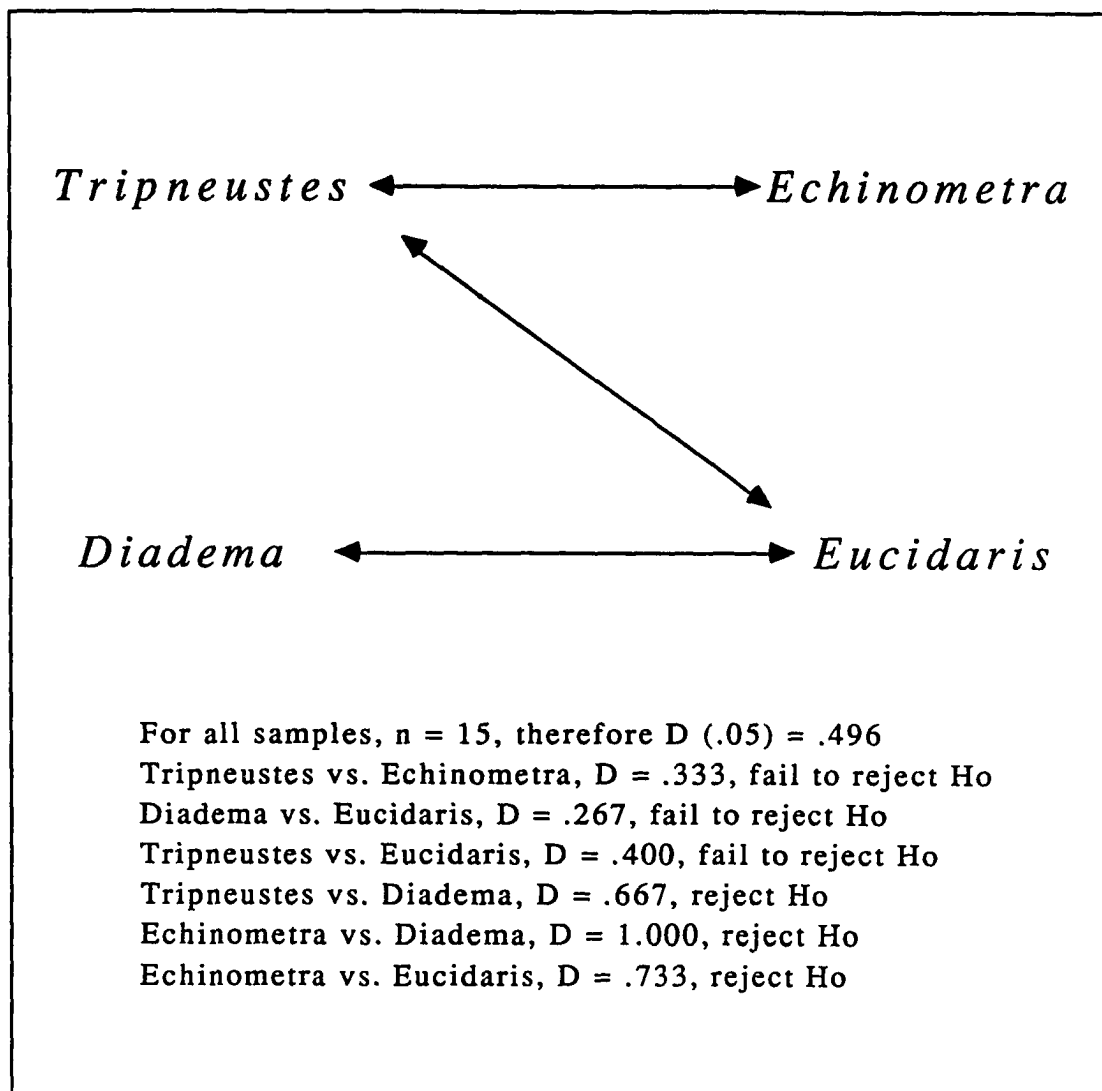


Table 2 -- Schematic representation of statistically significant and insignificant differences in the frequency distribution of states of disarticulation distinguished on the basis of tumbling experiments; where H_0 is that the histograms represent samples from statistically similar populations. Differences for species connected with lines are not significant at the $\alpha = .05$ level.

The contribution of Aristotle's Lantern material to the >2 mm fraction is relatively minor for all echinoids, and presumably mirrors their percent contribution in the initial skeleton. The elements present were rarely broken and commonly consisted of the ten demipyramids and, occasionally, teeth. For all echinoids, lantern elements were intact in all three size fractions studied. This suggests that after initial disarticulation by bleaching, tumbling had no effect on the condition of lantern material. The size of the various lantern elements (e.g. demipyramids, teeth, compasses, epiphyses) dictated their size distribution.

Consideration of all experimental results yields the following predictions of the condition of fossil echinoids in the absence of unusual taphonomic circumstances:

1. *Diadema*-- Tumbling results indicate that fossil occurrences of this echinoid will usually consist of fragmented material composed of spines and, secondarily, coronal material. Individual elements of the lantern, particularly demipyramids and teeth, may also be present. Observations of the sequence of decay and disarticulation suggest that occurrence of intact coronas with spines attached does not necessarily indicate anoxic decay but rather exceedingly rapid cessation of all decay (within 24 hours). The occurrence of intact bare coronas implies that decay was halted less than one week after death.

2. *Echinometra*-- Tumbling results demonstrate the durability of the echinometrid corona, and intact coronas (without peristomial or apical plates) are likely to occur (possibly transported) as fossils. Spines of echinometrids will be recognizable as fossils but not as

abundantly as diadematoid spines; lantern elements may also be present. Observations of the timing of disarticulation as a consequence of decay suggest that individuals preserved with spines attached could not have decayed longer than five days. No predictions can be made as to the timing of disarticulation of the corona.

3. *Eucidaris*-- Results of tumbling indicate that the robust spines of *Eucidaris* will be the most common representative of this echinoid in the fossil record. Coronas, when present, are most likely to be preserved as complete interambulacral segments that have broken along their ambulacral sutures. Coronal fragments may also occur. Lantern elements will rarely be preserved as fossils. Observations of decay suggest that, of the echinoids studied, *Eucidaris* is most likely to occur with spines attached. Such occurrences, as well as that of intact empty coronas imply decay of no longer than one week.

4. *Tripneustes*-- The relatively minor contribution of spine and lantern material to the >2 mm size fraction indicates that recognizable fossils of this echinacean will be composed almost entirely of coronal material. Moreover, tumbling results suggest a wide variation in condition of the material, including intact coronas lacking peristomial or apical plates, large sections of the corona and isolated test fragments.

5. In general, the preservational styles of *Echinometra* and *Tripneustes* will be similar, and those of *Diadema* and *Eucidaris* will be similar. However, significant differences in style of preservation can be expected to occur if either echinacean is compared to *Diadema*, and if *Echinometra* is compared to *Eucidaris*.

CHAPTER 4: SYNTHESIS

Taphonomic Predictions

The purpose of this chapter is to synthesize the results of field and laboratory analyses into predictions of taphonomic overprint, and to test the predictions. Examining exposed Pleistocene reef and near-reef facies for fossil occurrences of the same species studied in the field and laboratory experiments allows for a specific test of the predictions derived for each of them. Determination of the preservational style of the occurrences of all type species described for each family in the literature provides a general test of the predictions extended to each family in that it includes fossil occurrences in many different facies representing many different environments.

The preceding chapter has demonstrated that, in the environments studied, echinoids are rapidly reduced to two constituents which are then exposed to subsequent post-mortem processes: a corona devoid of organic matter and disarticulated skeletal elements (Aristotle's Lantern, spines and apical and peristomial plates). Consequently, the recognition of fossil material is largely a function of coronal rigidity and identifiability of individual skeletal elements. Taxonomic control of both coronal rigidity and the relative contribution of various skeletal elements to a recognizable (>2 mm) size fraction has been demonstrated. Moreover, degree of sutural interlocking and the morphology of lantern elements for each species are consistent at the familial level (Smith, 1980, 1981; Durham et al., 1966). Thus the following predictions of taphonomic overprint, summarized

in Table 3, are extended to each family represented by the species studied in the field and laboratory.

Cidaridae -- Fossils assigned to this family will occur, in order of decreasing relative frequency, as skeletal fragments (taphonomic code 7), fragments of corona larger than one interambulacrum in size (taphonomic code 6) and as intact coronas with no spines attached (taphonomic code 2). The frequency with which fragments (code 7) occur will be much higher than either of the two other preservational styles. The majority of the fragments described will be spine material followed by coronal material. Isolated lantern elements, apical plates and peristomial plates will rarely be described.

Diadematidae -- Diadematid fossils will be described primarily on the basis of fragmented material (code 7). Other taphonomic categories will be rare. The majority of the fragmented material will be spines followed by corona. Isolated lantern elements will be moderately rare in the data set; apical and peristomial plates will be rare.

Toxopneustidae -- In order of decreasing relative frequency, fossils will occur as intact bare coronas (code 2), fragments of corona larger than one interambulacrum in size (code 6) and as skeletal fragments (code 7). Skeletal fragments will almost entirely consist of coronal material. Unlike the *Cidaridae*, which are also predicted to exhibit these three styles of preservation, the distribution of fossil toxopneustids into the three taphonomic categories will be relatively equitable. Isolated spines, lantern elements, apical and peristomial plates will be described very rarely.

Echinometridae -- Fossils assigned to this family are predicted to occur as either intact coronas with no attached skeletal elements

<u>Family</u>	<u>Spines</u>	<u>Corona</u>	<u>Lantern</u>
Diadematidae	Abundant as fossils, both as whole and broken pieces.	Moderately abundant, but only as fragmented remains. Individual plates or groups of plates broken along sutures.	Moderately rare. Occurring as individual intact elements, primarily demipyramids and teeth.
Echinometridae	Moderately abundant as whole pieces.	Intact corona without apical system or peristome abundant. Large coronal fragments moderately rare. Coronal fragments rare.	Moderately rare. Occurring as individual intact elements, primarily demipyramids and teeth.
Toxopneustidae	Whole or broken pieces rare.	Intact corona without apical system or peristome, large sections of interambulacra, and test fragments all moderately abundant.	Rare.
Cidaridae	Intact primary spines very abundant.	Large sections of interambulacra abundant. Intact corona without apical system or peristome moderately abundant. Coronal fragments moderately rare.	Rare.

Table 3 -- Summary of taphonomic overprint predicted to affect fossil occurrences of species belonging to the four families under study. For all echinoids, the presence of apical or peristomial plates is expected to be very rare.

(code 2) or as large pieces of corona (code 6). Intact coronas will occur more frequently than partial coronas. Fragmented material (code 7) will occur rarely and be composed primarily of spines. Isolated lantern elements, apical and peristomial plates will be rare.

Differences between groups -- The families under study will fall into two groups on the basis of the frequency distribution of the taphonomic codes that I have discriminated for the literature data. Families Echinometridae and Toxopneustidae comprise one group; Families Diadematidae and Cidaridae comprise the second group. The distribution of preservational styles will be more similar within the defined groups than between them.

The Cockburntown Reef: A First Test of Taphonomic Predictions

Because of its Pleistocene age (White *et al.*, 1984), the fossil reef exposed at Cockburntown, San Salvador represents a logical "first step back" to test the taphonomic predictions derived from work in the field and laboratory. The same species of echinoids studied in the Recent existed in the Pleistocene and, with the exception of the lagoonal environment encountered in Graham's Harbor, the facies studied at Cockburntown are considered analogous (White *et al.*, 1984) to the environments encountered along the transects.

Along the three transects constructed in the Cockburntown quarry, a total of 13 m² of coral-rubblestone (backreef/reef) facies and 9 m² of calcarenite (shallow subtidal) facies were studied for the presence of echinoids. Fossil echinoids of any kind were rarely observed. The most common occurrence were intact tests whose intensely weathered condition made taxonomic assignment difficult

but may have been the irregular holoctypoid *Echinoneus*. The coral rubblestone facies yielded one of these echinoids and one fossil *Eucidaris tribuloides* (Fig. 30A). The specimen of *Echinoneus* occurred as an intact corona without spines or apical system. Absence of lantern elements was not the result of any taphonomic process; only juveniles of this group possess an Aristotle's Lantern (Rose, 1978). The fossil *Eucidaris* was represented by a lone, complete spine. A fragment of a mellitid sand dollar was also present in the coral-rubblestone facies. The calcarenite yielded five additional *Echinoneus* occurring as intact empty tests without spines or apical system. Sand dollar fragments were present in two of the quadrats superimposed on the calcarenite bedding plane, as was an intact, bare corona of (probably) a spatangoid (Plate 30B).

Constituent particle analyses of thin sections reveal that echinoderms are minor contributors to the rock comprising all facies, averaging 0.21% of the constituents. Values for the percent of echinoderm grains counted did not exceed 0.55% for any of the samples obtained.

Consideration of the preservational style and frequency of occurrence of echinoids at Cockburntown supports the taphonomic predictions derived from field observations and laboratory experimentation in the following ways:

1. *Rare occurrence*- - Results of population censuses and field experiments predicted that fossil echinoids would be rare in facies analogous to the environments under study.

2. *Lack of Echinometra and Diadema*-- Assuming that these echinoids were both common components of tropical reef ecosystems

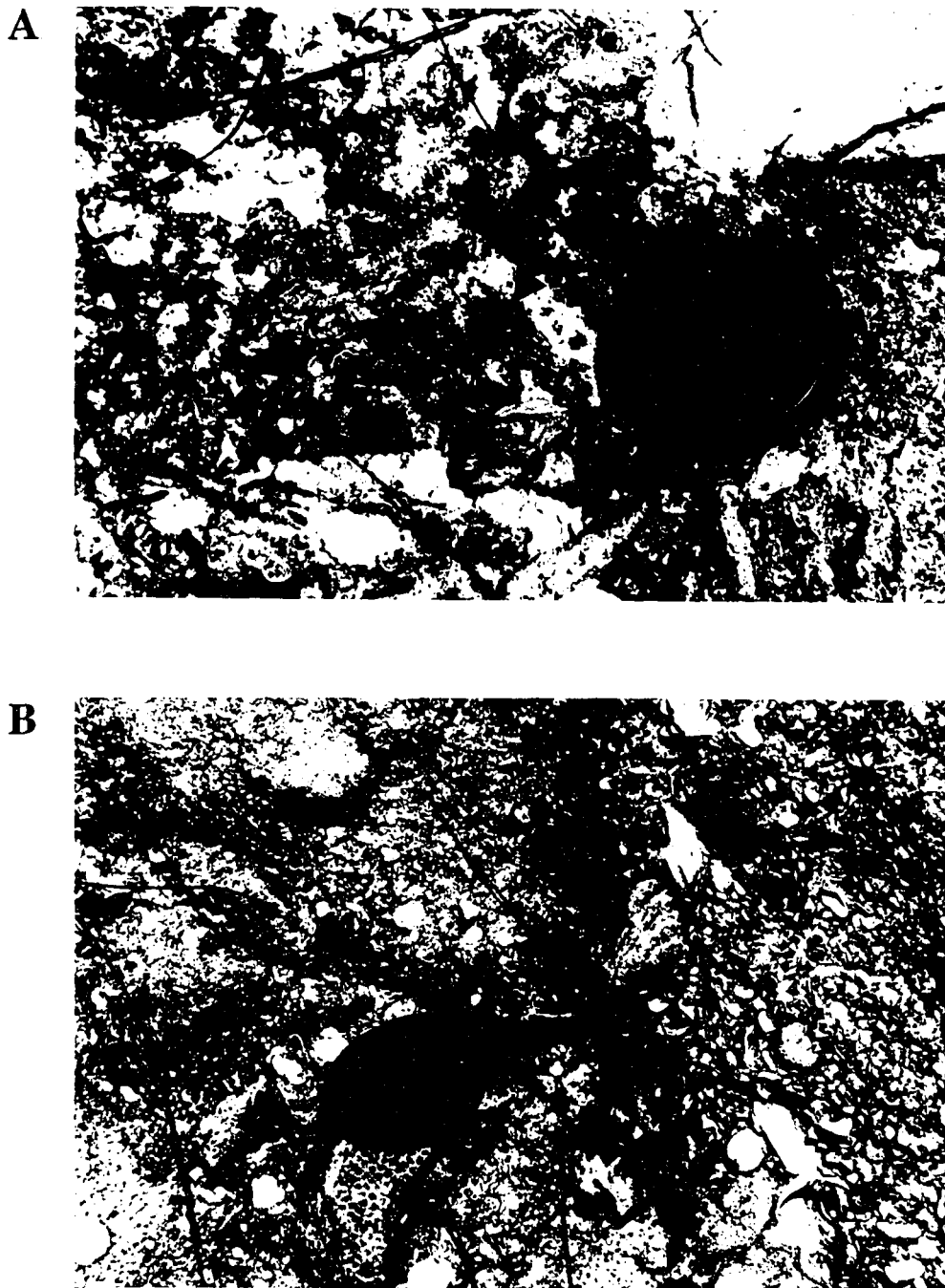


Figure 30 -- Examples of fossil echinoids observed in Pleistocene reef facies exposed near Cockburntown, San Salvador. A) Cidaroid spine (arrow) in the shallow subtidal facies; B) Corona of a probable spatangoid. Note abraded nature of the material.

during the Pleistocene, their absence from the reef facies is a result of the taphonomic factors delineated by the field and laboratory experiments. For both of these echinoids at the Cockburntown reef it may be stated that "lack of evidence is not evidence of lack", and additional bulk samples would be expected to contain spines and fragmented coronal material >2 mm in size.

3. *Condition of Eucidaris tribuloides*-- The presence of an intact spine of this echinoid agrees with predictions made from the results of tumbling experiments. Results of tumbling experiments suggest that examination of additional bulk samples from Cockburntown would yield additional spines.

4. *Minor constituent of the rock*-- Low values for the percentage of echinoderm material comprising the rock corroborate the results of constituent particle analyses performed on Recent sediment samples.

Echinoids are minor contributors to reef and near-reef facies analogous to the environments studied in the Recent. As a result, there is little direct evidence to support derived taphonomic predictions other than rarity of occurrence. The literature-derived data on preservational style provide a test of the predictions concerning the type of skeletal material likely to be present and its condition.

A Test of Taphonomic Predictions Using Literature-Derived Data

Through 1988, there have been 985 species of fossil echinoids described on the basis of fossil material and assigned to the families Cidaridae, Echinometridae, Toxopneustidae and Diadematidae. The distribution of the species into the families is not equitable (Table 4).

<u>Family</u>	<u>Subfamily</u>	<u>No. Genera</u>	<u>No. Species</u>	<u>No. Complete</u>	<u>% Complete</u>
Cidaridae	Cidarinae	13	609	443	72.7
	Rhabdocidarinae	9	195	131	67.2
	Stereocidarinae	4	74	54	73.0 (72.0)
	Goniocidarinae	1	14	12	85.7
	Histocidarinae	2	9	8	88.9
Diadematidae		6	32	21	65.6
Toxopneustidae		8	38	25	65.8
Echinometridae		6	9	8	88.9
TOTAL		60	981*	701**	71.4

Table 4 -- The distribution of fossil species in the database into higher taxonomic categories and the number of species for which taphonomic information is complete (stratigraphic information is complete for all species). The cidaroid Subfamily Ctenocidarinae, comprised predominantly of Recent genera, is excluded from the analysis since only one species has been assigned to that family on the basis of fossil material. Three species of cidaroid not assigned to any cidaroid subfamily by the original authors are also excluded.. The exclusion of these 4 species results in total numbers of species slightly different than reported in the text (delineated by * and **).

At the time of this writing, stratigraphic information has been compiled for all species. Taphonomic information has been compiled for 704 species, or approximately 71% of all known species. The completed subset of the entire database was sorted for each family on the basis of taphonomic condition (see Plate 6 for description of the taphonomic states discriminated).

Family Cidaridae

The cidaroids are the most diverse and abundant family for which preservation data were collected, comprising 91% of all echinoid species studied. A total of 648 type species of Cidaridae, representing 72% of known species, were characterized on the basis of their preservational style. Over 60% of the type species described fall into taphonomic code 7: skeletal fragments (Fig. 31). Intact whole tests with no skeletal elements attached (taphonomic code 2) comprise 20% of described type species. Broken coronal material at least as large as one interambulacrum comprises 10% of the type species. The remaining 10% of species are distributed into other taphonomic categories at relatively low numbers.

Further analysis of the type descriptions based on fragments indicates that 77% of the fragments described are isolated primary spines (Fig. 31). Coronal fragments (isolated plates broken along their boundaries or groups of plates still sutured but comprising a piece of corona no larger than an interambulacrum) represent an additional 13.2% of the species described. Isolated spines and coronal fragments occurring together are the material with which an additional 8.6% of type species are described. These three categories ac-

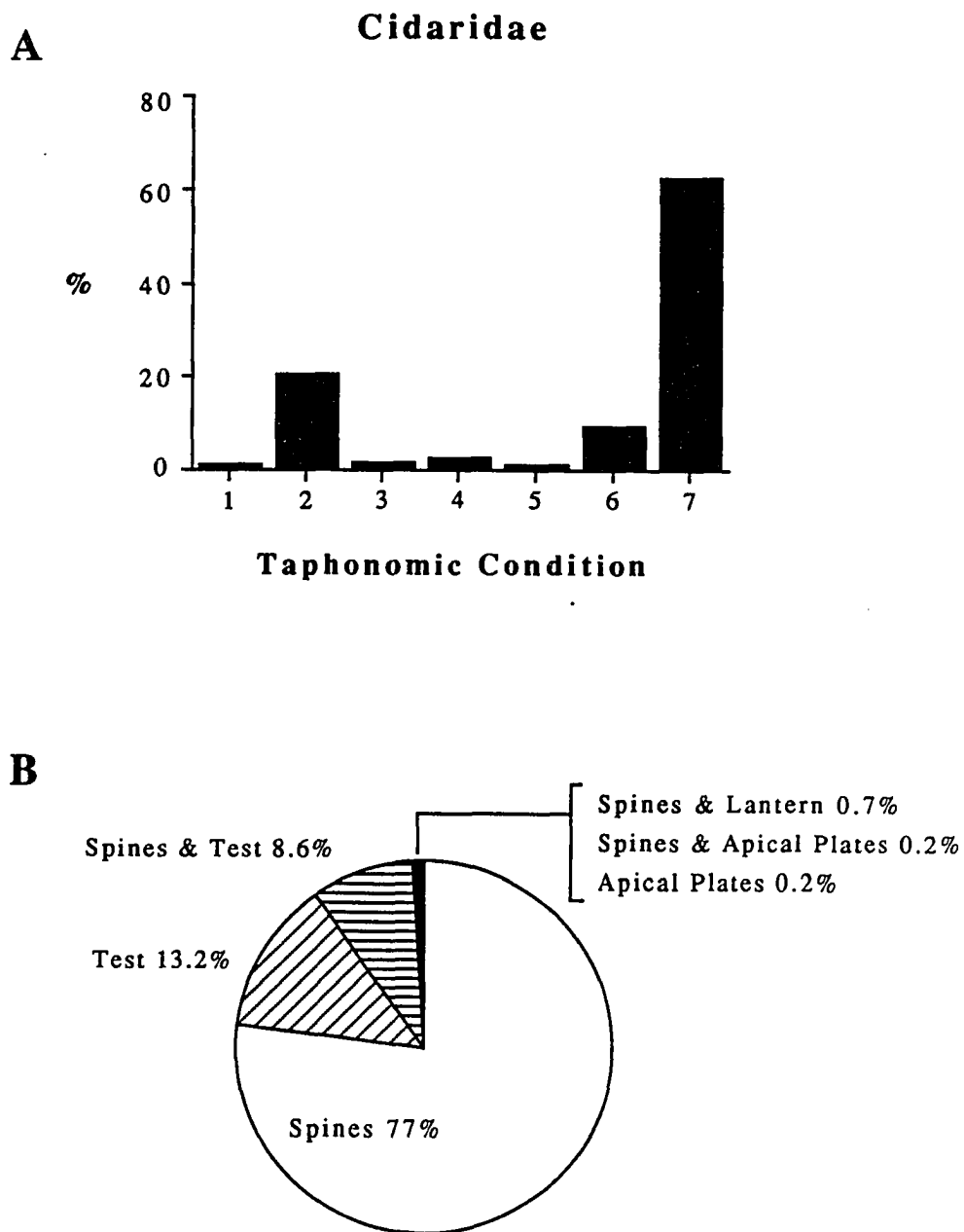


Figure 31 -- The distribution of preservational styles obtained from the literature for the Family Cidaridae. A) Relative frequency of each taphonomic code. B) Composition of taphonomic code 7 (skeletal fragments). For comparison with other families, frequencies of taphonomic codes are expressed as the percent of total species.

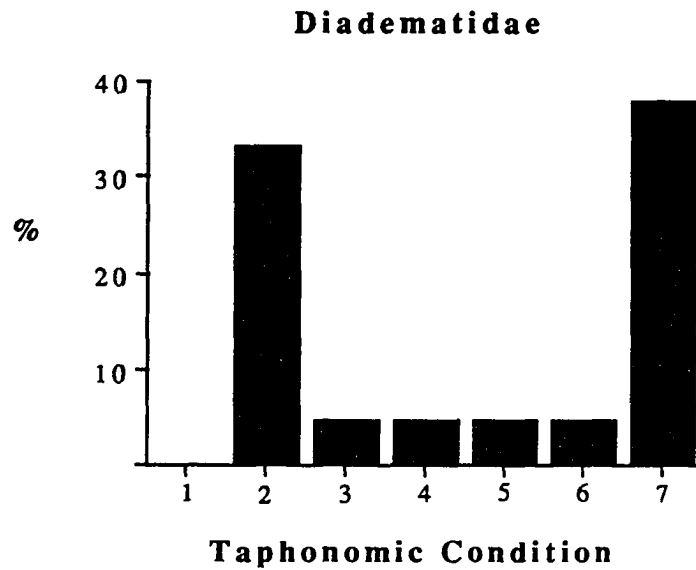
count for 98.8% of the species described on the basis of fragmented skeletal material. Isolated lantern elements are rarely described (3 species) as are isolated apical plates (2 species). Individual peristomial plates are not described in the literature examined.

Analysis of the fossil material on the basis of the presence or absence of selected skeletal elements (lantern, apical system and peristomial plates) reveals that they are rarely present with fossil cidaroid material. Of 650 fossil occurrences, lantern elements are described for 14 species. Three of these occurrences are as the isolated elements described above, while lanterns described for the remaining 11 species were inside (but not attached to) the peristome of an intact corona. Plates comprising the apical system were described as rarely as lantern elements, a total of 14 times. Two of the described occurrences were as isolated apical plates (described above) while the remaining 12 occurrences were complete apical systems, still attached to an intact corona. Finally, peristomial plates were exceedingly rare in the data set, described twice as attached to intact tests.

Family Diadematidae

A total of 21 species assigned to the Family Diadematidae were characterized on the basis of their preservation. The resulting data set represents 66% of known fossil species. Approximately 38% of the species examined are described on the basis of fragmented material (taphonomic code 7), the majority of which are spines (Fig. 32A, B). Intact tests with no skeletal elements attached (taphonomic code 2) are described for an additional 33% of examined species. With the exception of taphonomic code 1, each additional taphonomic condi-

A



B

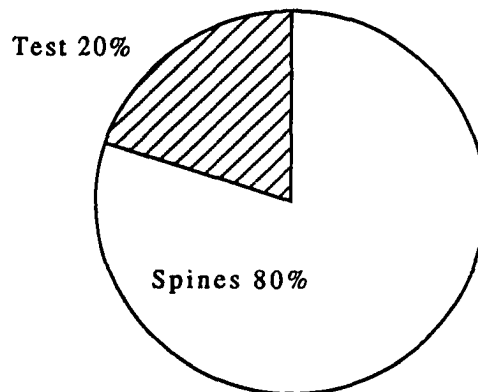


Figure 32 -- The distribution of preservational styles obtained from the literature for the Family Diadematidae. A) Relative frequency of each taphonomic code. B) Composition of taphonomic code 7 (skeletal fragments). For comparison with other families, frequencies of taphonomic codes are expressed as the percent of total species.

tion is represented by one occurrence in the data set analyzed.

Lantern elements, apical or peristomial plates do not occur as isolated skeletal elements.

Study of the presence/absence data collected for additional skeletal elements described for species of Diadematidae reveal that they rarely occur. Lantern elements are described once as occurring within the peristome of an intact corona. Apical plates are described twice, occurring as a complete apical system attached to an intact and a partial corona. Peristomial plates are not described in the data set.

Family Toxopneustidae

A total of 25 species (65.8% of known species) assigned to the Family Toxopneustidae were characterized according to preservational style. The condition of type fossil material is distributed into four taphonomic categories in relatively high percentages (Fig. 33). Forty percent of the species investigated are described on the basis of intact coronas with no attached skeletal elements (taphonomic code 2). Coronas that have been fractured or compressed but are otherwise complete and have no skeletal elements attached (taphonomic code 4) represent 28% of described species, while incomplete coronal material (taphonomic code 6) accounts for an additional 24% of the described species. Finally, isolated skeletal fragments (taphonomic code 7) have been used as type material for 8% of the described species. Fragments present are spines (for one species) and test plates (for one species). Analysis of presence/absence data obtained for additional skeletal elements reveals that the apical system has been described for 3 species, occurring

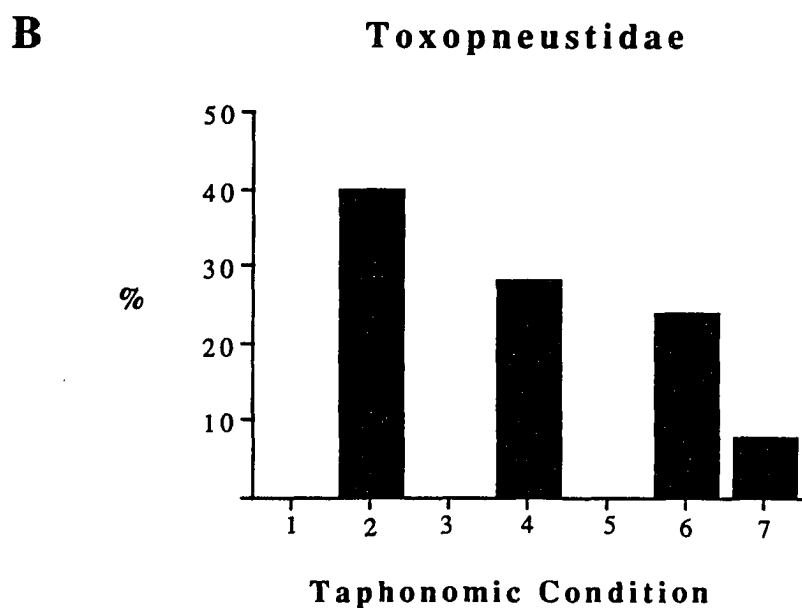
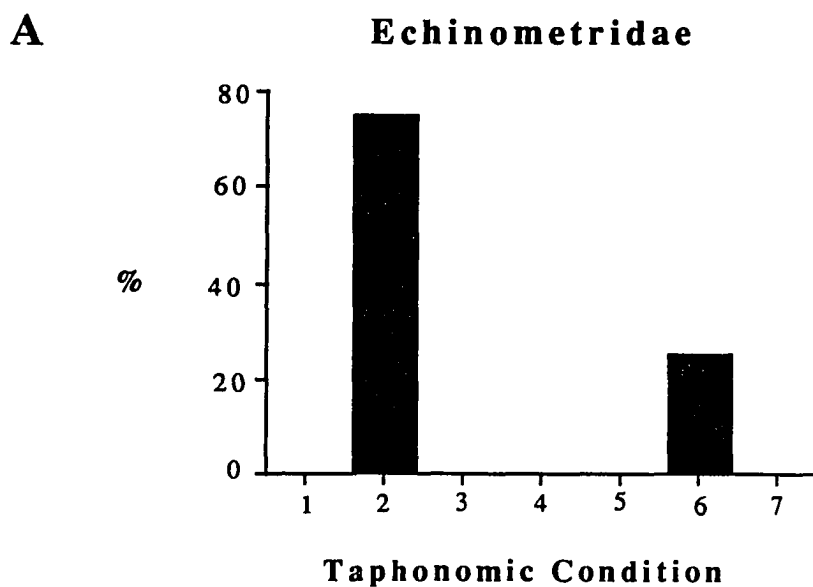


Figure 33 -- The distribution of preservational styles obtained from the literature for the Families Echinometridae (A) and Toxopneustidae (B). For comparison with other families, frequencies of taphonomic codes are expressed as the percent of total species.

attached to an intact test. Lantern elements and peristomial plates have not been described for the type material included in the data set.

Family Echinometridae

Compared to the three other families investigated, the Echinometridae are the most depauperate in terms of the number of species described on the basis of fossil material. A total of nine species placed in six genera have been described on the basis of fossil material through 1988. I have obtained taphonomic information for eight of the nine described species. Six of the eight species are described on the basis of an intact corona with no skeletal elements attached (taphonomic code 2) (Fig. 33A), while the remaining two species are described on the basis of incomplete tests (taphonomic code 6). No spines have been reported associated with the coronal material. Lantern elements were associated with (but not attached to) one intact corona and the apical systems were still attached to two additional intact coronas described.

Differences Between Groups

The Kolmogorov-Smirnov two-sample test was used to determine if statistically significant differences between the frequency distributions of preservational styles observed for each family occurred. There are no significant ($\alpha = .05$) differences between the histograms obtained for the Families Toxopneustidae, Echinometridae and Diadematidae (Table 5). Additionally, there is no significant difference between the histogram obtained for the Cidaridae and that

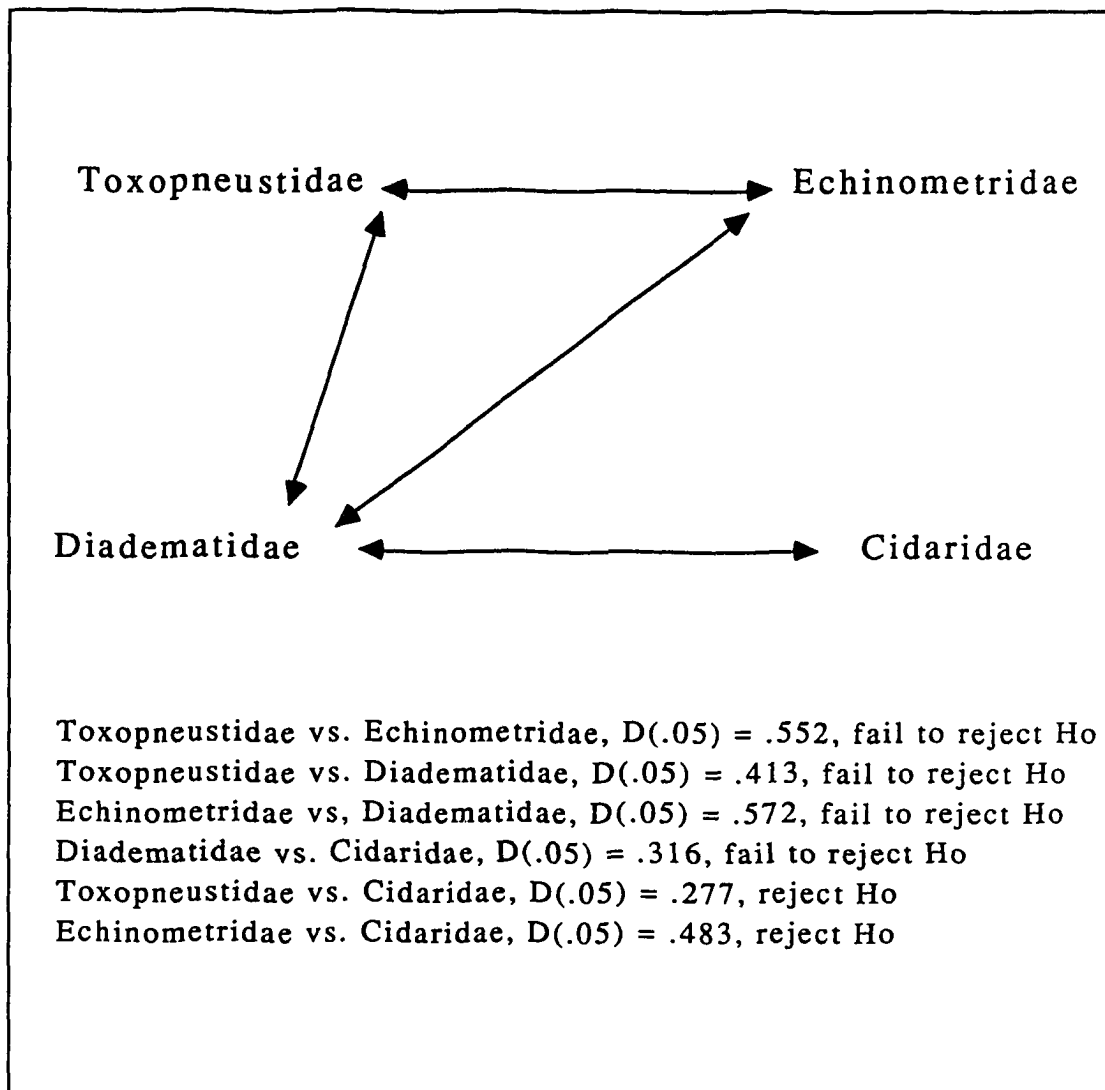


Table 5 -- Schematic representation of statistically significant and insignificant differences in the frequency distribution of states of disarticulation distinguished on the basis of literature-derived data; where H_0 is that the histograms represent samples from statistically similar populations. Differences for species connected with lines are not significant at the $\alpha = .05$ level.

for the Diadematidae. The histograms obtained for the Toxopneustidae and Echinometridae are both significantly different than the histogram obtained for the Cidaridae.

Discussion

Comparison of predicted and observed taphonomic states indicates that, at the familial level, the distribution of described species into the discriminated taphonomic categories corresponds to the predictions derived from field and laboratory analyses. A correspondence also exists between the predicted and observed frequency of occurrence of the skeletal elements studied during tumbling experiments. The agreement is particularly good for the Families Cidaridae, Echinometridae and Toxopneustidae.

The general condition of fossil cidaroid material was predicted to occur (in order of relative frequency) as fragmented material, sections of interambulacra separated along ambulacral sutures, and intact coronas with no skeletal elements attached (Table 3). Moreover, the majority of fragmented material was predicted to be spines. Observed taphonomic styles follow this pattern with the exception that taphonomic state 2 (intact corona) occurs more frequently than taphonomic state 6 (the category that includes complete sections of interambulacra) (Fig. 31A,B). Predicted styles of preservation were characterized quantitatively by generating a histogram of frequency distribution using the data obtained on the amount of test breakage incurred during tumbling experiments (Table 1). For comparison, disarticulation state 1 corresponds to taphonomic code 2, disarticulation states 2 and 3 correspond to taphonomic code 6, and disarticu-

lation state 4 corresponds to taphonomic code 7 (Compare Figures 10A,B and Fig. 29). A statistical comparison using the Kolmogorov-Smirnov two-sample test of the three state histograms obtained for predicted and observed preservational styles indicates that there is no significant difference ($\alpha = .05$) between predicted and expected values (Fig. 34A). The bimodal character of the histogram of observed preservational styles corroborates the conclusion, drawn from the decay experiments, that a disarticulation threshold of short duration exists for cidaroids: final burial prior to the threshold results in an intact corona whereas burial subsequent to the threshold results in coronal fragments. Occurrences of coronal material in intermediate states of preservation are rare because intermediate states of decay either do not occur or do not persist long enough to be preserved. Finally, the rarity of occurrence of lantern elements and apical and peristomial plates is in concurrence with the conclusions reached from field and laboratory work.

Any discussion of the correspondence or lack of correspondence of taphonomic predictions derived for the Family Echinometridae and observed fossil material must be prefaced with a reminder of the small number of observations. Only nine species have been described on the basis of fossil material, and data from eight of those have been recorded. The fact that few fossil species have been assigned to this family should not, however, invalidate a discussion of the condition of the material described. Fossil echinometrids were predicted to occur predominantly as intact coronas with no skeletal elements attached and, secondarily, as large coronal fragments (at least as large as an interambulacrum). Although

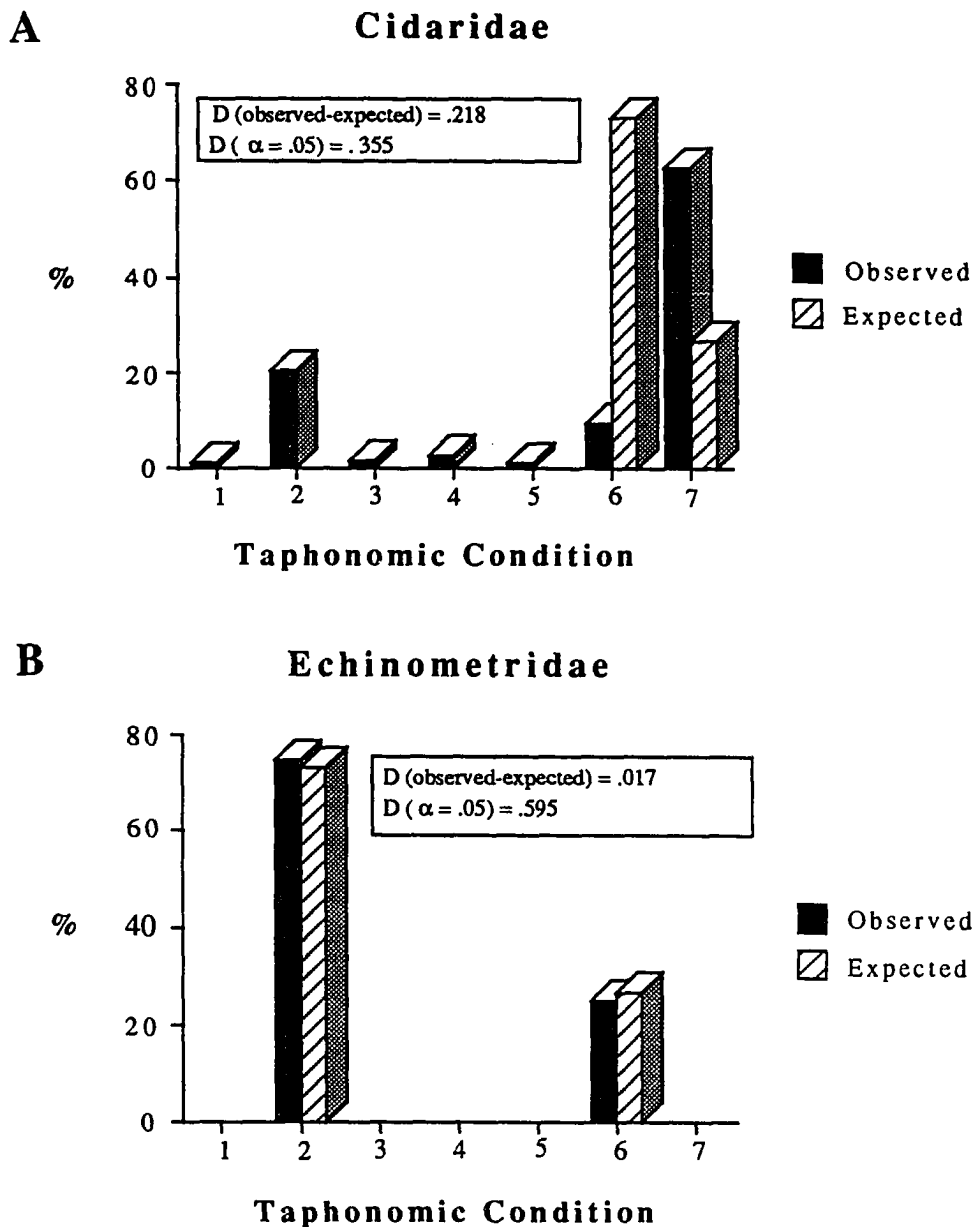


Figure 34 -- Comparison of the predicted distribution of preservational styles obtained from tumbling experiments with observed preservational styles obtained from the literature using the Kolmogorov-Smirnov two-sample test. Comparisons were made for taphonomic codes 2, 6 and 7 only. A) Family Cidaridae, B) Family Echinometridae. The distributions do not come from significantly different populations (at $\alpha = .05$).

spines were predicted to be moderately abundant, apical plates and lantern elements were predicted to occur rarely. The Echinometridae were the only family for which coronal fragments were predicted to be rare. The observed taphonomic condition of type echinometrid material corresponds to these predictions with the exception that no spines are described associated with the fossil material. Six of the eight described species occur as intact coronas (Fig. 33A); two of these still possess their apical system while one contains its lantern within (but not attached to) the peristome. As with the Cidaridae, a histogram of expected frequency distributions of preservational style was generated using the data obtained from the tumbling experiments (Table 1). Comparison of predicted and observed values using the same statistical analysis reveals no significant ($\alpha = .05$) difference in the histograms (Fig. 34B). The fact that fossil echinometrids occurred as either intact or partially intact coronas emphasizes the robustness of the corona rather than the presence of a disarticulation threshold -- recall that the results of decay experiments performed on *Echinometra* were inconclusive as to the timing of disarticulation.

After varied periods of tumbling, coronas of *Tripneustes* occurred in 3 of the 4 states of disarticulation discriminated for the tumbling experiments (Table 1). This led to the prediction that preservational styles of fossil material assigned to the Family Toxopneustidae would be equitably distributed between intact coronas with no attached skeletal elements (taphonomic code 2), large fragments (taphonomic code 6) and skeletal fragments (taphonomic code 7). The described fossil material corresponds to this prediction and, additionally, occurs as whole coronas lacking attached skeletal

elements that have been fractured or compressed but are otherwise intact (taphonomic code 4). The correspondence is quantitatively demonstrated by again using the Kolmogorov-Smirnov two-sample test to compare the histogram of observed styles of preservation with a histogram of predicted styles of preservation generated using data obtained from the tumbling experiments (Fig. 35A). No significant ($\alpha = .05$) difference was obtained. The observation of relatively large numbers of fractured and/or compressed coronas lacking spines (taphonomic code 4) is also logical: when subjected to varied periods of tumbling, coronas of *Tripneustes* were shown to suffer less breakage than all the echinoids studied except *Echinometra* (Fig. 28). The toxopneustid corona is weak enough to show the effects of destructive forces during preservation and yet strong enough to allow the preservation of intermediate states of disarticulation.

The "pan-taphonomic code" nature of fossils assigned to the Toxopneustidae is particularly apparent if the family's preservational style is compared to that of the other three families (compare Fig. 33B with Figs. 31A, 32A, and 33A). As already discussed for the Cidaridae and Echinometridae, the other families essentially have a bimodal distribution of taphonomic styles (taphonomic codes 2 and 7 for the Cidaridae and Diadematidae, codes 2 and 6 for the Echinometridae), while no such bimodality occurs in the Toxopneustidae. Finally, the rarity of occurrence of spines, lantern elements and peristomial plates predicted for the Toxopneustidae is borne out by the literature data. These elements are not described in the literature, although three species are described with their apical system attached.

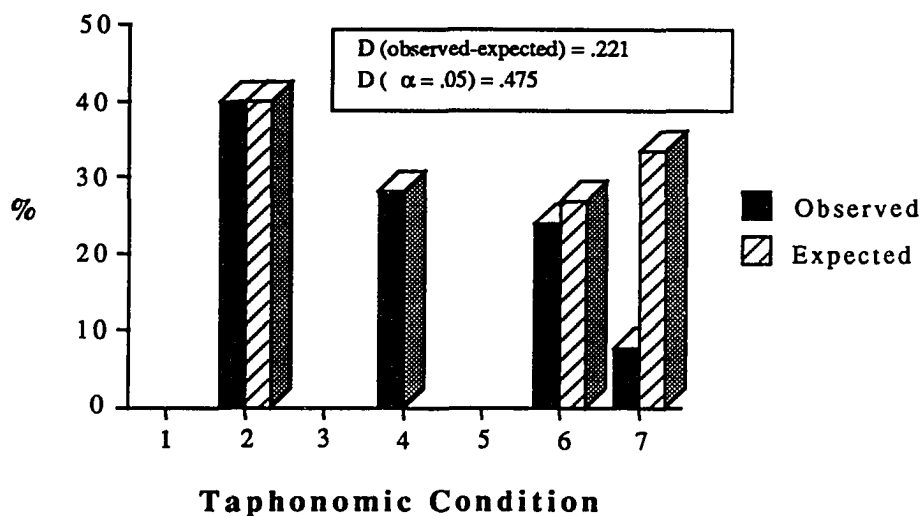
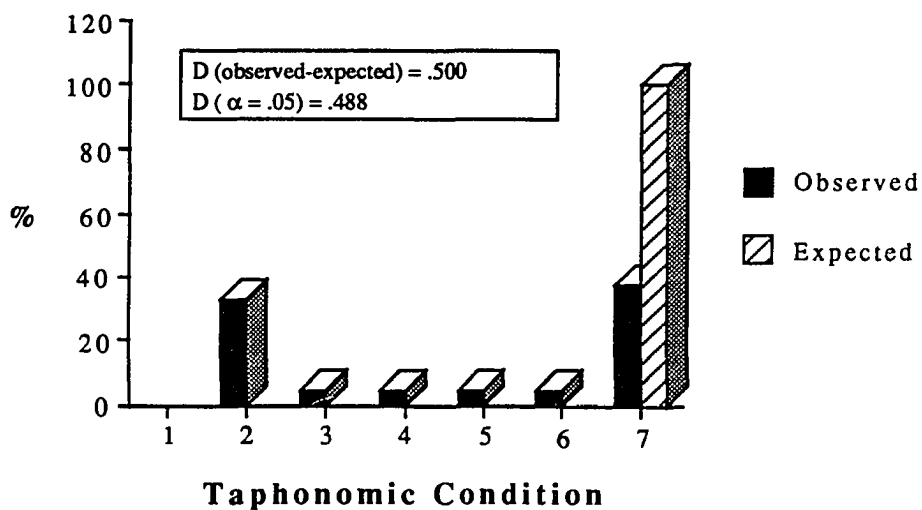
A**Toxopneustidae****B****Diadematidae**

Figure 35 -- Comparisons of the predicted distribution of preservational styles obtained from tumbling experiments with observed preservational styles obtained from the literature using the Kolmogorov-Smirnov two-sample test. Comparisons were made between taphonomic codes 2, 6 and 7 only. A) Family Toxopneustidae -- distributions do not come from significantly different populations. B) Family Diadematidae -- distributions are significantly different (at α = .05).

Type fossil material of species assigned to the Diadematidae was predicted to occur primarily as fragments, the majority of these being spines. Although the majority of the fragmented material is indeed spines (Fig. 32B), study of Fig. 32A reveals that the relative frequency of intact coronas with no skeletal elements attached (code 2) is greater than predicted. This is demonstrated quantitatively using the Kolmogorov-Smirnov two-sample test. The frequency distribution of observed styles of preservation is significantly different than that obtained using experimental data (Fig. 35B).

However, the bimodal histogram of observed preservational styles corroborates the conclusions obtained from the decay experiments: the diadematoïd corona is so fragile that unless final burial occurs very rapidly (resulting in exceptional preservation) only fragments will remain to be preserved. Recall that bleached echinoid carcasses were subjected to tumbling in order to approximate the condition of skeletal material observed during field experiments. The lack of correspondence between predicted and observed styles of preservation indicates that preservation of intact diadematoïd coronas does not usually occur under the circumstances observed in the field, where tests are rapidly denuded of all organic (connective) tissues. Put another way, the histograms that are compared represent "normal" taphonomic conditions (predicted preservational styles) vs. extraordinary taphonomic circumstances (observed preservational styles) in addition to normal disarticulation, and would not be expected to be statistically similar. While this would also be true for all the families studied, the extreme fragility of the diadematoïd skeleton magnifies this discrepancy.

If extraordinary circumstances of preservation are required for the presence of intact fossil coronas, they should occur much more rarely than fragmented material representing more common taphonomic conditions. There are two interrelated reasons for this discrepancy: 1) a bias exists in the condition of material used for type descriptions, and 2) lower level taxonomic classification of family members requires the presence of certain skeletal elements.

Type specimen bias -- The purpose of accumulating the literature data was to obtain representative taphonomic information for each family under study in the Recent. Since consideration of all fossil occurrences is beyond the scope of this study, the type material serves as a proxy for the entire family. The underlying philosophy of the typological species concept requires description of a type specimen so that it may be used for comparison with newly discovered fossil material. It is therefore possible that all families have been subjected to a "type specimen bias" in that taxonomists can be expected to choose the best material for descriptions of new species.

Examination of the preservation styles exhibited by the four families reveals that, without exception, a relatively high proportion of the described type material occurs as intact coronas lacking attached skeletal elements (taphonomic code 2). This agrees with the taphonomic predictions for the Toxopneustidae and Echinometridae. Although intact coronas of fossil Cidaridae were predicted to occur less frequently than large coronal fragments (i.e. sections of complete interambulacra, taphonomic code 6), the discrepancy was not sufficient to produce any statistically significant difference between predicted and observed distributions of preservational styles. However,

relatively frequent occurrences of intact coronas of fossil Diadematidae were not predicted. Consideration of the distribution of taphonomic states while acknowledging a possible bias towards intact coronas has no effect on the agreement between predicted and observed styles of preservation for the Toxopneustidae and Echinometridae: the Toxopneustidae would still exhibit a wide variation in the condition of fossil material and the Echinometridae would continue to be represented by a large proportion of intact coronas. However, a reduction in the frequency of occurrence of intact coronas relative to occurrences of fragmented material brings the observations from the literature data into closer agreement with the predictions derived for the Diadematidae. Similarly, a reduction in the frequency of occurrence of intact coronas relative to occurrences of large sections of corona would further reconcile predicted and observed styles of preservation of fossils assigned to Cidaridae.

Taxonomic factors -- The skeletal material required for taxonomic placement of specimens within the families under study is different in each group. A discussion of the relevant characteristics is important for determining the role that the discrimination of taxonomically useful features by echinoid workers has had on my assessment of the taphonomic overprint affecting fossil material described by those workers.

Fell (1966, p. U315) has stated that the only parts of a cidaroid skeleton of value in paleontology are whole or partial tests, ambulacral and interambulacral plates and primary spines.² Examination

² This is interesting from a taxonomic viewpoint since the primary type of the order and family, *Cidaris cidaris*, belongs to a small group of extant Atlantic

of the systematic taxonomy described in the Treatise reveals that, in general, overall appearance and ornamentation of the corona are important for discriminating between subfamilies, while spine morphology becomes important for distinguishing between genera (my experience with the literature data suggests that spine morphology becomes even more important at specific levels). Because coronal material is so important in classification, it becomes even more probable that species descriptions based on coronal material do indeed suffer the type specimen bias discussed above. The overwhelming number of species described on the basis of fossil spines is the product of their usefulness in taxonomy multiplied by their taphonomic resilience as demonstrated by the tumbling experiments. Similarly, the rarity of described lantern, apical system and peristomial plates may be considered the product of their lack of taxonomic usefulness at the subfamily and generic levels and the taphonomic vulnerability that I have demonstrated. This latter suggestion is corroborated by the observations, initially discussed above, that 1) the two occurrences of peristomial plates are described associated with a corona, 2) of 14 occurrences of apical plates, 12 are described associated with a corona and 3) of 14 occurrences of lantern elements, 11 are associated with a corona. Finally, both taphonomically and taxonomically, the two cidaroid species described on the basis of isolated api-

forms characterized by the presence of end teeth on a particular type of pedicellariae. These features are of very slight paleontological significance since pedicellariae are exceedingly rare as fossils. As a result no valid fossil species have yet been described for the genus *Cidaris*. However, as the primary type genus, generations of workers have assigned to it species whose precise generic position has not been established. Therefore, the name is without taxonomic validity.

cal plates and the three species described on the basis of isolated lantern elements must be viewed as extraordinary.³

Within the Order Diadematoidea, two families have fossil records, the Diadematidae and the Aspidodiadematidae (Durham et al., 1966; Smith, 1984). Although these families are distinguished mainly by the internal structure of their spines, the arrangement of apical plates in the apical system is also used (Durham et al., 1966). Genera are primarily distinguished on the basis of overall shape and ornamentation of the corona: characters that require more than an isolated plate or small coronal fragment to identify. As with cidaroid subfamilies, the importance of coronal material for distinguishing genera within the Diadematidae may have resulted in a bias towards the best-preserved material. Moreover, as discussed above, the fragility of the diadematoid test suggests that occurrences sufficiently complete to exhibit taxonomically useful characters also record exceptional taphonomic circumstances. This conclusion may be tested by further study of the sedimentological aspects of the units that contained the type material, and may explain the overall lack of described species in a group that has existed since at least the Lower Jurassic.⁴ The limited usefulness of isolated spines at the generic level helps to explain the lack of described occurrences even though results of the tumbling experiments indicated they are the most taphonomically resilient element of the diadematoid skeleton.

³ This is particularly true of the species based on lantern elements, since the morphology of the cidaroid lantern becomes taxonomically important at the level of Superorder.

⁴ It should be noted, however, that paucity of species does not reflect lack of abundance. The literature data I have collected contains no information as to abundance of preserved representatives of any of the families under study.

Finally, the lack of peristomial plates and association of the rare occurrences of both lantern elements and apical systems with coronal material is a product of their lack of taxonomic usefulness at the generic level and their demonstrated taphonomic vulnerability.

Coronal morphology is generally the most important characteristic for distinguishing fossil members of both the Toxopneustidae and Echinometridae. As a result, type specimen bias may have occurred in descriptions of new species. The good correspondence between predicted and observed preservational styles is the product of the usefulness of coronal material for taxonomic purposes and its demonstrated robustness when subjected to tumbling. Given this conclusion, the lack of described species assigned to the Echinometridae is perplexing. The Echinometridae is one of four families in the order Echinoida that were distinguished on the basis of the morphology of pedicillariae on extant forms by Mortensen (1943). Because such characters are essentially nonexistent in the fossil record, generic characters are presented in the Treatise so as to be mutually exclusive. Thus, taxonomists have been forced to work through classification in an "inside out" fashion: determining the ordinal assignment of fossil material, then generic placement, and finally familial placement. Perhaps these difficulties have resulted in an artificially depauperate family (in terms of species).

Differences between groups -- The conflicting results obtained by comparing predicted and observed preservational styles between families is best understood by considering differences in coronal rigidity. The Order Temnopleuroida (which contains the Family Toxopneustidae) differs from all other orders of regular echinoids in

having peg and socket structures on plate suture faces, and these bind the plates together after death (Smith, 1984). Echinoids belonging to the Order Echinoida (e.g. the Echinometridae) lack peg and socket jointing, but stereomic knobs interlock more extensively between plates in this group than in the cidarids and diadematids. The effect of these differences in skeletal microstructure on preservation potential has been demonstrated qualitatively by Kier's (1977) comparison of the number of echinoid species in the Miocene and Recent. The differences are quantitatively demonstrated by analyzing tumbling results on the basis of the amount of coronal breakage incurred (Fig. 28) and comparing the style of coronal breakage suffered among the four echinoids (Table 2). As predicted from results of that comparison, the observed distribution of preservational styles among the four families distinguishes two groups (Table 5). The Toxopneustidae and Echinometridae comprise group 1 and the distribution of preservational styles does not differ significantly between them. Similarly, the Cidaridae and Diadematidae comprise group 2 because the distribution of preservational styles does not differ significantly between them. Furthermore, the distribution of preservational styles observed among the Cidaridae is significantly different than that observed among the Echinometridae. Styles of preservation observed for the Cidaridae also differ significantly from those observed for the Toxopneustidae. Although this was not the case when tumbling results were analyzed, recall that the null hypothesis was not rejected only by a narrow margin. Moreover, this observation corroborates the findings of Kier (1977) and Smith (1984) discussed above.

The greatest departure of observed from predicted comparisons of the distribution of preservational styles occurs for the Family Diadematidae. Styles of preservation observed among the Diadematidae do not differ significantly from any other echinoid family. Results of decay and tumbling experiments indicated the extreme fragility of the diadematid corona in the absence of any connective tissues. As discussed above, the fragility of the diadematid corona dictates exceptional circumstances for its preservation; in the absence of unusual circumstances, only fragments will be preserved. The relatively high frequency of occurrence of exceptional taphonomic circumstances results in a bimodal distribution of preservational styles observed for the Diadematidae. This, in turn, accounts for the correspondence with the other three echinoid families, which, to varying degrees also have bimodal distributions of preservational styles.

In sum, members of the Echinometridae and Toxopneustidae have similarly robust coronas as a result of sutural interlocking. The corona is sufficiently sturdy to preserve the spectrum of preservational styles between an intact corona and disarticulated fragments. Members of the Cidaridae possess a corona which is not as robust as the echinacean groups but is still sufficiently sturdy to preserve a spectrum of preservational styles. Differences in skeletal microstructure among these three families are reflected by a range of preservational styles. Members of the Diadematidae possess coronas that are so fragile, only end members of the spectrum of taphonomic circumstances are preserved by fossil material (i.e. final burial is the cause of death or occurs extremely quickly -within days- after

death). Thus predictions of the distribution of preservational styles expected to occur under "normal" circumstances as well as predictions comparing that distribution to those of other echinoid families cannot be made.

A test of predictions at lower taxonomic levels

Given the patterns of preservation determined using literature occurrences, it is useful to test whether taxonomic level has an effect on the distribution of preservational styles. Put another way, since style of preservation has been shown to differ between families, is it consistent within families? The Family Cidaridae is recognized to contain six subfamilies by Durham et al. (1966). It is therefore appropriate to use the literature data obtained for the Cidaridae to test whether preservational styles within a family are consistent. Completed records of Cidaridae in the database were sorted to obtain taphonomic information for four of the six subfamilies.⁵

Histograms of the frequency distribution of preservational styles for each subfamily are presented in Figures 36 and 37. The Kolmogorov-Smirnov two-sample test was used to compare the frequency distributions generated with the subfamily data with that obtained using familial data. With the exception of the Subfamily Stereocidarinae, the distributions of preservational styles observed for the subfamilies do not differ significantly ($\alpha = .05$) from that obtained for the family. Thus the effects of skeletal microstructure,

⁵ Two subfamilies are excluded from the analysis. The Ctenocidarinae are comprised largely of Recent genera, while the Histocidarinae are a very small group (9 species).

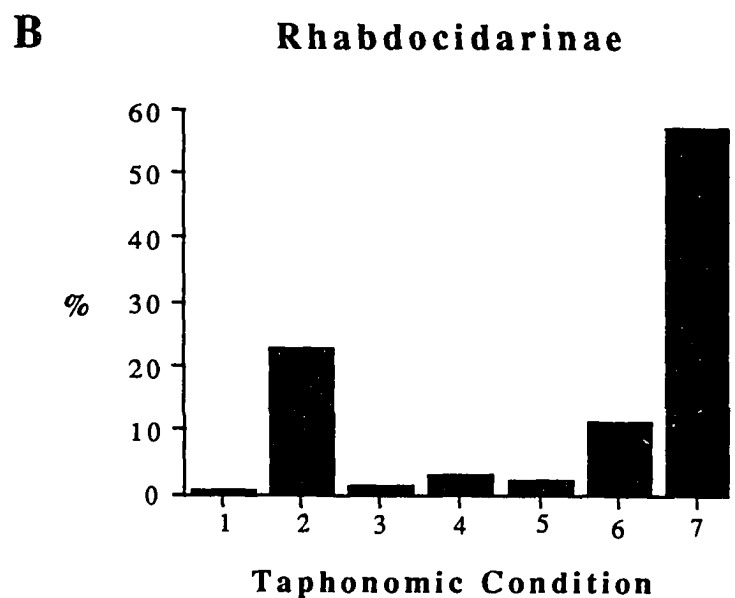
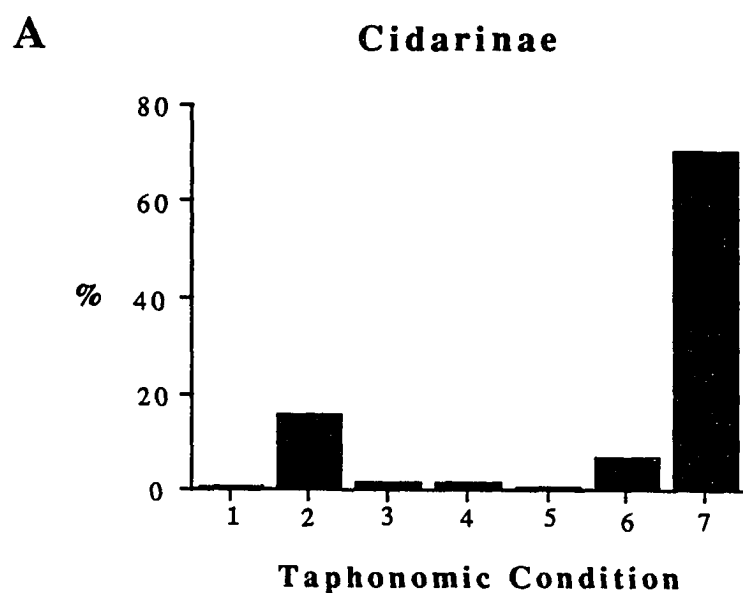


Figure 36 -- The distribution of preservational styles obtained from the literature for the Subfamilies Cidarinae (A) and Rhabdocidarinae (B).

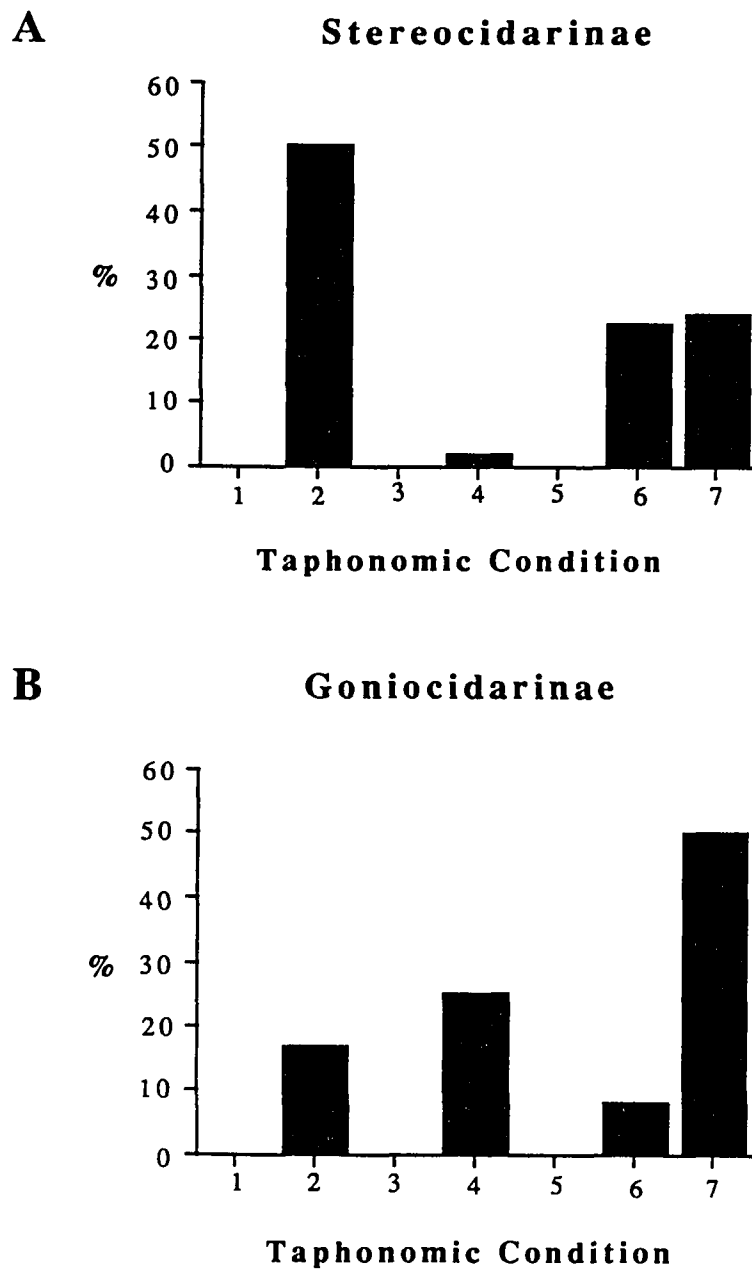


Figure 37 -- The distribution of preservational styles obtained from the literature for the Subfamilies Stereocidarinae (A) and Goniocidarinae (B).

type specimen bias and taxonomic bias are generally reflected for the Cidaridae at the next lower taxonomic level. This is logical since factors affecting preservational style such as extent of sutural interlocking are present at higher, and therefore lower, taxonomic levels.

The distribution of preservational styles in the Stereocidarinae differs from that of the family as a whole in the relative frequencies of occurrence of taphonomic codes 2 and 6 (Fig. 37A), suggesting that the Stereocidarinae possess a more robust corona relative to the rest of the family; the description of the characteristics of the subfamily describes the test as "robust and well-arched" (Fell, 1966, p. U235). Alternatively, members of the subfamily may be ecologically restricted to environments that favor preservation. The first hypothesis is testable, since the subfamily contains extant members that can be collected and subjected to additional tumbling experiments. The second hypothesis can also be tested by 1) determining the ecological occurrences of extant forms, and 2) assigning environments of deposition to the units enclosing fossil species for which taphonomic data has been collected.

It should be noted that extending taphonomic analyses to lower taxonomic levels increases the risk that taxonomic problems will obscure any pattern. As discussed earlier in this section, the Cidaridae as a group are without taxonomic validity. Assigning fossil species at increasingly low taxonomic levels becomes increasingly tenuous since, as discussed earlier, primary spines play an increasingly important role. Considering that more than one type of spine occurs on the same echinoid and that the spine ornamentation used to distinguish species is quite likely to be taphonomically vulnerable *sensu*

Brandt (1989), discussions of taxonomic control over taphonomic condition must be undertaken with caution.

CHAPTER 5: APPLICATION

A logical application of the results of this study is to assess the diversity history of each group with respect to the characteristic modes of taphonomic bias that have been demonstrated. The data on preservational style can be used to ascertain whether certain stratigraphic intervals are characterized by specific modes of preservation. By comparing such an analysis to the actual diversity history of a family, it can be determined what effect, if any, taphonomic bias has had on that family's diversity history. Because the data on type specimen preservation is particularly robust for the Family Cidaridae, the group was chosen for comparison of its diversity history with the preservational style of type species occurrences.

Using unpublished data on generic diversity kindly supplied by J. John Sepkoski (Univ. of Chicago), I have generated a spindle diagram of generic diversity for the Family Cidaridae (Fig. 38). At the series level, generic diversity increases relatively quickly from the origination of the family in the Middle Triassic through the Mesozoic. From the Paleocene through the Pleistocene, diversity remains relatively constant. The number of fossil genera ranges from one to twelve. The number of extant genera (33) was determined using lists compiled by Kier (1974) Kier and Lawson (1978), and the Zoological Record (1975-1988).

The number of type species of Cidaridae described from each stratigraphic interval is plotted along the left margin of the diversity diagram (Fig. 38). Although diversity increases towards the Recent, the number of type species described decreases as the Recent is ap-

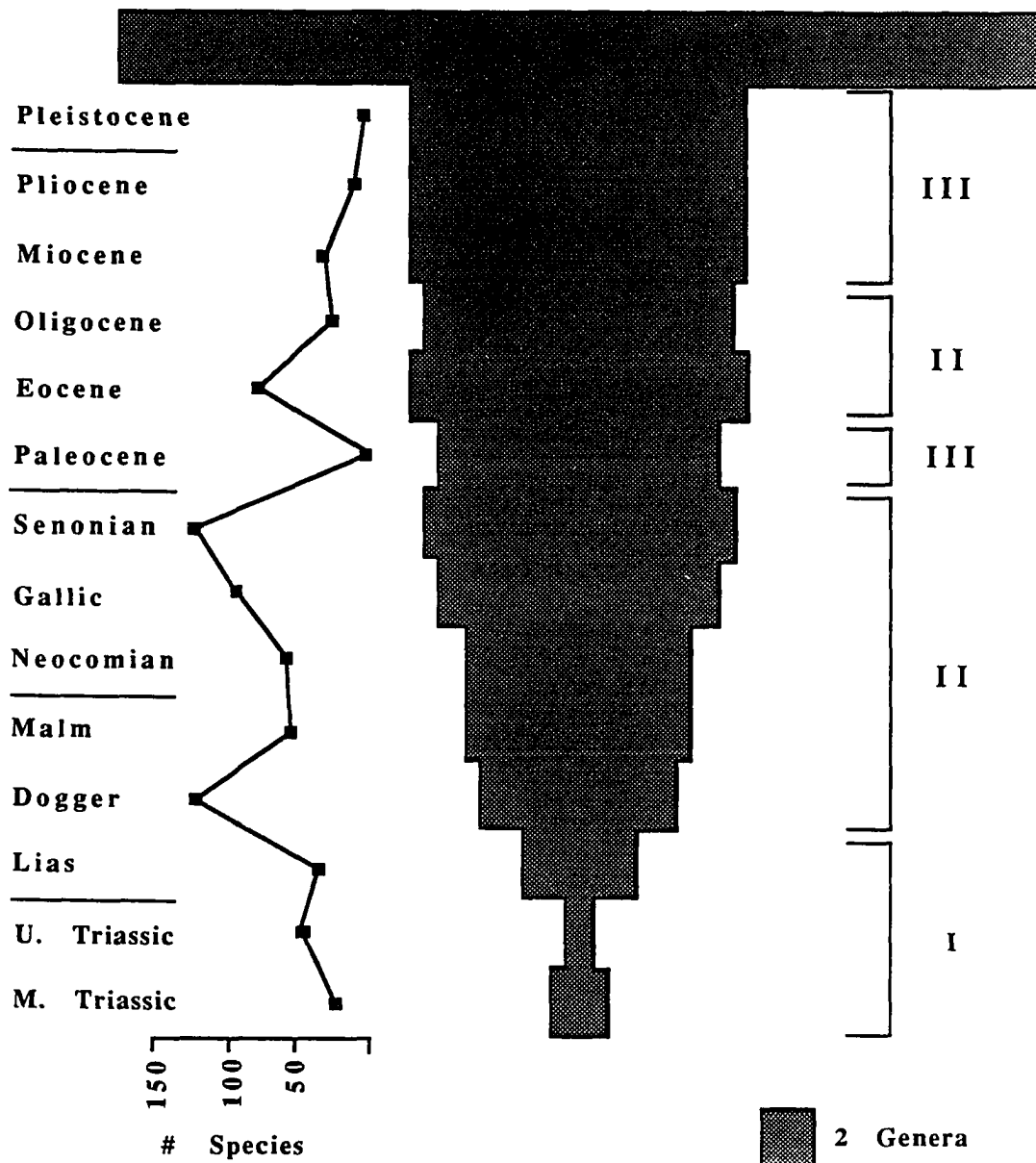


Figure 38 -- Generic diversity of the Family Cidaridae. Diversity of fossil forms from Sepkoski (unpublished data). Recent echinoid diversity compiled from Kier (1974), Kier & Lawson (1978) and the Zoological Record (1974-1988). The number of type species described from each series is plotted along the left margin of the spindle diagram. Results of cluster analysis are superimposed on the right margin of the diagram. See text for discussion.

proached. Raup (1979) was able to demonstrate that, as progressively younger rocks are sampled, the more likely it is that the fauna obtained will have an extant relative. This is one aspect of "Pull of the Recent", an apparent increase in diversity in progressively younger stratigraphic intervals. As discussed in Chapter 4, characters important for descriptions of cidaroids at the specific level are generally found on extant forms only. Thus, as progressively younger rocks are sampled, it is more likely that a fossil cidaroid will have an extant relative that exhibits characters that allow for taxonomic assignment at the specific level. Therefore, fewer new type species are described as the Recent is approached. Although perfectly logical, this "reverse" Pull of the Recent phenomenon was not expected.

To explore further the relationship of preservation to stratigraphic interval, Q-mode and R-mode cluster analysis of 13 samples (mid-Triassic-Pleistocene series) and 7 variables (taphonomic codes 1-7) was performed on all type species of Cidaridae described from each stratigraphic interval (Unweighted Pair-Group Method with Arithmetic Averaging; percent transformation of samples; quantified Dice similarity coefficient). Raw data are given in Appendix IV, and results are presented in the form of a two-way cluster analysis (Fig. 39).

Three distinct clusters are delineated on the basis of preservational style (Fig. 39).

I) "Spine-Dominated" -- These samples cluster together as a result of the overwhelming predominance of taphonomic code 7 (skeletal fragments) relative to all other preservational styles and a

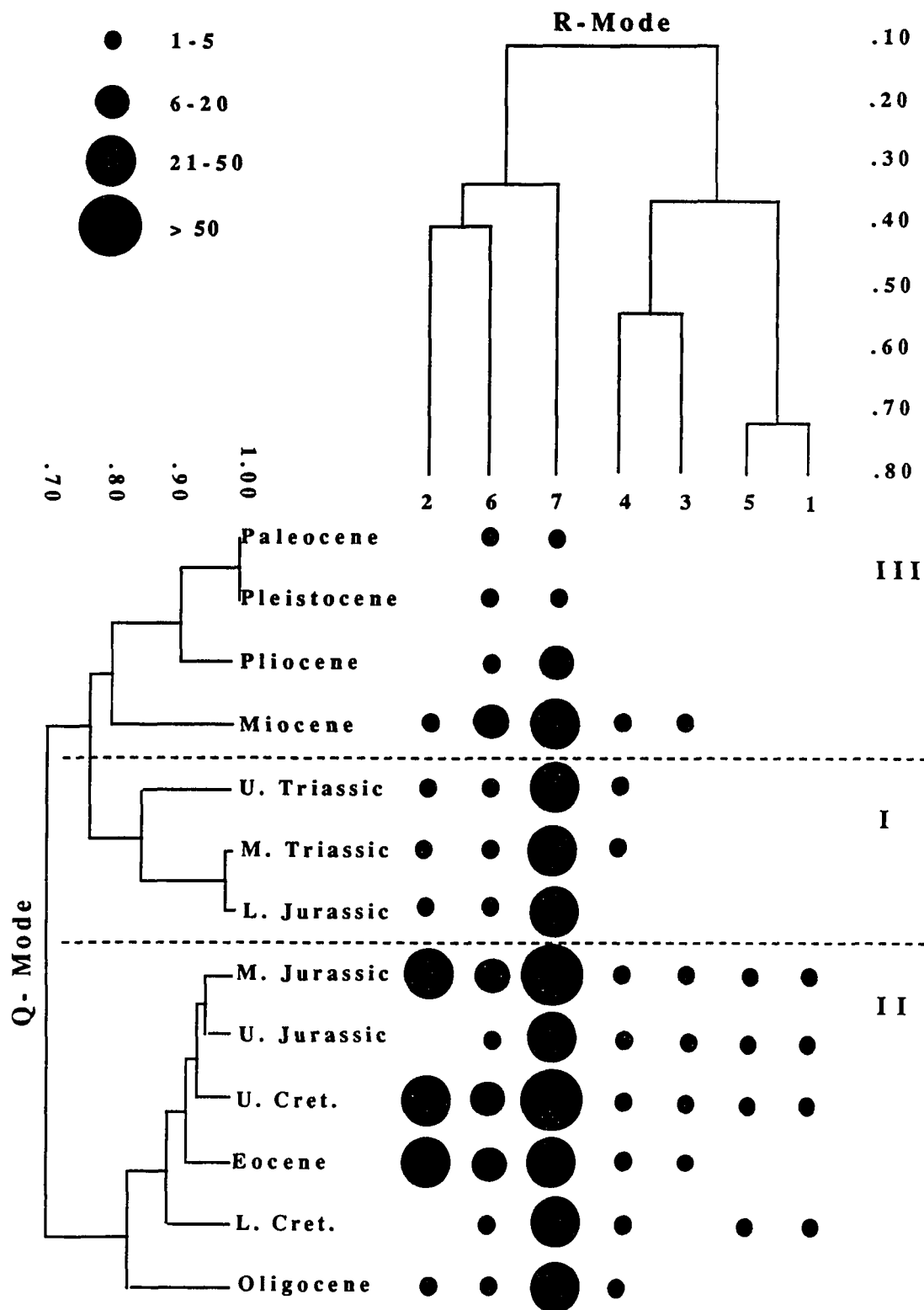


Fig. 39 -- Two-way cluster analysis of series and taphonomic code. Cophenetic correlation coefficient, Q-mode = .8482; R-mode = .9437.

lack of intermediate states of preservation. Recall that for the Cidaridae, 77% of the occurrences of skeletal fragments were spines (Fig. 31B). Large coronal fragments and intact denuded coronas also occur in the samples comprising this cluster. The middle and Upper Triassic, and Lias (Lower Jurassic) are characterized by this style of preservation.

II) "High Diversity" -- The samples cluster together because they contain the entire spectrum of preservational styles observed for fossil cidaroids. Skeletal fragments and intact denuded coronas (the end members of the preservation spectrum) are most common, and are represented by the bimodal distribution of preservational styles discussed in Chapter 4. All other styles of preservation occur in relatively low numbers in this cluster. With the exception of the Paleocene, all series from the Dogger (Middle Jurassic) through the Oligocene are characterized by this style of preservation.

III.) "Depauperate" --The final cluster contains samples characterized by relatively low numbers of described species that are represented by few preservational styles. Skeletal fragments and large coronal fragments are most common and intermediate states of preservation are rare. Note the virtual absence of intact denuded coronas (code 2) in this cluster as compared to Cluster I. The Paleocene, Miocene, Pliocene and Pleistocene are characterized by this style of preservation.

Comparison of the results of cluster analysis with the diversity history of the group (Fig. 38) indicates that, with the exception of the Paleocene, the dominant styles of preservation sort out stratigraphically. During their early history (Middle Triassic-Early Jurassic),

cidaroids are primarily represented by spines. This was apparent before the cluster analysis was performed since virtually all cidaroid type species described from the Triassic are spines collected from the St. Cassian beds of the Italian alps. The initial diversification of the family in the Middle Jurassic and generally continuing through the Eocene (from 4 to 12 genera) is characterized by an increase in both quality of preservation as well as the number of different preservational styles recorded. The few new fossil cidaroids described from the Miocene-Pleistocene are primarily represented by spines and large coronal fragments

If taphonomic overprint were a random phenomena, stratigraphic intervals would not be expected cluster from lowest to highest on the basis of preservational style of a particular invertebrate group. Thus the primary conclusions to be drawn from this analysis are: 1) there is a taphonomic signal affecting the diversity history of cidaroids, and; 2) taphonomic bias has changed systematically through time. Explaining these changes, however, is quite difficult since many factors are probably involved. For example, there are two alternative explanations for the coincidence of the initial adaptive radiation of the family and a change from "spine-dominated" preservation to "high taphonomic diversity" in the Middle Jurassic (Fig. 38):

A) The initial post-Paleozoic diversification of the cidaroids was the result of evolutionary changes that allowed for expansion into new ecospace (Kier, 1974). This expansion is perhaps expressed taphonomically by an increase in diversity of preservational style for two reasons: 1) environment can increase or decrease the preserva-

tion potential of an organism; some of the environments newly inhabited by cidaroids allowed additional modes of preservation; 2) Evolutionary changes that permitted ecologic expansion may also have produced a more robust skeleton. In either case, diversification of the group causes the diversification of preservational styles.

B) Alternatively, the diversification of preservational styles, particularly larger coronal fragments and intact coronas, provided additional material for the description of new taxa. As discussed in Chapter 4, overall appearance of the corona as well as its ornamentation are important for identification of cidaroids at lower taxonomic levels. Thus, in this scenario, the diversification of preservational styles causes a perceived diversification of the group.

Choosing between these contrasting hypothesis requires the accumulation of additional data and provides an agenda for future research on echinoid taphonomy in general. Specifically:

- 1) Accumulate data on general fossil cidaroid occurrences and test whether their preservational styles are different than those obtained for type species. This will help determine whether type species preservation provides a reasonable proxy for the entire group.

- 2) Complement the literature data with environmental information. Do cidaroids expand into environments that are sufficiently different to affect their preservation?

- 3) Evaluate the evolutionary trends in post-Paleozoic echinoids to determine whether subsequent morphological changes would enhance preservation potential.

4) Examine extensive cidaroid collections to refine taphonomic information further. Much complementary information (e.g. abrasion, boring, associations) is lost in the photographic (and in many cases lithographic) plates that accompany descriptions of type specimens.

5) Accumulate literature data on preservation of another contemporaneous echinoid group with an abundant fossil record to: A) determine whether any taphonomic bias can be demonstrated, and: B) compare the nature of that bias with that observed for cidaroids.

CHAPTER VI: CONCLUSIONS

1. The distribution of macro- and microscopic skeletal material of *Diadema antillarum*, *Echinometra lucunter*, *Eucidaris tribuloides* and *Tripneustes ventricosus* does not reflect the distribution of the living populations in tropical reef, near-reef, lagoonal and near shore environments.
2. Organic connective tissues of freshly killed specimens of *D. antillarum*, *E. lucunter* and *E. tribuloides* decay within six days in tropical reef environments. This results in a reduction of the skeleton to a corona devoid of spines, lantern elements and peristomial plates.
3. The above field observations suggest that fossil specimens of the echinoids under study will be rare. Moreover, the loss of organic connective tissue within six days' exposure in normal marine conditions suggests that recognition of fossil material depends on A) taxonomic differences in coronal rigidity related to sutural interlocking, and B) identifiability of isolated skeletal elements. Thus, the condition of fossil specimens will vary between taxa.
4. The prediction of rarity of occurrence of fossil echinoids is supported by examination of an exposure of Pleistocene reef and near reef facies. However, the scarcity of fossil material made more specific tests of the above predictions impossible.
5. A similar sequence of disarticulation of *Diadema*, *Echinometra* and *Eucidaris* occurs as a result of the decay of connective tissues. The spines detach, followed by the loss of the peristomial and apical plates, and Aristotle's Lantern. Finally, the corona disarticulates along ambulacral plate sutures. The timing of disarticulation differs for each species: spines of *Diadema* begin to detach after one day of decay whereas those of *Echinometra* detach after three days and those of *Eucidaris* detach after periods exceeding five days. Coronas of *Diadema* and *Eucidaris* were observed to disarticulate within seven and ten days of decay, respectively. Coronas of *Echinometra* did not disarticulate after ten days of decay.
6. Decay of organic tissue does not result in the flotation of echinoid skeletal material as has been reported in the literature.

7. The observations of Smith (1980, 1984) that echinacean groups have more extensive interlocking of stereom across plate suture faces than either Diadematoids or Cidaroids is corroborated by tumbling experiments. *Echinometra* undergoes the least amount of coronal damage, followed by *Tripneustes*, *Eucidaris* and *Diadema*.
8. The amount of skeletal material contributed to >2 mm, 1-2 mm, 500 μ - 1 mm, 125 μ - 500 μ , and <125 μ size fractions does not differ significantly between tumbling periods of one, ten and 100 hours.
9. Significant ($\alpha = .05$) differences between species exist in the composition of the >2 mm size fraction after tumbling. Carcasses of *Diadema* and *Eucidaris* contribute primarily spines to the >2 mm fraction. Carcasses of *Echinometra* and *Tripneustes* contribute primarily coronal material. However, for each echinoid, the relative amounts of spine, lantern and coronal material do not differ significantly between tumbling periods of one, ten and 100 hours.
10. For each echinoid the amount of coronal breakage inflicted by tumbling does not vary significantly between tumbling periods of one, ten and 100 hours. However, the amount of breakage does vary significantly ($\alpha = .05$) between species. *Diadema* suffer the most breakage, with an average breakage coefficient value of 173.47. *Echinometra* suffer the least breakage, exhibiting an average coefficient value of 4.65. Specimens of *Eucidaris* and *Tripneustes* fall within this range, with values of 89.36 and 34.31, respectively.
11. Tumbling experiments suggest that the preservational styles of fossil occurrences of the echinoids under study will vary between taxa. Members of the Family Diadematidae are predicted to occur primarily as skeletal fragments, mostly spines. Members of the Family Echinometridae are predicted to occur as intact coronas without spines, lantern elements, or apical and peristomial plates. Members of the Family Cidaridae are predicted to occur primarily as isolated spines, large coronal fragments, and as intact coronas devoid of spines, lantern elements, or apical and peristomial plates. Finally, members of the

Toxopneustidae are predicted to occur primarily as intact, partial or fragmented coronas only.

12. Four states of coronal disarticulation are discriminated from the tumbling experiments for quantitative comparison with literature-derived data of taphonomic bias affecting fossil echinoid occurrences: 1) intact corona; 2) coronal fragments larger than an interambulacrum; 3) complete interambulacrum; and, 4) coronal fragments smaller than an interambulacrum.
13. Through 1988, there have been 901 species assigned to the Family Cidaridae, 32 species assigned to the Family Diadematidae, 38 species assigned to the Family Toxopneustidae and 9 species assigned to the Family Echinometridae on the basis of fossil material.
14. The style of taphonomic bias predicted to affect type species described in the Families Cidaridae, Echinometridae and Toxopneustidae on the basis of field and laboratory analyses of extant species is supported by the literature data of their fossil occurrences. Moreover, for the Family Cidaridae, the distributions of preservational styles within subfamilies do not generally differ from that of the family: a bimodal distribution exists between spines and intact, denuded coronas.
15. The prediction that members of the Family Diadematidae will be represented primarily by skeletal fragments is not supported by the literature data. This is because the extreme fragility of the diadematoid corona dictates extraordinary circumstances of preservation that are not accounted for in the experiments performed.
16. The evolutionary history of the Family Cidaridae has a characteristic taphonomic overprint that has changed systematically since the apparent origination of the family in the Middle Triassic. Early members of the group are described primarily on the basis of spines. An increase in the "diversity" of preservational styles (ranging from exceptionally well preserved forms to isolated skeletal fragments) coincides with an increase in generic diversity beginning in the Middle Jurassic. Few type specimens, composed primarily of spines and large coronal fragments, are described from the Neogene and Pleistocene.

17. The number of described type species decreases from the Eocene through Pleistocene, illustrating a "reversed Pull of the Recent" stemming from the taxonomic utility of extant forms.

Literature Cited & Primary Database Records

- Airaghi, Carlo. 1902a. Echinidi terziari del Piemonte e della Liguria. *Palaeontographia Italica*, 7(1901):149-218, pls. 19-27.
- . 1905d. Echinodermi infracretacei dell'Isola de Capri. *Rivista Italiana de Paleontologia*, 11:82-90, pl. 1.
- Alkire, Leland G. Jr. 1988. Periodical Title Abbreviations: By Abbreviation. Gale Research Company, Book Tower, Detroit, Michigan.
- Allison, Peter A. 1988. The role of anoxia in the decay and mineralization of proteinaceous macro-fossils. *Paleobiology*, 14:139-154.
- Archiac, Adolphe d'. 1869. Introduction à l'étude de la paléontologie stratigraphique, v. 2. F. Savy, Paris, 616 p., 3 pl.
- Arnaud, Henri. 1898. Observations sur le *Cidaris pseudopistillum* Cotteau et *Brissopneustes aturensis*. *Actes, Société Linneenne de Bordeaux*, 53:103-119, pl. s.
- Arnold, Benjamin W., and Herbert L. Clark. 1927. Jamaica Fossil Echinoidea by Herbert L. Hawkins. *Museum of Comparative Zoology at Harvard College Memoirs*, 50(1):1-84, pls. 1-5.
- Aslin, C. J. 1968. Echinoid preservation in the Upper Estuarine Limestone of Bilsworth, Northamptonshire. *Geological Magazine*, 105:506-518.
- Assmann, P. 1925. Die fauna der Wirbellosen und die Diploporen der oberschlesischen Trias mit Ausnahme der Brachiopoden, Lamellibranchiaten, Gastropoden und Korallen. *Jahrbuch der Preusschen Geologischen Landesanstalt zu Berlin*, 46:504-527, pls. 8-9.

- . 1937. Revision der fauna der Wirbellosen der oberschlesischen Trias. *Abhandlungen der Koniglich Preussischen Geologischen Landesanstalt*, 170:1-134, pls. 1-21.
- Auerbach, J. 1846. Ueber eine neue Cidariten-Art, aus dem moskau-er-Jura. *Kaiserliche Russischen Min. Gessellschaft*, St. Petersburg, *Verhandlungen*, 1845-1846:199-200.
- Bak, R. P. M., and G. van Eys. 1975. Predation of the sea urchin *Diadema antillarum* Philippi on living corals. *Oecologia* (Berlin), 20:111-115.
- Bambach, Richard K. 1985. Classes and adaptive variety: The ecology of diversification in marine faunas through the Phanerozoic, in Valentine, James W. (ed.), *Phanerozoic Diversity Patterns, Profiles in Macroevolution*, Princeton University Press, Princeton, N.J. 441 p.
- Bantz, Hans-Ulrich. 1969. Echinoidea aus Plattenkalken der Altmühlalb und ihre Biostratonomie. *Erlanger Geologische Abhandlungen*, 78:1-35, Fig. 1, pls. 1-7.
- . 1969. Echinoidea aus Plattenkalken der Altmühlalb und ihre Biostratonomie. *Erlanger Geologische Abhandlungen*, 78:1-35, pls. 1-7.
- Bather, Francis A. 1909c. Triassic echinoderms of Bakony. *Resultate Wissenschaftlich Erforschung Baltonees*, 1(1): 1-288, pls. 1-18, text-figs. 1-63.
- Besaire, H., and J. Lambert. 1930. Notes sure quelques échinides de Madagascar at du Zululand. *Société Geologique de France, Bulletin Série 4*, 30:107-116, pls. 4-10.
- Besairie, H. 1930b. Recherches géologiques à Madagascar, contribution à l'étude des ressources minérales. *Société d'Histoire Naturelle de Toulouse, Bulletin*, 60:345-616, pls. 1-27.

- Bloos, G. 1973. Ein fund von Seeiegeln der Gattung *Diademopsis* aus dem Hettangium Württembergs und ihr Lebensraum. *Stuttgarter Beitrage Naturklasse (B)*, 5:1-25.
- Blyth Cain, J. D. 1968. Aspects of the depositional environment and palaeoecology of crinoidal limestones. *Scottish Journal of Geology*, 4:191-208.
- Boehm, August Joseph Georg). 1882. Ueber einige tertiäre Fossilien von der Insel Madura, nördlich von Java. *Kaiserliche Akademie der Wissenschaften in Wien, Mathematische-Naturwissenschaftliche Klass. Denkschriften*, 45:359-372, pls. 1-4.
- Boll, Ernest Friedrich August. 1846. *Geognosie der Deutschen Ostseeländer zwischen Eider und Oder*. Neubrandenburg, Berlin, 284 p., 2 pls.
- Boucot, A. 1953. Life and death assemblages among fossils. *American Journal of Science*, 25:25-40.
- Brandt, Danita S. 1989. Biotic versus taphonomic controls on trilobite granulosity: Implications for trilobite taxonomy, ecology and phylogeny. Abstracts of the 28th Geological Congress, Washington. D.C., 1:193-194.
- Brett, Carlton E., and Gordon C. Baird. 1986. Comparative taphonomy: A key to paleoenvironmental interpretation based on fossil preservation. *Palaios*, 1(3):207-227.
- Brito, I. M., and L. V. O. Ramirez. 1974. Equinódos do Mioceno Inferior do norte Brasil. *Anais da Academia Brasileira de Ciências*, 46(2):263-274, 14 pls.
- Bucaille, Ernest L. 1882-1883. Études sure les échinides de la Seine-Inférieure. *Société Geologique de Normandie, Bulletin*, 8:16-39.
- Buckland, William. 1836. *Geology and Mineralogy considered with reference to Natural Theology (Bridgewater Treatise VI)*. W. Pickering, London, 2 vols., 599 and 128 p.

- Caffin, R. 1867. Échinides des environs d'Evreux. Société des amis des sciences naturelles de Rouen, Bulletin, 2:54.
- Carpenter, Robert C. 1981. Grazing by *Diadema antillarum* (Philippi) and its effects on the benthic algal community. Journal of Marine Research, 39:749-765.
- Castex, L. 1947a. Notes sur quelques Échinides fossiles du Sud-Ouest de la France. Actes, Société Linneenne de Bordeaux, 93:25-42, pls. 1-2.
- Castex, L., and Jules M. Lambert. 1919-1920. Révision des Échinides des falaises de Biarritz. Actes, Société Linneenne de Bordeaux, 71:117-206, pls. 1-2.
- Chapman, Frederick, and F. A. Cudmore. 1934. The Cainozoic Cidaridae of Australia. National Museum of Melbourne, Memoir, 8:125-149, pls. 12-15.
- Checchia-Rispoli, Giuseppe. 1932c. Echinidi regolari del Maestrichtiano della Tripolitania. Bolletino, Rivista Uff. Geologia Italia, 57(3):3-16, pls. 1-2.
- Checchia-Rispoli, Giuseppe. 1907. Gli echinidi viventi e fossili della Sicilia. Parte seconda: Gli echinidi del Piano Siliciano de intorno di Palermo. Paleontographia Italica, 13:199-231.
- _____. 1933c. Illustrazioni di alcuni Echinidi del Maestrichtiano della Tripolitania raccolti da Ignazio Sanfilippo. Memorie Societa Geologica Italiana, 1:1-24, 2 pls., 8 text figs.
- Chiplonker, G. W., and R. M. Badve. 1972. Palaeontology of the Bagh Beds. II. Echinoidea. Proceedings of the Indian Academy of Science (B), 76(4):133-152, 2 figs., table.
- Clark, Hubert Lyman. 1933. A handbook of the littoral echinoderms of Puerto Rico and the other West Indian islands. New York Academy of Science, Scientific Survey of Puerto Rico and the Virgin Islands, 16(1):147 p., 7 pls.

- _____. 1945. Echinoidea, 312-328, pls. 41-43. *in* Ladd, Harry S., and J. Edward Hoffmeister (eds.), *The geology of Lau, Fiji*, Bernice P. Bishop Museum Bulletin, 181 Honolulu.
- Clark, William Bullock. 1893b. The Mesozoic Echinodermata of the United States. U. S. Geological Survey Bulletin, 97: 1-207, pls. 1-50.
- Clark, William Bullock, and Mayville W. Twitchell. 1915. The Mesozoic and Cenozoic Echinodermata of the United States. U.S. Geological Survey Monograph, 54:1-227, pls. 1-108 (p. 229-341).
- Clegg, E. L. G. 1933. Echinoidea from the Persian Gulf. *Palaeontologia Indica* (Memoirs of the Geological Society of India), 22(1):1-35, pls. 1-3, text-figs. 1-2.
- Colby, Norman D., and Mark R. Boardman. 1989. Depositional evolution of a windward high-energy lagoon, Graham's Harbour, San Salvador, Bahamas. *Journal of Sedimentary Petrology*, 59(5):819-834.
- Conrad, Timothy A. . 1850. Descriptions of one new Cretaceous and seven new Eocene fossils. *Journal of the Academy of Natural Sciences of Philadelphia*, Series 2, 2: 39-41.
- Cooke, C. Wythe. 1954. Pliocene echinoids from Okinawa. U.S. Geological Survey Professional Paper, 264-c:45-52, pls. 9-12.
- _____. 1955. Some Cretaceous echinoids from the Americas. U.S. Geological Survey Professional Paper, 264-E:87-112, pls. 18-29, 4 text-figs.
- _____. 1957a. Geology of Saipan, Mariana Islands. Echinoids. U.S. Geological Survey Professional Paper, 280-J:361-364, pl. 119.
- Cotteau, Gustave Honoré. 1849-1856. Études sur les Échinides fossiles du département de l'Yonne, Vol. 1, Terrain Jurassique. Paris, 374 p., 46 pls.

- _____. 1865b. Catalogue raisonné des Échinides fossiles du département d l'Aube. Congrès Scientifique de France, 31 Session(1864):260-330.
- _____. 1862-1867. Echinides, 894 p., pls. 1007-1204, bis. 1087, bis. *In* Orbigny, Alcide Dessalines d' (ed.), Paléontologie Française. Description zoologique et geologique de tous les animaux Mollusques et Rayonnées fossiles de France. A. Terrain Crétacés, 7 G. Masson, Paris.
- _____. 1875. Description des échinides tertiaires des iles St. Barthélemy et Anguilla. Kungliga Svenska Vetenskapsakademiens Handlingar, 13(6):1-48, pls. 1-8.
- _____. 1877. Description des echinides des terrains tertiaires moyens de la Corse. Bulletin Société d'Agriculture, Histoire Naturelle et Arts Utiles de Lyon,
- _____. 1879d. Notice sur les échinides Urgoniens recueillis par M. Barrois dans la Province Oviédo (Espagne). Annales de Société Géologique de Paris, 10(2):8 p., 1 pl.
- _____. 1858-1880. Échinides nouveaux ou peu connus. Série 1. Paris, p. 1-230, pls. 1-32.
- _____. 1875-1880. Échinides regulaires, 468 p., pls. 143-262. *In* Orbigny, Alcide Dessalines d' (ed.), Paléontologie Française. Description zoologique et geologique de tous les animaux Mollusques et Rayonnées fossiles de France. C. Terrains Jurassiques, 10(1) G. Masson, Paris.
- _____. 1880a. Descriptions des Échinides Tertiaires de la Belgique. Academie Royale des Sciences, des Lettres, et des Beaux-Arts de Belgique, Mémoires Couronnés et Mémoires Savants étranger, 43:90 p., 6 pls.
- _____. 1883. Échinides Jurassiques, Crétacés et Éocènes du Sud-Ouest de la France. Société des Sciences Naturelles de la Charente-Inférieure, Annales, 19:45-253.
- _____. 1884a. Die Echinide der Stramberger Schichten. Palaeontographica (Supplement), 2(5):1-40.

- 1880-1885. 960p., pls. 263-520. *In* Orbigny, Alcide Dessalines d' (ed.), *Paléontologie Française. Description zoologique et geologique de tous les animaux Mollusques et Rayonnées fossiles de France. D. Terrains Jurassiques*, 10(2) G. Masson, Paris.
- 1886a. Descripción de algunas especies de equinidos Nummulíticos de la Provincia de Gerona. Comisión del Mapa Geológico España, Boletín, 13(77-81):285-289.
- 1887d. Catalogue des Échinides recueillis par M. Roussel dans le terrain Crétacé des Petites Pyrénées et des Corbières. Société Geologique de France, Bulletin Série 3, 15:639-665, pls. 16-20.
- 1885-1889. 672 p., pls. 1-200. *In* Orbigny, Alcide Dessalines d' (ed.), *Paléontologie Française. Description zoologique et geologique de tous les animaux Mollusques et Rayonnées fossiles de France. E. Terrains Tertiaires, Éocène 1*, G. Masson, Paris.
- 1882-1893. Échinides nouveaux ou peu connus, Deuxième série. Extrait du Bulletin Société Zoologique de France, No. 1 (1882): 1-19, pls. 1-2; No. 2 (1883): 20-36, pls. 2-4; No. 3 (1884): 37-51, pls. 5-6; No. 4 (1885): 53-66, pls. 7-8; No. 5 (1886): 69-89, pls. 9-10; No. 6 (1887): 91-103, pls. 11-12; No. 7 (1888): 105-121, pls. 13-14; No. 8 (1889): 123-134, pls. 15-16; No. 9 (1890): 135-148, pls. 17-18; No. 10 (1891): 149-162, pls. 19-20; No. 11 (1892): 163-174, pls. 20-21; No. 12 (1893): 175-185, pls. 23-24,
- 1889-1894. 789 p., pls. 201-384. *In* Orbigny, Alcide Dessalines d' (ed.), *Paléontologie Française. Description zoologique et geologique de tous les animaux Mollusques et Rayonnées fossiles de France. F. Terrains Tertiaires Éocène 2*, G. Masson, Paris.
- 1894. Sur quelques espèces d'Échinides du Liban, p. 346-360, pls. 1-2. *In* Association Française pour l'avancement des sciences Compte rendu de la 22me session. Besançon, 1893, 22

- . 1895. Description des Échinides recueillis par M. Lovisato dans le Miocene de la Sardaigne. Société Geologique de France Mémoires Paléontologie No. 13, 5(2):1-56, pls. 3-7.

Cotteau, Gustave Honoré, and Victor Gauthier. Échinides fossiles, *in* Morgan J. de (ed.), Mission scientifique en Perse. Tome troisième, Études géologiques. Partie II. Paléontologie, Première partie, Paris, 107 p., 16 pls.

Cotteau, Gustave Honoré, Pierre Alphonse Peron, and Victor Gauthier. 1876. Étages Urgo-Aptien et Albien, 90 p., 8 pls. *In* Échinides fossiles de l'Algerie, 1, (3) Paris.

- . 1878. Étage Cénomanién, 144 p., 8 pls. *In* Échinides fossiles de l'Algerie, 1, (4) Paris.

- . 1879. Étage Cénomanién, 145-234, pls. 9-16. *In* Échinides fossiles de l'Algerie, 1, (5) Paris.

- . 1879. Étage Turonien, 110 p., 8 pls. *In* Échinides fossiles de l'Algerie, 2, (6) Paris.

- . 1881. Étage Sénonien, 118 p., 8 pls. *In* Échinides fossiles de l'Algerie, 2, (7) Paris.

- . 1883. Terrain Jurassique, 79 p., 8 pls. *In* Échinides fossiles de l'Algerie, 1, (1) Paris.

Cotteau, Gustave Honoré, Peron Pierre Alphonse, and Victor Gauthier. 1884. Étage Sénonien, 119-197, pls. 9-20. *In* Échinides fossiles de l'Algerie, 2, (8) Paris.

Cotteau, Gustave Honoré, Pierre Alphonse Peron, and Victor Gauthier. 1884. Étages Tithonique et Néocomien, 99 p., 9 pls. *In* Échinides fossiles de l'Algerie, 1, (2) Paris.

- . 1885. Étage Éocène, 89 p., 8 pls. *In* Échinides fossiles de l'Algerie, 3, (9) Paris.

- . 1891. Étage Miocène et Pliocène, 273 p., 8 pls. *In* Échinides fossiles de l'Algerie, 3, (10) Paris.

- Cotteau, Gustave Honoré, and Jules Triger. 1855-1869. *Échinides du Département de la Sarthe, considérés au point de vue zoologique et stratigraphique*. J. B. Baillière et fils, Paris, 455 p., 75 pls., 2 tables.
- Cregin, Frank W. 1893. A contribution to the invertebrate paleontology of the Texas Cretaceous. Geological Survey of Texas Fourth Annual Report, :139-294, pls. 24-46.
- Cuttress, B. M. 1976. A new *Prionocidaris* (Echinodermata: Echinoidea) from the middle Miocene of Florida. *Proceedings of the Biological Society of Washington*, 89(12):191-198, 2 figs.
- . 1980. Cretaceous and Tertiary Cidaroida (Echinodermata: Echinoidea) of the Caribbean area. *Bulletins of American Paleontology*, 77(309):1-221.
- Dacqué, E. 1939. Die fauna der Regensburg-Kelheimer Oberkreide. *Abhandlungen der Bayerischen Akademie der Wissenschaften* (new series), 45:1-218, 117 pls.
- Dames, Wilhelm Barnim. 1878. Die Echiniden der vicentinischen und veronischen Tertiärlagerungen. *Palaeontographica*, 25: 1-100, pls. 1-11.
- DeGregorio, A. 1930b. Fossili triassici della Cave di Billiemi presso Palermo. *Annales de Géologie et de Paleontologie*, 54: 1-40, pls. 1-7.
- Démoly, F. 1928. Note de M. Jules Lambert sur des Échinides de la Savoie et de l'Isère. *Bulletin Société d'Histoire Naturelle de Savoie Chambéry*, 21:139-153, pl. 1.
- Desor, Pierre Jean Edouard. 1855-1858. *Synopsis des Échinides fossiles*. Paris & Wiesbaden: i-lxviii, 1-490, pls. 1-44.
- Desor, Pierre Jean Edouard, and P. de Loriol. 1872. *Echinologie Helvétique, description des oursins fossiles de la Suisse. Echinides de la période Jurassique*. Paris & Wiesbaden, 441 p., 61 pls.

- Döderlein, Ludwig Heinrich Philipp. 1902. Bericht über die von Herrn. Prof. Semon bei Amboina und Thursday Island gesammelten Echinoidea, p. 43-84; pls. 58-65, *in* Semon, H. P., Zoologisch Forschungsreisen in Australien um dem Malayischen Archipel, Bd. 5(6), Medizinischnaturwissenschaft Gesellschaft Jena, Denkschriften, 8(2):683-726, pls. 58-65.
- Duncan, Peter Martin. 1886. Note on the Echinoidea of the Cretaceous Series of Lower Narbadá Valley, with remarks upon their geological age. Records of the Geological Survey of India, 20 (1887):81-92.
- Duncan, Peter Martin, and W. Percy Sladen. 1883. The fossil Echinoidea of Kachh and Kattywar. Palaeontologia Indica, Series 14 (Memoirs of the Geological Survey of India), 1(4): 104 p., 13 pls.
- . 1882-1886. Fossil Echinoidea of Western Sind and the Coast of Biluchstán and of the Persian Gulf, from the Tertiary Formations, 392 p., 58 pls. *In* Tertiary and Upper Cretaceous fauna of western India, 1, (3), Palaeontologia Indica (Memoirs of the Geological Survey of India), Series 14, v. 1.
- Durham, J. W., H. B. Fell, A. G. Fischer, P. M. Kier, R. V. Melville, D. L. Pawson, and C. D. Wagner. 1966. Echinoids, *in* Moore, R. C. (ed.), Treatise on Invertebrate Paleontology, Part U: Echinodermata 3, University of Kansas Press and the Geological Society of America, Lawrence, Kansas.
- Ebert, Theodor. 1889. Die echiniden des Nord-und Mitteldeutschen Oligocäns. Abhandlungen zur geologischen Specialkarte von Preussen und den Thüringischen Staaten (Prussia. Geologische Landesanstalt), 9(1):1-111, 10 pls., text-figs.
- Efremov, J. A. 1940. Taphonomy; a new branch of geology. Pan-American Geologist, 74:81-93.

- El-Din Mahmoud. I.G. 1955. Études paléontologiques sur la faune Crétacique du Massif du Moghara (Sinai-Egypte). Publications de l'Institut du Desert d'Égypte, 8:1-195, fogs. 4-81, pls. 1-19.
- Fagerstrom, J. A. 1964. Fossil communities in paleoecology: their recognition and significance. Geological Society of America Bulletin, 75:1197-1216.
- Felix, J. P., and Hans Lenk. 1891. Uebersicht über die geologischen Verhältnisse des mexicanischen Staates Puebla. Palaeontographica, 37(5-6):117-139, pl. 30.
- Fell, Howard Barraclough. 1954. Tertiary and Recent Echinoidea of New Zealand. New Zealand Geological Survey Palaeontological Bulletin, 23:62 p., 15 pls., 15 text-figs.
- . 1962a. A new Cretaceous echinoid from the Franciscan Formation of California. Transactions of the Royal Society of New Zealand. Zoology, 2:27-30. 1 pl.
- . 1966. Cidaroids, p. U312-U338, in Moore, R. C. (ed.), Treatise on Invertebrate Paleontology, Part U: Echinodermata 3, University of Kansas Press and the Geological Society of America, Lawrence Kansas.
- Forbes, Edward. 1850c. Notes on the Echinodermata, In Dixon, Frederick (ed.), The geology and fossils of the Tertiary and Cretaceous Formations of Sussex, xvi + 422 + xvi p., 45 pls., text-figs., London.
- . 1852. Monograph of the Echinodermata of the British Tertiaries. Palaeontographical Society, London, 6:i-vii, 1-36, pls. 1-4, text-figs.
- Fourtau, Rene. 1912c. Contribution à l'étude des Échinides fossiles de la Syrie. Memoires d'Institut Égyptien, Cairo, 7(2):41-68, pls. 12-14.
- Fourtau, René. 1901c. Notes sur les Échinides fossiles d'Égypte. Bulletin Institut Égyptien, Série 4, 2(2):31-199, pls. 1-6.

- _____. 1909. Description des Échinides fossiles recueillies par MM. W. F. Hume et John A. Ball dans le désert Libyque et le nord du désert Arabique. Mémoires Institut Égyptien, Cairo, 6(2):93-175, pls. 6-9.
 - _____. 1914b. Catalogue des invertbrés fossiles de l'Égypte représentés dans les collections du Musée de Géologie au Caire. Terrains Crétacés, Ière partie, Échinodermes. Gouvernement d'Égypte, Cairo, 110 p., 8 pls.
 - _____. 1921. Catalogue des invertébrés fossiles de l'Égypte représentés dans les collections du Musée de Géologie au Caire. Terrains Crétacés, Troisième partie, Échinodermes (Supplément). Geological Survey of Egypt Palaeontological Series, 5:i-vi, 1-101, pls. 1-11.
- Fritsch, Karl Wilhelm Georg von. 1877. Die Echiniden der Nummuliten-Bildungen von Borneo. Die Eocänformation von Borneo und ihre Versteinerungen. Palaeontographica Supplement, 3(1):85-92, pl. 13.
- Gauthier, Victor. 1889a. Description des Échindes fossiles recueillis en 1885 et 1886 dans la region sud des hauts plateaux de la Tunisie par M. Philippe Thomas. Exploration Scientifique, Tunisie, 116 p., 6 pls.
- _____. 1891. Note sur quelques Échinides de l'Yonne. Bulletin de la Société des Sciences Historiques et Naturelles d l'Yonne, 44:75-96, pls. 1-2.
 - _____. 1899b. Révision des Échinides fossiles de l'Égypte, in Fourtau, René, Mémoires Institut Egyptien, 3:605-740, 4 pls.
 - _____. 1902a. 109-190, pls. 17-24. In Morgan, J. de (ed.), Mission scientifique en Perse. Études géologiques, partie 3, Paléontologie, Première partie, Échinides fossiles (Supplément), 3, Paris.
 - _____. 1902c. in Fourtau, René 1901c, Notes sur les Échinides fossiles d'Égypte, Bulletin Institut Égyptien Série 4, 2(2): 31-199, pls. 1-6.

- . 1903a. Contribution à l'étude des Échindes fossiles VII. Genre *Ganbirretia* Gauthier. Société Géologique de France Bulletin, Série 4, 3:19-29, pl. 1.
- Geinitz, Hanns Bruno. 1871-1875. Elbthalgebirge in Sachsen. Palaeontographica, 20(1,2):319 p., 12 pls.
- Ginsburg, Robert N. 1956. Environmental relationships of grain size and constituent particles in some south Florida sediments. American Association of Petroleum Geologists Bulletin, 40:2384-2387.
- Goldfuss, Georg August. 1826-1844. Petrefacta Germaniae, Albbildungen und Beschreibungen der Petrifacten Deutschlands und der angrenzenden, 1(1826):. Länder, Dusseldorf, 200 p. pls. 1-71.
- Grant, Ullyses S IV, and LEO George Hertlein. 1938b. The West American Cenozoic Echinoidea. University of California at Los Angeles, Publications in Mathematics and Physical Sciences, 2:i-ivi, 1-225, pls. 1-20, text figs. 1-17.
- Gras, Claude J. A. 1848. Description des oursins fossiles du département de l'Isère, précédée de notions élémentaires sur l'organisation et la glossologie de cette classe de zoophytes et suivie d'une notice géologique sur les divers terrains d'Isère. Bulletin Société des Statistique Sciences Naturelles et Arts Industriels Département de l'Isère, 4: 289-390, pls. 1-6; supplément p. 444-451, pl. 1.
- Greenstein, Benjamin J. 1989. Mass mortality of the West-Indian echinoid *Diadema antillarum* (Echinodermata: Echinoidea): A natural experiment in taphonomy. Palaios, 4(5):487-492.
- Greenstein, Benjamin J., and David L. Meyer. 1985a. Actuopaleontology of reef-dwelling echinoderms at Bonaire, Netherlands Antilles. Ohio Academy of Science Annual Meeting, Abstracts with Programs, 85(2):19-20.
- . 1985b. Mass mortality of the West-Indian echinoid *Diadema antillarum*: A natural experiment in taphonomy. Geological Society of America Abstracts with Programs, 17(7):p. 598.

- Gregorio, Antoine de. 1890. Monographie de la faune éocène de l'Alabama. Annales de Géologie et de Paléontologie, Livres 7-8:1-216, pls. 1-46.
- Gregory, John W. 1893. The Jurassic fauna of Cutch. Palaeontologia Indica (Memoirs of the Geological Survey of India Series 9, 2(1):11 p., 2 pls.
- . 1897a. On the affinities of the Echinothuridae; and on *Pedinothuria* and *Helicodiadema*, two new genera of Echinoidea. Quarterly Journal of the Geological Society of London, 53:112-122, pl. 7, text-figs. 1-3.
- . 1898. A collection of Egyptian fossil Echinoidea. Geological Magazine, new series, decade 4, 5:149-161, pls. 5-6.
- Guembel, Carl Wilhelm. 1861-1869. Geognostische Beschreibung des Königreichs Bayern. Part II. Geognostische Beschreibung des ostbayerischen Grenzgebirges oder des Bayerischen und Oberpfälzer Waldgebirges. Gottia, viii + 968 p. 16 pls. text-figs.
- Harland, W. B., A. V. Cox, P. G. Llewellyn, C. A. G. Pickton, A. G. Smith, and R. Walters. 1982. A Geologic Time Scale. Cambridge University Press, Cambridge, 131 p.
- Hassan, M. Y. 1969. Contributions to the echinoid fauna of the Maestrichtian-Paleocene strata of south western Egypt. Proceedings of the Egyptian Academy of Science, 22:15-19, pl. 1.
- Hawkins, Herbert Leader. 1912f. The species of *Cidaris* from the lower Greensand of Faringdon. Geological Magazine, decade 5, 9:529-540, pls. 25-26.
- Hawkins, H. L., and S. M. Hampton. 1927. The occurrence, structure and affinities of *Echinocystis* and *Palaeodiscus*. Quarterly Journal of the Geological Society of London, 83: 574-603.

- Hendler, Gordon. 1977. The differential effects of seasonal stress and predation on the stability of reef-flat echinoid populations. *Proceedings of the Third International Coral Reef Symposium, Miami*, 3:217-233.
- Herklots, Janus Adrian. 1854. Fossiles de Java. Description des restes fossiles d'animaux des terrains Tertiaires de l'Ile de Java recueilles par F. Junghuhn. Pt. IV. Échinodermes. Leide, p. i-iv, 1-24, 5 pls.
- Hess, H. 1974. Eine Echinodermen-fauna aus dem mittleren Dogger des Aargauer Juras. *Schweizerische Palaeontologische Abhandlungen*, 92(1972):1-133, 90 figs., 26 pls., 10 tables.
- Himmelman, J. H., and D. H. Steele. 1971. Foods and predators of the green sea urchin *Strongylocentrotus droebachiensis* in Newfoundland waters. *Marine Biology*, 9:315-322.
- Hughes, Roger N., and Helen P. Hughes. 1981. Morphological and behavioural aspects of feeding in the Cassidae (Tonnacea, Mesogastropoda). *Malacologia*, 20(2):385-402.
- Innocenti, Giulia Degli. 1924a. Due nuovi echinidi dell'Eocene Istriano. *Rivista Italiana di Paleontologia e Stratigraphia*, 30:41-46, pl. 2.
- Jackson, Robert Tracy. 1922. Fossil Echini of the West Indies. Carnegie Institute, Washington, Publication 306:i-iv, 1-103, pls. 1-18.
- Jeannet, Alphonse. 1927. Un *Paracidaris* nouveau du Jura argovien. *Eclogae Geologicae Helvetiae*, 20(3):393-396, pl. 12.
- . 1928a. Contribution à l'étude des Échinides tertiaires de la Trinité et du Vénézuëla. *Memoires de Société Paléontologique Suisse (Schweizerische Paläontologische Gesellschaft Abhandlungen)*, 48:1-49, pls. 1-6, text-figs. 1-12.

- _____. 1929. Révision des *Rhabdocidaris* du Jurassique supérieur Suisse. Abhandlungen der Schweizerischen Palaeontologischen Gesellschaft, 48(3):1-45, figs. 1-17, pls. 1-5.
 - _____. 1933d. Sur quelques Échinides néocomiens du Vorarlag. Eclogae Geologicae Helvetiae, 26:233-234.
 - _____. 1933e. Sur quelques *Leiocidaris* jurassiques suisses. Mémoires de la Société Paléontologique Suisse, 53:1-7, 1 pl.
 - _____. 1955. Sur quelques Échinides fossiles étrangers. Société Géologique de France, Bulletin Série 6, 5:553-561, pls. 25-26, text-figs 1a-1b.
- Jeannet, Alphonse, and R. Martin. 1937. Ueber neozoische Echinoidea aus dem Niederländisch-Indischen Archipel. Leidsche Geologische Mededeelingen (Later Leidse Geologische Mededelingen), 8(6):215-308, figs. 1-67.
- Johnson, R. G. 1957. Experiments on the burial of shells. Journal of Geology, 65:527-535.
- _____. 1960. Models and methods for the analysis of the mode of formation of fossil assemblages. Geological Society of America Bulletin, 71:1075-1086.
- Jones, Brian. 1987. Biostratigraphy of a modern ophiuroid: A study of preservation potential. Unpublished Student Project, West Indies Lab, St. Croix U.S. Virgin Islands,
- Kew, William Stephen Webster. 1920. Cretaceous and Cenozoic Echinoidea of the Pacific Coast of North America. University of California at Berkeley, Department of Geology Bulletin, 12:23-236, pls. 3-42, 5 text-figs.
- Kidwell, Susan M., and Tomasz K. Baumiller. in press. Experimental disintegration of regular echinoids: roles of temperature, oxygen and decay thresholds. Paleobiology,

- _____. 1989. Post-mortem disintegration of echinoids: Effects of temperature, oxygenation, tumbling and algal coats. Abstracts of the 28th International Geological Congress, Washington, 2:188-189.

- Kier, Porter M. 1958. New American Paleozoic echinoids. Smithsonian Miscellaneous Collections, 135(9)

- _____. 1965. Evolutionary trends in Paleozoic echinoids. Journal of Paleontology, 39:436-465.

- _____. 1966. A new echinoid from the Cretaceous Pierre Shale of eastern Wyoming, in Gill, J. R., Cobban, W. A., The Red Bird section of the Upper Cretaceous Pierre Shale, United States Geological Survey Professional Paper 393-A, U.S. Government Printing Office,

- _____. 1968. Triassic echinoids of North America. Journal of Paleontology, 42(4):1000-1006.

- _____. 1974. Evolutionary trends and their functional significance in the post-Paleozoic echinoids. Journal of Paleontology, 48(Supplement):Paleontological Society Memoir 5: 1-95.

- _____. 1977. The poor fossil record of the regular echinoid. Paleobiology, 3(2):168-174.

- Kier, Porter Martin. 1963. Tertiary echinoids from the Caloosahatchee and Tamiami Formations of Florida. Smithsonian Miscellaneous Collections, 145(5):1-63, pls. 1-18, text-figs. 1-58.

- _____. 1972. Tertiary and Mesozoic echinoids of Saudi Arabia. Smithsonian Miscellaneous Contributions, Paleobiology, 13: 1-41, 7 figs., 10 pls., 2 tables.

- _____. 1977. Triassic echinoids. Smithsonian Contributions to Paleobiology No. 30. Smithsonian Institution Press, Washington, 88 p.

- . 1984. Echinoids from the Triassic (St. Cassian) of Italy, their lantern supports and a revised phylogeny of Triassic echinoids. *Smithsonian Contributions to Paleobiology* No. 56. Smithsonian Institution Press, Washington, 41 p.
- Kier, Porter Martin, and Mary Hurd Lawson. 1978. Index of living and fossil echinoids, 1924-1970. *Smithsonian Contributions to Paleobiology* No. 34. Smithsonian Institution Press, Washington, 182 p.
- Kier, Porter M., and Richard E. Grant. 1965. Echinoid distribution and habits, Key Largo Coral Reef Preserve, Florida. *Smithsonian Miscellaneous Collections*, 149:1-68.
- Kier, Porter M., and Mary H. Lawson. 1978. Index of living and fossil echinoids 1924-1970. *Smithsonian Contributions to Paleobiology*, No. 34:182 p.
- Klipstein, August von. 1843-1883. *Mitteilungen aus dem Gebiete der Geologie und Palaeontologie. Beiträge zur geologischen (und topographischen) Kenntniss der östlichen Alpen*, Giessen, 2 vols.
- Koch, Antal. 1885. Die alttertiären Echiniden Siebenbürgens. *Jahrbuch Kaiserliche Ungarischen Geologische Anstalt. Mittheilungen*, 7:47-132.
- König, H. 1982. Unterpermische Seeigel aus Kreta (Griechenland). *Mittheilungen, Neues Jahrbuch fuer Geologie und Palaeontologie*, 1982(3):167-175.
- Krenkel, H. 1928. Echiniden der pommerschen Kreide. *Abhandlungen aus dem geologisch-palaeontologischen Institut der Universität Greifswald*, 7:1-32, pls. 1-3.
- Kutscher, M. 1988. Die echinodermen des Magdeburger Grunsandes (Mittel-Oligozan). *Abhandlungen Ber Naturk Vorgeschichte*, 12(6):3-14.
- Lambert, J., and V. Pérebaskine. 1929. Notes sur quelques Échinides du Soudan. *Bulletin Société Géologique de France, Série 4*, 29:471-477, pl. 38.

- Lambert, J., and P. Thiéry. 1909. Notes échinologiques. I. Sur le genre *Cidaris*. II. Sur les genres d'Échinides proposés par Brandt en 1835. III. Sur les genres de sous-famille des Diadematidae. Bulletin des Société des Sciences Naturelle, Haute-Marne, 6(23-24):43-60, pl. 1.
- Lambert, Jules M. 1892. Recherches sur le Échinides de l'Aptien de Grandpré. Société Géologique de France, Bulletin Série 3, 20:38-100, pls. 2-4.
- _____. 1899a. Note sur les Échinides de la Craie de Ciply. Société Belge de Géologie, de Paléontologie, et d'Hydrologie Bulletin (Later, Société Belge de Géologie Bulletin) Série 2, 11:1-50, pls. 2-5.
- _____. 1899b. Études sur quelques Échinides de l'Infra-Lias et du Lias. Bulletin Société des Sciences Historiques et Naturelles de l'Yonne, 53(2):3-57, pl. 1.
- _____. 1902a. Description des Échinides fossiles de la province de Barcelone. Société Géologique de France, Mémoires Paléontologie 24, 9:1-58, 4 pls., 5 text-figs.
- _____. 1906b. Description des Échinides fossiles de la province de Barcelone. Deuxième et troisième parties, Échinides des terrains Miocène et Pliocène. Appendice: Genre *Hemiheliopsis*. Société Géologique de France, Mémoires Paléontologie, 14(1907)(2-3):59-128, pls. 6-10.
- _____. 1908a. Notes sur quelques Échinides de la Haute-Garonne, II. Société Géologique de France, Bulletin Série 4, 8: 360-375.
- _____. 1908c. Note sur les Échinides du Calcaire Pisolithique du bassin de Paris. Association Française pour l'avancement du Science, Comptes Rendu 1907, 36(1):201-202.
- _____. 1907-1909. Description des Échinides fossiles des terrains miocéniques de la Sardaigne. Mémoires Société Paléontologique Suisse, 34,35(1907,1909):1-142, 11 pls.

- 1909a. Revision de quelques Cidaridae de la Baie. Société des Sciences Historiques et Naturelles de l'Yonne, Bulletin, 62:113-175.
- 1909c. Observations à l'occasion de l'étude de quelques Échinides de l'Ardeche et du Gard. Annales, Société Linnéenne d'Lyons, 56:93-98.
- 1909d. Liste critique des Échinides du Calcaire à Baculites du Cotentin. Société Linnéenne de Normandie, série 6, 2:3-30, pl. 1.
- 1910a. Les Échinides des Iles Snow-Hill et Seymour. Wissenschaftlich Ergebnisse Schwedischen Südpolar Expedition, 1901-1903, 3(2):1-15, pl. 1.
- 1911c. Étude sur les Échinides Crétacés de Rennes-les-Bains et des Corbières. Bulletin Société d'Études Scientifique de l'Aude, 22:66-183, pls. 1-3.
- 1911f. Description des Échinides Crétacés de la Belgique, principalement de ceux conservés au Musée Royal de Bruxelles. II. Échinides de l'étage Senonien. Mémoires Musée Royal d'Histoire Naturelle de la Belgique, 4:81 p., 3 pls.
- 1912a. Études géologiques et paléontologiques sur le Bordelais, par l'Abbé Labrie et J. Lambert. I. Revision des Échinides fossiles du Bordelais. Échinides Éocènes. Actes Société Linneenne de Bordeaux, 66:45-120, pls. 1-3.
- 1913f. Échinides Calloviens du plateau de Césareda (Portugal). Communications Servicos Geologicos Portugal, 9: 69-76, pl. 1.
- 1915b. Revision des Échinides fossiles du Bordelais. II. Échinides de l'Oligocène. Actes Société Linneenne de Bordeaux, 69:13-59.
- 1910-1916. Descriptions des Échinides néogènes du Bassin de Rhône. Mémoires Société Paléontologique Suisse, 37(1910-1911):1-48, pls. 1-3.

- _____. 1916b. Sur l'existence de l'étage Valangien dans l'Aube et dans l'Yonne (avec observations sur les Échinides). Mémoires Société Académique d'Agriculture des Sciences, Artes et Belles-Lettres du Département de l'Aube, 80(troisième série):19-94.
- _____. 1916d. Note sur quelques Échinides de la Grande Oolite (Bathonien) et du Callovien du Massif de Porto-de-Moz (Portugal). Communications Servicos Geologicos Portugal, 11(1915-1916):85-96, pl. 1.
- _____. 1918a. Revision des Échinides du Nummulitique de la Provence et des Alpes Françaises. Mémoires Société Paléontologique Suisse, 43:1-161, pls. 1-2.
- _____. 1920c. Échinides fossiles des environs de Santander. Annales. Société Linnéenne de Lyo, 66(1919):1-32, pls. 1-3.
- _____. 1920f. Notes sur quelques Échinides du Crétacé inférieur de la Provence. Notes Provençales, 11:1-23, pls. 1-2.
- _____. 1920h. Échinides fossiles des environs de Santander recueillis par M.L. Mengaud. Annales. Société Linnéenne de Lyon, 66:1-56, pls. 1-3.
- _____. 1924a. Note sur les Échinides de la collection Ambayrac. Riviera Scientifique et Mineralogique, 2(1):3-8.
- _____. 1924b. Sur un Échinide nouveau du Bassin de Paris. Société Géologique de France, Comptes rendu, 1924:p. 98, 1 fig.
- _____. 1924c. Sur un échinide nouveau du Rhétien des Préalpes bernoises. Eclogae Geologicae Helvetiae, 18(3):448-450, figs. 1-2.
- _____. 1927a. Révision des Échinides fossiles de la Catalogne. Memorias Museo de Ciencias Naturales Barcelona, Seria Geologico, 1(1):1-102, pls. 1-4.
- _____. 1928d. Révision des Échinides fossiles du Bordelais III. Échinides du Miocène. Actes. Société Linnéenne de Bordeaux, 79:71-125.

- _____. 1931. Note sur le groupe des *Oligopygus*, la nouvelle famille des Haimeidae, et sur quelques Échinides fossiles de Cuba. Société Géologique de France. Bulletin série 5, 1: 289-304, pl. 17, 3 text-figs.
- _____. 1931-1932. Étude sur les Échinides fossiles du Nord de l'Afrique. Mémoires Société Géologique de France. Mémoire 16 nouveau série 7, pt. 2(1931):1-108, pls. 1-4, pt. 4(1932):109-228, 4 pls.
- _____. 1932. Sur quelques échinides du Tithonique et de l'Éocène des environs de Chambéry. Bulletin de Société d'Histoire Naturelle de Savoie, 22:250-263.
- _____. 1933a. Échinides de Madagascar communiqués par M. H. Besairie. Annales Géologiques du Service des Mines Madagascar, 3:1-49, pls. 1-4.
- _____. 1933b. Échinides fossiles du Maroc. Protectorat de la République Française au Maroc, Service des Mines et de la Carte Géologique, Notes et Mémoires, 27:27-79, figs. 1-3, pls. 1-3.
- _____. 1933c. Note sur quelques échinides de la région de Chatillon-sur-Seine. Bulletin de la Société Géologique de France, Notes et Mémoires, 5(3):173-180, pl. 7.
- _____. 1933d. Supplément à la revision des échinides fossiles de la Catalogne. Bulletin de la Institució Catalana d'història Natural, 33(4-5):183-195, figs. 1-2, pl. 4.
- _____. 1935a. Note sur les Échinides Jurassiques et les oscillations du détroit Poitevin. Bulletin. Société Géologique de France, série 5, 4:523-536, pls. 26-27.
- _____. 1935b. Sur quelques échinides fossiles de Valence et d'Alicante communiqués par M. le Prof. Darder Pericás. Boletín de la Sociedad Española de Historia Natural, 35(7): 359-371, pls. 41-42.

- _____. 1935d. Notes sur quelques Échinides fossiles. III. Échinides du Mexique. Bulletin. Société Géologique de France, série 5, 5:365-376, pl. 16, text-figs. 1-2.
- _____. 1935f. Échinides crétacés d'Espagne. I. Sur quelques échinides crétacés des provinces de Burgos, Palencia et Leon, communiqués par M. Raymond Ciry; II. Sur quelques échinides crétacés d'Espagne, communiqués par M. le Prof. Royo y. Gomez. Boletín de la Sociedad Española de Historia Natural, 35(10):513-526, pls. 57-58.
- _____. 1936c. Nouveaux échinides fossiles de Madagascar. Annales Géologiques du Service des Mines, Madagascar, 6:1-32, pls. 1-4.
- _____. 1937f. Échinides fossiles du Maroc. Notes et Mémoires. Service des Mines et Carte Géologique, Maroc, 39:39-109, pls. 1-4, 4 text fogs.
- Lambert, Jules M., and L. H. Savin. 1905. Note sur quelques Échinides de diverses régions. Bulletin Société Statistique des Sciences Naturelles et Arts Industriels, Département d'Isère, Série 4, 8:306-315.
- Lambert, Jules M., and Savin L.H. 1906. Note sur deux Échinides nouveaux des Alpes Maritimes. Annales Société des Lettres des Sciences et d'Arts Alpes Maritimes, 20:67-68; 96-97, 1 pl.
- Lambert, Jules M., and P. Thiéry. 1908. Révision des Échinides Jurassiques du Département de la Haute-Marne. Bulletin Société Naturelle. Haute-Marne, Année 20:32 p., pl. 4.
- _____. 1909-1925. Essai de nomenclature raisonnée des Échinides. Librairie L. Ferrière, Chaumont, 607 p., 15 pls., 51 text-figs.
- Laube, Gustav Carl. 1864. Die fauna der Schichten von St. Cassian. I. Abt. Echiniden. Denkschriften der Kaiserlichen Akademie der Wissenschaften, Mathematische-Naturwissenschaftliche Klasse. Vierundzwanzigster Band, 24(1865):223-296.

- _____. 1868. Ein Beitrag zur Kenntniss der Echinodermen des vicentischen Tertiärgebietes. Kaiserliche Akademie der Wissenschaften in Wien, Mathematische-Naturwissenschaftlich Klasse, Denkschriften, 29(2):1-38.
- Laube Gustav Carl. 1871. Die echinoiden der Österreich-Ungarischen obere Tertiäerablagerungen. Kaiserlich-Koenigliche Geologische Reichsanst. in Wien, Abhandlungen, 5(3):55-74, 4 pls.
- Lawrence, D. R. 1968. Taphonomy and information losses in fossil communities. Geological Society of America Bulletin, 82:237-265.
- _____. 1971. The nature and structure of paleoecology. Journal of Paleontology, 45:593-607.
- Leonardi, Piero, and Lovo M. 1950. Nuove forme di echinodermi della fauna cassiana di Cortina d'Ampezzo. Studi Trentini Scienze Nat., Trent, 27:3-10, pls. 1-2.
- Lessios, H. A., D. R. Robertson, and J. D. Cubit. 1984. Spread of *Diadema* mass mortality through the Caribbean. Science, 226:335-337.
- Loriol, Perceval d'. 1880b. Monographie des Échinides contenus dans les couches nummulitiques de l'Égypte. Mémoires Société des Sciences Physiques et d'Histoire Naturelles, Genève, 27: 59-148, 11 pls.
- Loriol, Perceval d'. 1882a. Description des Échinides des environs de Camerino (Toscane) précédés d'une notice Stratigraphique. Mémoires Société des Sciences Physiques et d'Histoire Naturelles Genève, 28:1-32, 3 pls.
- Loriol, Perceval d'. 1887-1888. Recueil d'études paléontologiques sur la Faune Crétacique du Portugal. Description des Échinodermes. Acad. Real Science Lisboa, Mémoires Comm. Geologicos Portugal, 2:1-122, 22 pls.

- _____. 1888a. Matériaux pour l'étude stratigraphique et paléontologique de la Province d'Angola. Description des Échinides de la Province d'Angola. Mémoires Société des Sciences Physiques et d'Histoire Naturelle Genève, 30, pt. 1(2):97-114, pls. 6-8.
 - _____. 1884-1905. Notes pour servir à l'étude des échinodermes série 1, no. 5 (1897). Mémoires Société des Sciences Physiques et d'Histoire Naturelle Genève, 32(9):1-26, 3 pls.
 - _____. 1884-1905. Notes pour servir à l'étude des échinodermes série 1, no. 7 (1899). Mémoires Société des Sciences Physiques et d'Histoire Naturelle Genève, 33, pt. 2(1):1-34, 3 pls.
 - _____. Faune Jurassique du Portugal: Échinodermes. Acad. Real Science Lisboa, Comm. Geologicos Portugal, Lisbon, 179 p., 29 pls.
- Loriol, Perceval de. 1873a. Echinologie Helvétique. Description des oursins fossiles de la Suisse, Deuxième partie. Échinides de la période Crétacée. Chez H. Georg, Libraire, Genève, Bale, Lyon, 398 p., 33 pls.
- _____. 1875a. Echinologie helvétique. Descriptions des oursins fossiles de la Suisse. Troisième partie. Échinides de la période Tertiaire. Mémoires de la Société Paléontologique Suisse, 2:1-142, pls. 1-23.
 - _____. 1882b. Eocaene Echinoideen aus Aegypten und der libyschen Wüste. Palaeontographica, 30(2):59 p., 11 pls.
 - _____. 1885. Premier supplément à l'Echinologie Helvétique. Mémoires Société Paléontologique Suisse, 12(3):1-25.

- . 1884-1905. Notes pour servir à l'étude des échinodermes. Série 1, No. 1(1884): p. 605-643, 4 pls.; No. 2(1887): p. 365-407; No. 3(1891): 31 p., 3 pls.; No. 4(1894): p. 467-497, pls. 22-24; No. 6(1897): p. 142-178, pls. 6-8; No. 8(1900): p. 55-96, pls. 6-9; No. 9(1901): 48 p., 3 pls.; No. 10(1902): 32 p., 4 pls.; Série 2, No. 1(1903): 50 p., 3 pls.; No. 2(1904): 68 p., 4 pls.; No. 3(1905): 32 p., 2 pls. Series 1 Nos. 1 and 2 in *Recueil Zoologique Suisse*, vols. 1 and 4; No. 3 in *Mémoires de la Société de Physique et d'Histoire Naturelle de Genève*, v. 8 (supplement); Nos. 4, 6 and 8 in *Revue Suisse de Zoologie et annales du Musée d'Histoire Naturelle de Genève*, vols. 2,5 and 8; Nos. 9, 10 and Series 2, Nos. 1, 2 and 3 publ. by Bâle et Genève,
- . 1909. Notes sur quelques espèces d'Échinides fossiles de Syrie. *Revue Suisse de Zoologie*, 17:219-248, 1 pl.
- MacDonald, K. B. Paleocommunities: toward some confidence levels, p. 87-106, in Scott, R. W., and West R.R. (eds.), *Structure and Classification of Paleocommunities*, Dowden, Hutchinson and Ross, Stroudsburg, PA.
- Malaroda, R. 1951. Il lattorfiano del Montecchio di Costozza (Colli Berici). Parte prima. I. Macrofossili. *Memorie Museo di Storia Naturale Verona*, 2:147-210, pls. 1-7.
- Maury, Carlotta J. 1936. O Cretaceo de Sergipe. *Memorias Servicos Geologicos et Minas, Brazil*, 3:i-xxv, 1-283, 28 pls.
- Mayer-Eymar, Carl David Wilhelm. 1898a. Neue Echiniden aus dem Nummulitengebilden Aegyptens. *Vierteljahresschrift Naturforschende Gesellschaft in Zuerich*, 53:46-56, pls. 3-6.
- Meneghini, Giuseppe. 1862. Echinodermi fossili Neogenici di Toscana. *Neues Jahrbuch für Mineralogie, Geologie und Palaöntologie*, :638-639.
- . 1867-1881. Monographie des fossiles du Calcaire Rouge ammonitique (Lias supérieur) de Lombardie et de l'Apennin Central. *Lombarde ou Description des fossiles de Lombardie*, Série 4:242 p., 32 pls.

- Mercier, Jean. 1932. Études sur les Échinides du Bathonien de la bordure occidentale du Bassin de Paris. Mémoires Société Linnéenne de Normandie, nouvelle série, Géologie, 2:1-273, 11 pls., 34 text-figs.
- . 1937c. Échinides du Lias de la bordure du Massif Armoricaïn. Bulletin de la Société Géologique de Normandie et des amis du Museum de Havre, 39:12-42, pl. 1.
- Meyer, David L., and Kaniaulono B. Meyer. 1986. Biostratigraphy of Recent crinoids (Echinodermata) at Lizard Island, Great Barrier Reef, Australia. *Palaos*, 1(3):294-302.
- Michalet, Louis Eugene. 1895. Le Bathonien des environs de Toulon et ses Échinides. Description d'un nouveau genre *Heteropedina*. Bulletin Société Géologique de France, série 2, 23:50-75, 5 figs.
- Michelin, Hardouin. 1845. Zoophytes, Échinodermes et Stellérides de l'île Maurice, publiée avec le matériaux et les notes laissés par J. Desjardins, sous la direction et par les soins de M.F.E. Guérin Meneville. Mag. Zool. Anat. Comp. et Palaeont, 1:27 p., 6 pls.
- . 1860. Description de quelques Échinides nouveaux, in Goubeit, J. Quelques mots sur l'Étage Éocène moyen dans le bassin de Paris, Bulletin Société Géologique de France série 2, 17:137-149, pl. 2.
- Mortensen, Theodor. 1943. A monograph of the Echinoidea. *Camarodonta* II, 3(3):446 p., 215 text-fig., atlas, 66 pls.
- Müller, A. H. 1951b. Grundlagen der Biostratonomie. Deutsche Akademie der Wissenschaften zu Berlin, Abhandlungen; Klasse für Mathematische und allgemeine Naturkunde, 1950(3):147 p., text figs. 1-79.
- . 1955. Beiträge zur Stratonomie und Ökologie des germanischen Muschelkalkes. *Geologie*, 4:285-297.

- _____. Fossilization (Taphonomy), p. A2-A78, in Robison, R. A., and C. Teichert (eds.), *Treatise on Invertebrate Paleontology (A): Introduction*, University of Kansas Press, Lawrence Kansas.
- _____. *Lehrbuch der Paläozoologie. I. Allgemeine Grundlagen*, 2nd Edition. G. Fischer, Jena, 405 p., 228 text-figs.
- Nicklès, Tousaint Joseph) René. 1892. *Recherches géologiques sur les terrains secondaires et Tertiaires de la Province d'Alicante et du sud de la province de Valence*. Annales Hébert, 1:1-219, pls. 1-10 (echinoderms pp. 202-204).
- Nisiyama, Syozo. 1966. The echinoid fauna from Japan and adjacent regions. Part 1. *Palaeontological Society of Japan Special paper*, No. 11:277 p., 18 pls.
- Olson, E. C. 1980. Taphonomy: its history and role in community evolution, p. 5-19, in Behrensmeyer, A. K., and A. P. Hill (eds.), *Fossils in the making. Vertebrate Taphonomy and Paleoecology*, University of Chicago Press, Chicago, 338 p.
- Ooster, William Alexandre. 1865. *Synopsis des Échinodermes fossiles des Alpes Suisses*. Genève et Bâle, 131 p., 29 pls.
- Oppenheim, Paul. 1900-1901. Die Priabonaschichten und ihre Fauna, im Zusammenhange mit gleichalterigen und analogen Ablagerungen vergleichend betrachtet. *Palaeontographica*, 47(1900-1901):1-348, pls. 1-21.
- _____. 1902b. Revision der tertiären Echiniden Venetiens und des Trentino, unter Mittheilung neuer Formen. *Deutsche Geologische Gesellschaft, Zeitschrift*, 54:159-283, pls. 7-9, 23 text-figs.
- Orbigny, Alcide Dessalines d'. 1849. *Cours élémentaire de Paléontologie et de Géologie Stratigraphique*, Vol. 1. Chapitre de la Fossilization. V. Masson, Paris, p. 34-69.
- Parona, Carlo Fabrizio. 1892. Revisions della fauna Liassica di Gozzano in Piemonte. *Memorie Reale Accademia de Scienze*, Torino, Serie 2, 43:1-59.

- Pávay, Elek. 1873. Die geologische Verhältnisse der Umgebung von Klausenburg. Mitteilungen Jahresberichte Kaiserliche Ungar. Geol. Anstalt, Budapest, 1(1871):351-441.
- . 1874. Die fossilen Seeigel des Ofnermergels. Kaiserliche Ungar. Geologische Anstalt, Budapest, Jahresberische, 3(2): 1-188, 8 pls.
- Peterson, C. H. 1976. Relative abundances of living and dead molluscs in two California lagoons. *Lethaia*, 9:137-148.
- Petitot, M. L. 1961. Contribution à l'étude des Échinides fossiles du Maroc (Jurassique et Crétacé). Notes et Mémoires du Service Geologique du MAroc, 146(1959):1-183, 6 figs., atlas; p. 1-72, 17 pls.
- Philip, G. M. 1963b. A new genus of regular echinoid from the lower Eocene of British Somaliland. *Journal of Paleontology*, 37(5):1104-1109, figs. 1-3.
- . 1963d. The Tertiary echinoids of southeastern Australia. I. Introduction and Cidaridae (1). *Proceedings of the Royal Society of Victoria*, 76(2):181-226, 6 pls., 5 text-figs.
- . 1964. The Tertiary echinoids of southeastern Australia. II. Cidaridae (2). *Proceedings of the Royal Society of Victoria*, 77(2):433-478.
- . 1965b. The Tertiary echinoids of southeastern Australia. III. Stirodonta, Aulodonta and Camarodonta. *Proceedings of the Royal Society of Victoria*, 78:181-196, 4 pls., 4 text-figs.
- . 1969. The Tertiary echinoids of southeastern Australia. IV. Camarodonta (2). *Proceedings of the Royal Society of Victoria*, 82(2):233-276, 16 pls., 8 text-figs.
- Philippi, Rudolphe Amandus. 1860. Reise durch die Wüste Atacama...im Sommer 1853-1854. Halle, ix + 192 + 62 p., 27 pls., map.

- Plotnik, Roy E. 1986. Taphonomy of a modern shrimp: Implications for the Arthropod fossil record. *Palaios*, 1(3): 286-293.
- Pomel (Nicolas) Auguste. 1888b. Sur le *Thagastea wetterlei*, nouveau genre d'Échinide éocène d'Algérie, et observations sur le groupe des Fibulariens. *Academie des Sciences (Paris) Comptes rendus*, 106(5):373-374.
- . Paléontologie ou description des animaux fossiles de l'Algérie. Échinodermes, Livraison 2. Alger 1887, Paris.
- Quenstedt, Friedrich August von. 1858. *Der Jura*. Tübingen, 5 pts, vi + 842 p., 103 pls.
- . 1875. *Petrefactenkunde Deutschlands*. Pt. 1 Echiniden, v. 3. Fues's Verlag (R. Reisland), Leipzig.
- . 1882-1885. *Handbuch der Petrefaktenkunde*. Tübingen, viii + 1239 p., 100 pls., text-figs.
- Raup, D. M. 1979. Biases in the fossil record of species and genera. *Bulletin of the Carnegie Museum of Natural History*, 12:85-91.
- Ravn, Jesper Peter Johannes. 1928. De regulaere Echinider i Danmarks Kridtaflejringer. *Kongelige Danske Videnskabernes Selskab Skrifter Ser. 9* (also *Communic. Paléont.* Copenhagen, v. 29: 1-62, pls. 1-6), 1(1):1-63, 6 pls.
- Régis, M. B. 1977. Organization microstructurale du stérom de l'échinoïde *Paracentrotus lividus* (Lamarck) et ses éventuelles incidences physiologiques. *Comptes rendus de la Academie des Sciences, Paris, Série D*285:189-192.
- Remes, MAuric. 1905. Nachtrage zur fauna von Stramberg. VI. Crinoiden-, Asteriden- und Echinoiden-Reste aus dem weissen Kalkstein von Stramberg. *Beiträge Paläontologie Österreich-Ungarns und des Orients*, 18:59-63, pl. 7.

- Reyment, R. A. 1986. Nekroplanktonic dispersal of echinoid tests. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 52(3-4):347-349.
- Richter, Rudolph. 1922. Flachseebeobachtungen zur Paläontologie und Geologie III-IV. *Senckenbergiana*, 4:103-141, pl. 1.
- . 1931. Tierwelt und Umwelt im Hunsrückschiefer; zur Entstehung eines schwarzen Schlammsteins. *Senckenbergiana*, 13:299-342.
- . 1937. Die "Salter'sche Einbettung" als Folge und Kennzeichen des Häutungsvorganges. *Senckenbergiana*, 19(413-431)
- . 1942. Die Einkippungsregel. *Senckenbergiana*, 25:181-206.
- Roemer, Friedrich Adolph. 1840-1841. Versteinerungen des Norddeutschen Kreidegebirges. Hannover, iv + 145 p., 16 pls.
- Roman, J. 1976. Échinides Éocènes et Miocènes du Qatar (Golfe Persique). *Annales de Paleontologie*, 62(1):49-85, 13 figs., 4 pls.
- Rose, E. P. F. 1978. Some observations on the Recent Holoctypoid *Echinoneus cyclostomus* and their palaeoecological significance. *Thalass. Jugoslav*, 12: 299-306.
- Rosenkranz, D. 1971. Zur Sedimentologie und Ökologie von Echinodermen-Lagerstätten. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, 138(2):221-258.
- Ruhrmann, G. 1971a. Riffe-ferne Sedimentation unterdevonischer Krinoidenkalke im Kantabrischen Gebirge (Spanien). *Neues Jahrbuch Für Geologie und Paläontologie Mh. Jg.*, 1971(4): 231-248.
- . 1971b. Riffe-nahe Sedimentation paläozoischer Krinoiden Fragmente. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, 138:56-100.

- Sanchez Roig, Mario. 1952a. Nuevos géneros y especies de equinodermos fósiles Cubanos. *Memorias Sociedad Cubana de Historia Natural "Felipe Poey"*, 21(1):1-30, pls. 1-15.
- Sánchez Roig, Mario. 1926b. Contribución a la paleontología Cubana. Los equinodermos fósiles de Cuba. *Boletín Minas Haban*, 10:1-179, pls. 1-43.
- . 1949. Paleontología Cubana. I. Los equinodermos fósiles de Cuba. Habana, p. 1-302, pls. 1-50.
- . 1953a. Nuevos equinidos fósiles de la fauna Cubana. II. Nuevos equinoideos fósiles de Cuba. *Anales Academia de Ciencias Médicas, Físicas, y Naturales de la Habana*, 91(2): 135-176.
- Sandberger, Carl Ludwig Fridolin von. 1863. Die conchylien des Mainzer Tertiärbeckens. Wiesbaden, v + 458 p., 35 pls.
- Sandor, M. 1981. Mitteltriadische Echinoiden des Aggteleker Karstes (Nordungarn. *Evi Jelent magy. K.Foldt Intez.*, 1979-1981:279-331.
- Savin, Louis H. 1902. Note sur quelques Échinides du Dauphiné et autres régions. *Bulletin Société Statistique des Sciences Naturelles et Arts Industriels, Département d'Isère, Série 4*, 6:265-287, pls. 1-4.
- . 1903b. Catalogue raisonné des Échinides fossiles du Département de la Savoie. *Bulletin Société d'Histoire Naturelle Savoie, Chambéry, Série 2*, 8:59-249, 3 pls.
- . 1905. Revision des Échinides fossiles du Département de l'Isère. *Bulletin Société Statistique des Sciences Naturelles et Arts Industriels, Département d'Isère, Série 4* (also *Travaux Laboratoire de Géologie, Faculte des Sciences de Grenoble*, v. 7: 150-363, pls. 1-8), 8:109-324, pls. 1-8.
- Schäfer, Wilhelm. 1962. *Aktuo-Paläontologie nach studien in der Nordsee*. Kramer, Frankfurt am Main, 668 p., 277 text-figs.

- _____. 1972. Ecology and palaeoecology of marine environments. Oliver & Boyd, Edinburgh, 569 p.

Schaueroth, Karl von. 1865. Verzeichniss der Versteinerungen im Herzogl. Naturalien cabinet zu Colburg (No. 1-4328), mit Angabe der Synonymen und Beschreibung, Colburg, xv + 327 p., 30 pls.

Schlüter, Clemens August Joseph. 1883-1892. Die regulären Echiniden der Norddeutschen Kreide. K. Preussische Geologische Landesanstalt, Berlin, Abhandlungen (also Geologisches Jahrbuch), 4-5:1-315, 21 pls.

- _____. 1897b. Ueber einige baltische Kreide-Echiniden. Deutsche Geologische Gesellschaft Zeitschrift, 49:409-430.

Schmitz, E. 1970. Ein interessanter Cidarisstachel im Feuersteingeschiebe. Meyniana, 20:37-38, pl. 1.

Schopf, T. J. M. 1978. Fossilization potential of an intertidal fauna: Friday Harbor, Washington. Paleobiology, 4:261-270.

Seilacher, Adolph. 1970. Begriff und Bedeutung der Fossil-Lagerstätten. Neues Jahrbuch für Geologie und Paläontologie, Monatshefte, 1970:34-39.

- _____. 1973. Biostratinomy: The sedimentology of biologically standardized particles, p. 159-177, in Ginsburg, Robert N. (ed.), Evolving concepts in sedimentology, Johns Hopkins University Press, Baltimore.

Seilacher, Adolph, and F. Westphal. 1971. Fossil Lagerstätten, p. 327-335, in Sedimentology of parts of Central Europe, Guidebook of the 8th International Sedimentological Congress,

Seilacher, Adolph, and E. Seilacher. 1976. Palökologie, Konstruktionen, Sedimentologie, Diagenese und Vergesellschaftung von Fossilien. Zentralblatt für Geologie und Paläontologie, 2(5-6):227-233.

- Seilacher, A., W. E. Reif, and F. Westphal. 1985. Sedimentological, ecological and temporal patterns of fossil lagerstätten, in Whittington, H. B., Conway Morris, S., Extraordinary Fossil Biotas: Their ecological and evolutionary significance, *Philosophical Transactions of the Royal Society of London*, B311:1-192.
- Sepkoski, J. J. Jr. 1981. A factor analytic description of the Phanerozoic marine fossil record. *Paleobiology*, 7:36-53.
- Seunes, Jean. 1888b. Échinides Crétacés des Pyrénées. I. *Bulletin Société Géologique de France Série 3*, 16:791-816, pls. 28-31.
- Shalem, N. 1933. Sopra un giacimento cenomaniano a Brachiopodi in Palestina. *Revista Italiana de Paleontologia*, 39:17-28, pl. 2.
- Simonelli, Vittorio. 1889. Terreni e fossili dell'Isola de Pianosa nel Mar Tirreno. *Bolletín Revista Comitato Geologia Italia, Series 2*, 10:193-237, pls. 3-7.
- Smith, Andrew B. 1980. Stereom microstructure of the echinoid test. *The Palaeontological Association Special Papers in Palaeontology*, 25:1-81.
- . 1981. Implications of lantern morphology for the phylogeny of post-Palaeozoic echinoids. *Palaeontology*, 24:779-801.
- . 1984. Echinoid Palaeobiology, Special Topics in *Palaeontology* 1. George Allen & Unwin, London, 190 p.
- Socin, Costantino. 1941. Nota preliminare sulla fauna echinologica dell'oligo-Miocene somelo. *Atti Reale Accademia de Scienze, Torino*, 77:1-10.
- Spencer, W. K. 1950. Asterozoa and the study of Palaeozoic faunas. *Geological Magazine*, 87:393-408.

- Stanton, R. J. Jr. 1976. Relationship of fossil communities to original communities of living organisms, *in* Scott, R. W., and R. R. West (eds.), *Structure and Classification of Paleocommunities*, Dowden, Hutchinson & Ross, Stroudsburg PA, 291 p.
- Stefanini, Giuseppe. 1909. Echinidi del Miocene medio dell'Emilia. Parte seconda. *Palaeontographia Italica*, 15: 1-57.
- Steinmann, Gustav. 1881a. Ueber Tithon und Kreide in der peruanischen Anden. *Neues Jahrbuch für Mineralogie Geologie und Palaöntologie*, 2:130-153, pls. 6-8.
- Stephenson, D. G. 1968. Some Miocene Cidaridae (Echinoidea) from Kenya. *Journal of Natural History*, 2(4):553-568. figs. 1-2.
- Stoppani, Antonio. 1860-1865. Géologie et paléontologie des couches à *Avicula contorta* en Lombardie. *Paléontologie Lombardie, ou description des fossiles de Lombardie publiée à l'aide de plusieurs savants*, Milan, Série 3, 267 p., 60 pls.
- Taramelli, Torquato. 1874. Di alcuni Echinidi eocenici dell'Istria. *Annales Reale Istituto Veneto di Scienze, Lettere, ed Arti, Series 4*, 3:951-976, pls. 1-2.
- Tauber, A. F. 1951. *Tripneustes ventricosus austriacus* nov. ssp., ein tropischer Seeigel aus dem Torton des Wiener Beckens. *Sitzungsberichte Österreichische Akademie der Wissenschaften (Abstract I)*, 160(3-4):303-320, pl. 1.
- Thièry, P. 1928. Consideration phylogéniques sur les Cidaridae. *Archives de Zoologie expérimentale et générale*, 67(4): 179-181.
- Thièry, P., J. Lambert, and R. Collignon. 1928. Note sur quelques Échinides de la région de la Voulte. *Travaux du Laboratoire de Géologie de la Faculté des Sciences de Lyon*, 13(11):81-103, pl. 21.

- Tornquist, Alexander Johannes Heinrich). 1908. Die Diadematoïden des Wurtembergischen Lias. Deutsche Geologische Gesellschaft Zeitschrift, 60:378-430, pls. 15-19.
- Valette, Aurélien. 1898. Note sur quelques radioles d'Échinides du Corallien Inférieur du Département de l'Yonne. Bulletin Société des Sciences Historiques et Naturelles de l'Yonne, 52:121-150.
- . 1907-1908. Revision des Échinides fossiles de l'Yonne. II. Bulletin Société des Sciences Historiques et Naturelles de l'Yonne, 60:9-191.
- . 1911. Description de quelques Échinides nouveaux de la Craie (Supplement). Bulletin Société des Sciences Historiques et Naturelles de l'Yonne, 2me Sem., 1910: 121-151.
- . 1921. Note sur quelques Échinodermes Crétacés de l'Yonne. Bulletin Société des Sciences Historiques et Naturelles de l'Yonne, 1920:17-34, 6 figs.
- Valette, Aurélien, and Jules M. Lambert. 1913. Description de quelques Échinides nouveaux de la Craie (2me Supplement). Bulletin, 132 Sem. Société de Sciences Historiques et Naturelles de l'Yonne, 1913:1-46, figs. 1-18.
- Venzo, Sergio. 1934b. Il Ladinico superiore della Isola de Rodi (Egeo). II. La fauna. Palaeontographia Italica, 34:142-170, pl. 13.
- Vinassa de Regny, Paolo Eugenio. 1903. Fossili del Montenegro. I. Fauna dei calcari rossi e grigi del Sutorman. Memorie Reale Accademia delle Scienze, Istituto di Bologna, Series 5, 10:447-471, pls. 1-2.
- Wanner, J. 1902. Die fauna der obersten weissen Kreide der libyschen Wüste. Palaeontographica, 30(2):91-152, pls. 13-19.

- . 1941. Neue Beiträge zur Kenntnis der permischen Echinodermen von Timor. *Palaeontographica*, 4:297-314, pls. 25-26.
- Weber, G. 1934. Échinodea du Jurassique et du Crétacé de Crimée, I. Transactions of the United Geological and Prospecting Service of the USSR, 312:1-99, pls. 1-12.
- Weigelt, Johannes. 1919. Geologie und Nordseefauna. Der Steinbruch, 14:228-231; 244-246, text-figs. 1-10.
- . 1927. Rezente Wirbeltierleichen und ihre paläobiologische Bedeutung. Max Weg, Leipzig, xvi + 227 p., 28 text-figs., 37 pls.
- . 1928b. Die Pflanzenreste des mitteldeutschen Kuperschiefers und ihre Einschaltung ins Sediment. Fortschritte der Geologie und Paläontologie, Berlin.
- Weisbord, N. E. 1934. Some Cretaceous and Tertiary echinoids from Cuba. *Bulletins of American Paleontology*, 20(70c): 1-270, pls. 1-9.
- . 1971. Bibliography of Cenozoic Echinoidea including some Mesozoic and Paleozoic titles. *Bulletins of American Paleontology*, 59(263):314 p.
- White, Brian, Karen Kurkijy, and Curran H. Allen. 1984. A shallowing-upward sequence in a Pleistocene coral reef and associated facies, San Salvador, Bahamas, p. 53-70, in Teeter, James W., *Proceedings of the Second Symposium on the Geology of the Bahamas*,
- Whitfield, H., and R. Hovey. 1906. Remarks on and description of Jurassic fossils of the Black Hills. *Bulletin of the American Museum of Natural History*, New York, 22(23): 389-402, pls. 42-52.
- Whitney, Marion I., and Lewis B. Kellum. 1966. Echinoids of the Glen Rose Limestone of Texas. *Papers, Michigan Academy of Sciences, Arts and Letters*, 51:241-263, pls. 1-2.

- Wilson, M. V. H. 1988. Taphonomic processes: Information loss and information gain. *Geoscience Canada*, 15(2):131-148.
- Woods, Henry. 1908. Echinodea, Brachiopoda and Lamellibranchia from the Upper Cretaceous Limestone of Need's Camp, Buffalo River. *Annals of the South African Museum*, 7:13-20.
- Wright, Thomas W. 1851a. On the Cidaridae of the Oolites, with descriptions of some new species of that family. *Annals and Magazine of Natural History*, Series 2, 8:241-280.
- . 1855a. On fossil echinoderms from the Island of Malta; with notes on the stratigraphical distribution of the fossil organisms in the Maltese beds. *Annals and Magazine of Natural History*, Series 2, 15:101-127; 175-196; 262-277, pls. 4-7.
- . 1855-1860. Monograph of the British fossil Echinodermata of the Oolitic formations. I. Echinoidea. *Palaeontographical Society Monograph*, London, 481 p., 43 pls.
- . 1864. On the fossil Echinidae of Malta. With additional notes on the Miocene beds of the island, and the stratigraphical distribution of the species therein; by A. Leith Adams. *Quarterly Journal of the Geological Society of London*, 20:471-491, pls. 21-22.
- . 1864-1882. Monograph of the British fossil Echinodermata of the Cretaceous formations. I. Echinoidea. *Palaeontographical Society Monograph*, London, 371 p., 80 pls.
- Yoshiwara, Shigeyasu Takunga). 1898a. Preliminary notice of new Japanes echinoids. *Annotationes Zoologicae Japonenses*, 2:57-61, pl. 2.
- Zardini, Rinaldo. 1976. Fossili di Cortina. Atlante degli echinodermi Cassiani (Trias medio-superiore) della regione dolomitica attorno a Cortina d'Ampezzo. Cortina d'Ampezzo, Belluno, Italy, p. 3-29, 22 pls.

APPENDIX 1

This appendix contains a list of all type species described for the Families Diadematidae, Cidaridae, Echinometridae and Toxopneustidae on the basis of fossil material. Taxonomy follows that of the Treatise. This list is complete through 1988 and was compiled using information from Lambert and Thiéry's (1909-1925) monograph and Kier and Lawson's (1978) update. Species described since 1974 were obtained from the Zoological Record. Stratigraphic information and primary reference are included with each entry. Species marked with a * are those for which taphonomic information is complete and were used in the analysis of preservational style presented in the text. The references listed here are fully cited in the bibliography. Local stage names not incorporated in the Harland et al. (1982) time scale are followed by the Harland et al. equivalents in parentheses.

Two reference works proved invaluable for fleshing out the often-times sketchy bibliographic information in the Lambert and Thiéry monograph. These were Wiesbord's Bibliography of Cenozoic Echinoidea including some Mesozoic and Paleozoic Titles (1971), and Journal Title Abbreviations: By Abbreviation (Alkire, 1988). Obtaining primary references would have been difficult without these sources.

Family DiadematidaeGenus: *Diadema*

Unknown

- | | |
|-------------------------|-----------------|
| <i>D. calamare</i> | Döderlein, 1902 |
| <i>D. desori</i> | " |
| * <i>D. desjardinsi</i> | Michelin, 1845 |

Miocene

- | | |
|--------------------------------|--------------------|
| <i>D. ficheuri</i> | Pomel, 1887 |
| <i>D. regnyi</i> | Lambert, 1907-1909 |
| * <i>D. vetus</i> (Aquitanian) | Lambert, 1931c |

Eocene

- | | |
|-------------------------|----------------|
| * <i>D. principeana</i> | Weisbord, 1934 |
|-------------------------|----------------|

Genus: *Centrostephanus*

Senonian

- | | |
|-------------------------|--------------|
| * <i>C. ebroicensis</i> | Caffin, 1867 |
|-------------------------|--------------|

Oligocene	
* <i>C. nanus</i>	Sandberger, 1863
Miocene	
<i>C. calarensis</i>	Lambert, 1907-1909
<i>C. airaghii</i>	"
<i>C. sahelensis</i>	Pomel, 1887
* <i>C. sacyi</i> (Burdigalian)	Lambert, 1928
* <i>C. habanensis</i>	Lambert & Thiéry, 1909-1925
Genus: <i>Eodiadema</i>	
Carnian	
* <i>E. regulare</i>	Laube, 1864
L. Jurassic	
* <i>E. lacostei</i>	Lambert, 1933b
Hettangian	
* <i>E. collenoti</i>	Cotteau, 1880-1885
* <i>E. lobatum</i>	Wright, 1855-1860
<i>E. olifax</i>	Tornquist, 1908
<i>E. parvatum</i>	"
* <i>E. thoralis</i>	Petitot, 1961
Charmouthian (L. Jur.)	
* <i>E. laqueatum</i>	Quenstedt, 1875
* <i>E. minutum</i>	Cotteau, 1880-1885
<i>E. sondelfingense</i>	Tornquist, 1908
Toarcian	
<i>E. pusillum</i>	Lambert, 1899b
Genus: <i>Palaeodiadema</i>	
Turonian	
<i>P. gauthieri</i>	Lambert, 1931c
Senonian	
* <i>P. fragile</i>	Wright, 1864-1882
* <i>P. geinitzi</i>	Lambert & Thiéry, 1909
	Geinitz, 1871
Paleocene/U. Cret	
* <i>P. multiforme</i>	Ravn, 1928
Oligocene	
<i>P. reingarde</i>	Kutscher, 1988

Genus: *Pedinothuria*

Jurassic

* *P. cidaroides** *P. barottei*

Gregory, 1897a

Lambert & Thiery, 1909-1925

Family CidaridaeGenus: *Minicidaris**Minicidaris minihagali*

Deraniyagala, 1961

Subfamily HistocidarinaeGenus: *Histocidaris*

Duntroonian-Waitakian (Olig.)

* *H. mckayi*

Fell, 1954

Miocene

* *H. oranensis* (Tortonian)

Lambert, 1931c

Helvetian (Pleist.)

H. geneffensis

Lambert, 1931d

Genus: *Polycidaris*

Charmouthian (L. Jur.)

* *P. edwardsi*

Wright, 1855-1860

Bajocian

* *P. collenoti*

Cotteau, 1875-1880

* *P. gauthieri*

"

Bathonian

* *P. blainvillei*

"

Oxfordian

* *P. nonarius*

Quenstedt, 1875

Rauracian (M. Jur.)

* *P. trouvillensis*

Cotteau, 1875-1880

Subfamily CtenocidarinaeGenus: *Notocidaris*

Pliocene

* *N. vellai*

Fell, 1954

Subfamily GoniocidarinaeGenus: *Goniocidaris*

Eocene

- * *G. habanensis*

Sanchez Roig, 1949

Oligocene

- * *G. hebe*
- * *G. holguinensis*
- * *G. murrayensis*
- * *G. pusilla*

Fell, 1954

Sanchez Roig, 1949

Chapman & Cudmore, 1934

Fell, 1954

Miocene

- * *G. affinis*
- * *G. depressa*
- * *G. granulata*
- G. halaensis*
- * *G. noetlingi*
- * *G. praecipua*

Duncan & Sladen, 1883

"

"

Archaic & Haime, 1853

Roman, 1976

Philip, 1964

Pliocene

- * *G. mortenseni*
- * *G. tubaria hallettensis*
- G. jorgensis*

Chapman & Cudmore, 1934

Philip, 1964

Loriol, 1902

Subfamily StereocidarinaeGenus: *Stereocidaris*

Cenomanian

- * *S. carteri*
- S. hannoverana*
- * *S. hudsenthensis*
- * *S. sarracenorum*

Wright, 1864-1882

Schlüter, 1892

Cooke, 1955

Fourtau, 1921

Turonian

- * *S. lallieri*
- * *S. sceptrifera*
- S. silesiaca*
- S. subhercynica*

Lambert, 1909a

Cotteau, 1862-1867

Schlüter, 1892

"

Senonian

- * *S. filamentosa*
- * *S. griffei*
- * *S. pseudohirudo*
- S. jaekeli grandior*
- * *S. merceyi*
- S. hureoe*
- S. sancti*

Cotteau, 1862-1867

Lambert, 1909a

Cotteau, 1862-1867

Krenkel, 1928

Cotteau, 1862-1867

Valette & Lambert, 1913

Valette, 1920

Cretaceous

- S. rugensis*
- S. jaekeli undulifera*
- S. jaekeli latior*

Krenkel, 1928

"

"

<i>S. jaekeli</i>	"
<i>S. bolli</i>	"
* <i>S. baileyi</i>	Fell, 1962a
Eocene	
<i>S. destefanni</i>	Innocenti, 1924a
* <i>S. cudmorei</i>	Philip, 1964
* <i>S. fosteri</i>	"
* <i>S. hispida</i>	"
* <i>S. inermis</i>	"
* <i>S. intricata</i>	"
Pliocene	
* <i>S. grandis fusana</i>	Nisiyama, 1966
* <i>S. hutchinsoni</i>	Fell, 1954
Genus: <i>Phalcrocidaris</i>	
Cenomanian	
* <i>P. atropa</i>	Cotteau, Peron & Gauthier, 1879
* <i>P. insignis</i>	Cotteau, 1862-1867
Turonian	
<i>P. wollemanni</i>	Schlüter, 1892
Senonian	
<i>P. darupensis</i>	Schlüter, 1892
* <i>P. punctillum</i>	Cotteau, 1862-1867
* <i>P. senonensis</i>	Gauthier, 1891
Eocene	
* <i>P. nummulitica</i>	Cotteau, 1889-1894
Plio-Pleistocene	
* <i>P. japonica multipora</i>	Nisiyama, 1966
Genus: <i>Typocidaris</i>	
Sequanian (M. Jur.)	
* <i>T. marginata</i>	Cotteau, 1875-1880
Valanginian	
* <i>T. folcariensis</i>	Gauthier, 1891
Neocomian	
* <i>T. malum</i>	Cotteau, 1862-1867
Barremian	
* <i>T. baumbergeri</i>	Jeannet, 1933d
Aptian	
* <i>T. arduennensis</i>	Lambert, 1892
* <i>T. farringdonensis</i>	"
* <i>T. proxima</i>	Fourtau, 1921

* <i>T. gauthieri</i>	"
Albian	
* <i>T. thalebensis</i>	Lambert, 1931c
Cenomanian	
* <i>T. beyrouthensis</i>	Loriol, 1909
* <i>T. cenomaniensis</i>	Cotteau, 1862-1867
* <i>T. essenensis</i>	"
<i>T. praehirudo</i>	Lambert, 1894
* <i>T. vesiculosa</i>	Wright, 1864-1882
Turonian	
* <i>T. hirudo</i>	Cotteau, 1862-1867
* <i>T. strehlensis</i>	Geinitz, 1871-1875
Senonian	
* <i>T. ambigua</i>	Cotteau, 1862-1867
* <i>T. boriesi</i>	Lambert, 1909a
* <i>T. campaniensis</i>	Cotteau, 1862-1867
<i>T. chercherensis</i>	Fourtau, 1909
* <i>T. ovata</i>	Lambert, 1909a
* <i>T. pseudohirudo</i>	Cotteau, 1862-1867
<i>T. pseudopistillum</i>	Arnaud, 1898
* <i>T. royanus</i>	Cotteau, 1862-1867
* <i>T. serrata</i>	"
* <i>T. spanophyma</i>	Lambert, 1909a
* <i>T. subvesiculosa</i>	"
<i>T. wrighti</i>	Wright, 1864-1882
* <i>T. corbaricus</i>	Lambert & Thiéry, 1909-1925
Maastrichtian	
* <i>T. falgarensis</i>	Lambert, 1933d
Danian	
<i>T. rosenkrantzi</i>	Ravn, 1928
<i>T. danica</i>	"
Genus: <i>Temnocidaris</i>	
Senonian	
* <i>T. magnifica</i>	Cotteau, 1862-1867
* <i>T. baylei</i>	"
* <i>T. danica</i>	"
Subfamily Rhabdocidarinae	
Genus: <i>Rhabdocidaris</i>	
Unknown	
<i>R. ovata</i>	Philipi, 1860
Carmouthian (Pliensbachian)	
* <i>R. impar</i>	Cotteau, 1875-1880
* <i>R. moreau</i>	"

Liassic (L. Jur.)	
* <i>R. villae</i>	Meneghini, 1867-1881
Domerian (L. Jur.)	
* <i>R. chouberti</i>	Lambert, 1937b
Toarcian	
* <i>R. heuvelini</i>	Cotteau & Triger, 1855-1869
* <i>R. major</i>	Cotteau, 1875-1880
Bajocian	
* <i>R. crassissimi</i>	Cotteau, 1875-1880
* <i>R. ferryi</i>	Cotteau, 1880-1885
* <i>R. fowleri</i>	Wright, 1855-1860
* <i>R. horrida</i>	Cotteau, 1875-1880
<i>R. lafayi</i>	Lissajous, 1903-1904
* <i>R. rhodani</i>	Cotteau, 1875-1880
* <i>R. turbeti</i>	Lambert, 1933b
Bathonian	
* <i>R. helicoides</i>	Gauthier, 1903a
* <i>R. kisombyensis</i>	Lambert, 1936c
* <i>R. bigoti</i>	Mercier, 1931
Callovian	
* <i>R. copeoides</i>	Cotteau, 1875-1880
* <i>R. gregoryi</i>	Gregory, 1893
* <i>R. guttata</i>	Cotteau, 1875-1880
* <i>R. lusitanica</i>	Lambert, 1913f
<i>R. sagresensis</i>	Loriol, 1890-1891
* <i>R. thurmanni</i>	Cotteau, 1875-1880
Rauracian (M. Jur.)	
* <i>R. censoriensis</i>	Cotteau, 1875-1880
* <i>R. megalacantha</i>	"
* <i>R. ritteri</i>	"
* <i>R. trigonacantha</i>	"
Sequanian (M. Jur.)	
<i>R. arrudaensis</i>	Loriol, 1890-1891
<i>R. arsenoensis</i>	"
* <i>R. asperrima</i>	Desor & Loriol, 1872
<i>R. boccagei</i>	Loriol, 1890-1891
* <i>R. clavator</i>	Desor & Loriol, 1872
* <i>R. maxima</i>	"
<i>R. mira</i>	Loriol, 1890-1891
* <i>R. mitrata</i>	Quenstedt, 1875
* <i>R. nobilis</i>	Desor & Loriol, 1872
* <i>R. orbignyana</i>	Cotteau, 1875-1880
<i>R. pereirae</i>	Loriol, 1890-1891
<i>R. roquettei</i>	"
* <i>R. triaculeata</i>	Quenstedt, 1875
* <i>R. trilatera</i>	"

* <i>R. triptera</i>	Cotteau, 1875-1880
* <i>R. trispinata</i>	Quenstedt, 1875
* <i>R. virgata</i>	Cotteau, 1875-1880
* <i>R. bononiensis</i>	"
* <i>R. durandi</i>	Cotteau, 1880-1885
<i>R. yailensis</i>	Weber, 1934
Oxfordian	
* <i>R. caprimontana</i>	Cotteau, 1875-1880
* <i>R. cristata</i>	Desor & Loriol, 1872
* <i>R. herculis</i>	"
* <i>R. janitoris</i>	Cotteau, 1875-1880
* <i>R. sarthacensis</i>	"
* <i>R. tricarinata</i>	Quenstedt, 1875
Kimmeridgian	
* <i>R. boehmi</i>	Bantz, 1969
* <i>R. cotteaui</i>	Jeannet, 1929
* <i>R. desori</i>	"
* <i>R. mayri</i>	Bantz, 1969
* <i>R. nunlisti</i>	Jeannet, 1929
* <i>R. orbignyformis</i>	"
* <i>R. rauraca</i>	"
* <i>R. stingelini</i>	"
Hauterivian	
<i>R. arginensis</i>	Weber, 1934
<i>R. buraganensis</i>	"
Neocomian	
<i>R. cascaensis</i>	Loriol, 1887-1888
<i>R. delgadoi</i>	"
<i>R. delphinensis</i>	Savin, 1905
<i>R. gevreyi</i>	Savin, 1902
<i>R. insuetus</i>	Loriol, 1887-1888
* <i>R. jauberti</i>	Cotteau, 1862-1867
* <i>R. kiliani</i>	Cotteau, 1882-1893
<i>R. lacertosus</i>	Loriol, 1887-1888
* <i>R. pavimentatus</i>	Loriol, 1873a
<i>R. petitclerei</i>	Savin, 1902
<i>R. salvae</i>	Nickles, 1892
* <i>R. thunensis</i>	Loriol, 1873a
* <i>R. tournali</i>	Cotteau, 1862-1867
<i>R. triangularis</i>	Schlüter, 1892
* <i>R. tuberosa</i>	Cotteau, 1862-1867
Urgonian (L. Cret.)	
* <i>R. cortazari</i>	Cotteau, 1879d
Aptian	
<i>R. jacobi</i>	Savin, 1905
Albian	
* <i>R. brasiliensis</i>	Maury, 1936

Cenomanian	
<i>R. abdaensis</i>	Loriol, 1900
<i>R. libanoticus</i>	"
<i>R. orientalis</i>	"
Senonian	
<i>R. cometes</i>	Boll, 1846
<i>R. schlönbachi</i>	Schlüter, 1892
Eocene	
<i>R. gaillardoti</i>	Gauthier, 1902c
* <i>R. libyensis</i>	Gregory, 1898
* <i>R. lorioli</i>	Mayer-Eymar, 1898a
* <i>R. mespilum</i>	Cotteau, 1889-1894
* <i>R. navillei</i>	Cotteau, 1882-1893
* <i>R. oxyrine</i>	Meneghini, 1862
<i>R. posthumus</i>	Pavay, 1874
* <i>R. pouechi</i>	Cotteau, 1889-1894
* <i>R. ranikoti</i>	Duncan & Sladen, 1882-1886
* <i>R. sindensis</i>	"
* <i>R. rovasendai</i>	Airaghi, 1902a
* <i>R. ugolinorum</i>	Oppenheim, 1902b
* <i>R. vidali</i>	Cotteau, 1886a
* <i>R. zitteli</i>	Loriol, 1882b
Oligocene	
* <i>R. anhaltina</i>	Ebert, 1889
* <i>R. deserta</i>	"
Miocene	
* <i>R. compressa</i>	Cotteau, 1895
Pliocene	
<i>R. rosaria</i>	Lambert, 1907-1909
Genus: <i>Chondrocidaris</i>	
Miocene	
* <i>C. clarkii</i>	Cahpman & Cudmore, 1934
* <i>C. marianica</i>	Nisiyama, 1966
* <i>C. problepteryx</i>	Clark, 1945
Genus: <i>Megacidaris</i>	
L. Jurassic	
* <i>M. cottreai</i>	Mercier, 1937c
Genus: <i>Parhabdocidaris</i>	
U. Jurassic	
* <i>R. vorusensis</i>	Thièry, 1928

Genus: *Phyllacanthus*

Aptian

P. tysoni

Whitney & Kellum, 1966

P. texanus

Duntroonian (Olig.-Mioc.)

** P. titan*

Fell, 1954

Janjukian (Olig.-Mioc.)

** P. duncani gambierensis*

Philip, 1963d

Oligocene-Pliocene

** P. ducani*

Chapman & Cudmore, 1934

Miocene

** P. clarkii impersus*

Philip, 1963d

** P. dubius sundaica*

Jeannet & Martin, 1937

** P. priscus*

Brito & Ramirez, 1974

** P. wellmanae* (Kapitean)

Fell, 1954

Pliocene

** P. serratus*

Philip, 1963d

Pleistocene

** P. tylotus*

Clark, 1945

Genus: *Aulacocidaris*

Ptérocérian (L. Cret.)

A. lamberti

Savin, 1903b

Valangian

** A. sanctae-crucis*

Cotteaun, 1862-1867

Cenomanian

** A. schlumbergeri*

Cotteau, 1883

A. thomasi

Cotteau, 1858-1880

Genus: *Leiocidaris*

Oxfordian

** L. cartieri*

Desor & Loriol, 1872

Kimmeridgian

** L. tobleri*

Jeannet, 1933d

Sequanian (M. Jur.)

** L. rollieri*

Jeannet, 1933d

Cretaceous

** L. leoni*

Sanchez Roig, 1926b

Neocomian

L. hilsii

Schlüter, 1892

Barremian	
<i>L. karakachi</i>	Weber, 1934
Albian	
* <i>L. thiebaudi</i>	Jeannet, 1955
* <i>L. doncieuxi</i>	Lambert & Thiery, 1909-1924
Cenomanian	
<i>L. angulata</i>	Gauthier, 1889a
<i>L. balli</i>	Fourtau, 1914b
<i>L. bonolai</i>	Gauthier, 1902c
* <i>L. ludovici</i>	Fourtau, 1912c
<i>L. stefannii</i>	Shalem, 1933
Turonian	
* <i>L. subvenulosa</i>	Cotteau, Peron & Gauthier, 1879
Senonian	
<i>L. aegyptica</i>	Fourtau, 1914b
<i>L. capelloi</i>	Loriol, 1887-1888
<i>L. crameri</i>	"
* <i>L. hemigranosus</i>	Clark, 1893b
* <i>L. morgani</i>	Gauthier, 1902a
* <i>L. pouyannei</i>	Cotteau, 1862-1867
* <i>L. venulosa</i>	"
Maastrichtian	
* <i>L. tripolitana</i>	Checchia-Rispoli, 1933c
<i>L. sanfilippoi</i>	Checchia-Rispole, 1932c
* <i>L. mudrugensis</i>	Sanchez Roig, 1949
Eocene	
<i>L. abbatei</i>	Gauthier, 1902c
* <i>L. almerai</i>	Lambert, 1902a
* <i>L. altai</i>	Dames, 1878
* <i>L. balestrai</i>	Oppenheim, 1902b
* <i>L. blancheti</i>	Cotteau, 1889-1894
* <i>L. boffilli</i>	Lambert, 1902a
<i>L. boussaci</i>	Castex & Lambert, 1920
* <i>L. canaliculata</i>	Duncan & Sladen, 1882-1886
* <i>L. carolinensis</i>	Clark & Twitchell, 1915
* <i>L. cottreaui</i>	Lambert & Pérébaskine, 1929
<i>L. granulata</i>	Gauthier, 1902c
* <i>L. itala</i>	Laube, 1868
* <i>L. mezzoana</i>	"
<i>L. minichensis</i>	Gauthier, 1899b
* <i>L. mitchelli</i>	Clark & Twitchell, 1915
* <i>L. montserratensis</i>	Lambert, 1902a
* <i>L. mortensoni</i>	Lambert, 1933a
<i>L. oppenheimi</i>	Lambert, 1912-1915
<i>L. pentacrinorum</i>	Lambert, 1916d
* <i>L. pseudojurassica</i>	Laube, 1868
<i>L. scampicchioii</i>	Taramelli, 1874

Oligocene

- * *L. spinidentatus*
- * *L. cojimarensis*

Sanchez Roig, 1949

"

Miocene

- * *L. adamsi*
- L. antarctica*
- * *L. loveni*
- L. scillae*
- L. sismondai*
- L. thyriger*

Wright, 1864

Loriol, 1902

Cotteau, 1875

Lambert, 1907-1909

"

Simonelli, 1889

Genus: *Porocidaris*

Paleocene

- P. farafrensis* (Landinian)

Hassan, 1969

Eocene

- * *P. anomala*
- * *P. lopezi*
- P. ruinae*
- P. schmideli*
- * *P. tuberculosa*

Duncan & Sladen, 1882-1886

Sanchez Roig, 1953a

Oppenheim, 1902b

Loriol, 1880b

Michelin, 1850

Genus: *Prionocidaris*

Eocene

- * *P. marshalli* (Bartonian)

Fell, 1954

Duntroonian-Otaian (Olig.)

- * *P. haasti*

Fell, 1954

Miocene

- * *P. cookei*
- * *P. katherinae*
- * *P. scoparia*
- * *P. praeverticillata* (Aquitanian)

Cuttress, 1976

Cuttress, 1980

Chapman & Cudmore, 1934

Stephenson, 1968

Plio-Pliocene

- * *P. malindiensis*

Stephenson, 1968

Subfamily Cidarinae

Genus: *Prophyllacanthus*

Miocene

- * *P. eocenicus*

Cuttress, 1980

Genus: *Zardinechinus*

Carnian

- * *Z. lancedelli*
- * *Z. giulini*

Kier, 1977

Kier, 1984

Genus: *Leurocidaris*

Carnian

- * *L. montanaro*

Kier, 1977

Genus: *Paurocidaris*

Carnian

- * *P. rinbianchi*

Kier, 1977

Genus: *Cidaris*

Unknown

- C. hawkinsi*
- * *C. mortoni*

Hawkins, 1912f
Clark & Twitchell, 1915

Permian

- C. jonkeri*
- C. bitauniensis*

Wanner, 1941
"

Triassic

- * *C. anellatus*
- * *C. ecki*
- * *C. longispina*
- * *C. mirandus*
- * *C. percostatus*
- * *C. remifera*
- * *C. shastensis*
- * *C. tuberculinus*

De Gregorio, 1930b
Assmann, 1925
Assmann, 1937
De Gregorio, 1930b
"
Assmann, 1937
Clark & Twitchell, 1915
De Gregorio, 1930b

Carnian

- * *C. aculeata*
- * *C. aculeata fusiformis*
- C. adunca*
- C. aggtelekensis*
- * *C. alata*
- * *C. alpina*
- * *C. austriaca*
- C. batheri*
- * *C. bionica*
- * *C. coralliophila*
- * *C. costalarensis*
- * *C. costata*
- * *C. costeanensis*
- * *C. crenulata*
- * *C. dorsata coronata*
- * *C. dorsata jugulata*
- * *C. forminensis*
- * *C. fustis*
- * *C. giauensis*
- * *C. glabra*
- C. gladius*
- * *C. leonardi*
- * *C. magna*

Zardini, 1976
"
Sandor, 1981
"
Laube, 1864
Zardini, 1976
Desor, 1855-1858
Sandor, 1981
Zardini, 1976
"
"
"
"
Leonardi & Lovo, 1950
"
"
Zardini, 1976
Laube, 1864
Zardini, 1976
"
Sandor, 1981
Zardini, 1976
Leonardi & Lovo, 1950

* <i>C. milierensis</i>	Zardini, 1976
* <i>C. ovata</i>	"
<i>C. palaformis</i>	Sandor, 1981
* <i>C. petersii</i>	Laube, 1864
* <i>C. plana</i>	Zardini, 1976
* <i>C. pusilla</i>	Leonardi & Lovo, 1950
* <i>C. pyramidalis</i>	"
* <i>C. quadrialata</i>	Zardini, 1976
* <i>C. quadariserrata</i>	"
* <i>C. raiblana capitata</i>	Leonardi & Lovo, 1950
* <i>C. reticulata</i>	Zardini, 1976
* <i>C. roemeri</i>	Laube, 1864
* <i>C. scrobiculata rumerlensis</i>	Leonardi & Lovo, 1950
* <i>C. seelandica</i>	Zardini, 1976
* <i>C. semicostata</i>	Laube, 1864
<i>C. serraedentata</i>	Sandor, 1981
* <i>C. spongiosa</i>	Zardini, 1976
* <i>C. staulinensis</i>	Leonardi & Lovo, 1950
* <i>C. sulcata</i>	Zardini, 1976
* <i>C. tenuicostata</i>	"
* <i>C. trapezoidalis</i>	"
* <i>C. triserrata</i>	Laube, 1864
* <i>C. trigona</i>	"
* <i>C. trigona cuspidata</i>	Leonardi & Lovo, 1950
* <i>C. undulatus</i>	Quenstedt, 1875
* <i>C. verticillata</i>	Zardini, 1976
* <i>C. zardini</i>	Leonardi & Lovo, 1950
* <i>C. decorata</i>	Bather, 1909c
* <i>C. decoratissima</i>	"
* <i>C. fasciculata</i>	"
* <i>C. linearis</i>	"
* <i>C. mayeri</i>	"
* <i>C. parastadifera</i>	"
* <i>C. schwageri</i>	"
* <i>C. similis</i>	"
* <i>C. subspinulosa</i>	"
* <i>C. waechteri</i>	"
* <i>C. wissmanni</i>	
Norian	
<i>C. gilletae</i>	Lambert, 1927a
<i>C. regnyi</i>	Vinassa de Regny, 1903
<i>C. transversa</i>	Schafhaufl, 1859
Rhaetian	
<i>C. alternata</i>	Stoppani, 1860-1865
<i>C. caudex</i>	"
<i>C. lanceata</i>	"
<i>C. spina-christi</i>	"
<i>C. stipes</i>	"
Jurassic	
* <i>C. plumasensis</i>	Clark & Twitchell, 1915
<i>C. spathulatus</i>	Auerbach, 1846

Sinemurian	
* <i>C. erbaensis</i>	Meneghini, 1867-1881
* <i>C. itys</i>	Cotteau, 1875-1880
* <i>C. jarbus</i>	"
Charmouthian (Pliensbachian)	
* <i>C. deslongchampsii</i>	Cotteau, 1875-1880
* <i>C. terrenzii</i>	Parona, 1892
Toarcian	
<i>C. impressa</i>	Lambert, 1899b
* <i>C. pandarus</i>	Cotteau, 1875-1880
* <i>C. posidoniae</i>	Quenstedt, 1875
Domerian (L. Jur.)	
* <i>C. gemenosensis</i>	Lambert & Thiéry, 1909-1924
Liassic (L. Jur.)	
* <i>C. rouxi</i>	Lambert & Thiéry, 1909-1924
Bajocian	
<i>C. andreae</i>	Lissajous, 1903-1904
<i>C. cesaredensis</i>	Loriol, 1890-1891
* <i>C. honorinae</i>	Cotteau, 1875-1880
* <i>C. lamellosa</i>	Cotteau, 1875-1880
* <i>C. ovispina</i>	Quenstedt, 1875
<i>C. quiosensis</i>	Loriol, 1890-1891
* <i>C. torulosus</i>	Quenstedt, 1875
<i>C. triculenta</i>	Loriol, 1890-1891
Bathonian	
* <i>C. aspernata</i>	Desor & Loriol, 1872
* <i>C. guerangeri</i>	Cotteau, 1875-1880
* <i>C. julii</i>	"
<i>C. mattosensis</i>	Loriol, 1890-1891
* <i>C. mulleri</i>	Desor & Loriol, 1872
* <i>C. taxacantha</i>	Loriol, 1873a
Callovian	
* <i>C. allobrogica</i>	Desor & Loriol, 1872
<i>C. sagresensis</i>	Loriol, 1890-1891
Rauracian (M. Jur.)	
* <i>C. schlumbergeri</i>	Cotteau, 1875-1880
* <i>C. silicea</i>	"
Sequanian (M. Jur.)	
* <i>C. acrolineata</i>	Cotteau 1875-1880
* <i>C. basseto</i>	"
<i>C. choffati</i>	Loriol, 1890-1891
<i>C. gomesi</i>	"
* <i>C. millepunctata</i>	Cotteau, 1875-1880
<i>C. submarginata</i>	Felix & Lenk, 1891

Oxfordian	
* <i>C. cartieri</i>	Desor & Loriol, 1872
* <i>C. psammosa</i>	"
* <i>C. rarefacta</i>	Quenstedt
Kimmeridgian	
* <i>C. normanna</i>	Cotteau, 1875-1880
Tithonian	
<i>C. aizyensis</i>	Loriol, 1902
* <i>C. bellefourchensis</i>	Whitfield & Hovey, 1906
* <i>C. californicus</i>	Clark, 1893b
* <i>C. catenifera</i>	Desor & Loriol, 1872
<i>C. mauritanicus</i>	Loriol, 1902
<i>C. moravica</i>	Remes, 1905
* <i>C. nesseldorfensis</i>	Loriol, 1901
<i>C. savini</i>	Loriol, 1902
<i>C. subpunctata</i>	Cotteau, 1884a
* <i>C. zetes</i>	Loriol, 1901
Cretaceous	
* <i>C. dixiensis</i>	Clark & Twitchell, 1915
Hauterivian-Valangian	
<i>C. theodosiae</i>	Weber, 1934
<i>C. enissalensis</i>	"
Valangian	
* <i>C. bernouillensis</i>	Lambert, 1916b
Neocomian	
<i>C. avenacea</i>	Savin, 1905
* <i>C. campichei</i>	Loriol, 1873a
<i>C. cherennensis</i>	Savin, 1905
* <i>C. cornifera</i>	Cotteau, 1862-1867
* <i>C. cydonifera</i>	"
<i>C. gevreyi</i>	Savin, 1905
<i>C. guiasensis</i>	Loriol, 1887-1888
* <i>C. heteracantha</i>	Cotteau, 1862-1867
<i>C. hirsuta</i>	Schlüter, 1892
<i>C. jacobi</i>	Savin, 1905
* <i>C. justiana</i>	Loriol, 1873a
* <i>C. lardyi</i>	Cotteau, 1862-1867
* <i>C. ligeriensis</i>	"
<i>C. maresi</i>	Cotteau, 1858-1880
<i>C. mexilhoeirensis</i>	Loriol, 1887-1888
* <i>C. neocomiensis</i>	Cotteau, 1862-1867
* <i>C. pretiosa</i>	"
* <i>C. problematica</i>	"
* <i>C. puntatissima</i>	"
Aptian	
<i>C. coxwiellensis</i>	Hawkins, 1912f

* <i>C. kiliani</i>	Cotteau, 1882-1893
* <i>C. plexa</i>	Lambert, 1892
* <i>C. mullerriedi</i>	Lambert, 1935d
* <i>C. sinea</i>	Fourtau, 1921
Albian	
* <i>C. gaultina</i>	Wright, 1864-1882
<i>C. stylophora</i>	Gras, 1848
<i>C. vafellus</i>	Loriol, 1888a
Cenomanian	
* <i>C. angulata</i>	Cotteau, Peron & Gauthier, 1879
* <i>C. berthelini</i>	Cotteau, 1862-1867
<i>C. cragini</i>	Loriol, 1904
* <i>C. dallonii</i>	Lambert, 1924b
<i>C. daglensis</i>	Gauthier, 1889a
* <i>C. dixiensis</i>	Cragin, 1893
* <i>C. dixonii</i>	Cotteau, 1862-1867
* <i>C. eliasensis</i>	Loriol, 1901
<i>C. figueirensis</i>	Loriol, 1887-1888
<i>C. junqueiroensis</i>	"
* <i>C. leenhardtii</i>	Loriol, 1900
<i>C. mamarozensis</i>	Loriol, 1887-1888
* <i>C. mourguei</i>	Cotteau, 1882-1893
* <i>C. pseudospinulosa</i>	Cotteau, 1862-1867
* <i>C. rousseli</i>	Cotteau, 1887d
* <i>C. sorigneti</i>	Cotteau, 1862-1867
* <i>C. tehamaensis</i>	Clark & Twitchell, 1915
* <i>C. texanus</i>	Clark, 1893b
<i>C. thomasi</i>	Gauthier, 1899b
* <i>C. velifera</i>	Cotteau, 1862-1867
* <i>C. zumeffeni</i>	Lorio, 1901
Turonian	
* <i>C. fusiformis</i>	Cotteau, 1862-1867
Santonian	
* <i>C. meslei</i>	Lambert, 1931c
Campanian	
* <i>C. mahafalensis</i>	Besairie, 1930b
Maastrichtian	
<i>C. majungensis</i>	Lambert, 1933a
Senonian	
<i>C. aftabensis</i>	Cotteau & Gauthier, 1895
<i>C. asperula</i>	Roemer, 1840-1841
<i>C. baltica</i>	Schlüter, 1892
* <i>C. beaugei</i>	Seunes, 1888b
* <i>C. beausetensis</i>	Cotteau, 1882-1893
* <i>C. coronglobus</i>	Quenstedt, 1875
* <i>C. excavata</i>	Cotteau, 1862-1867
* <i>C. faujasi</i>	Desor, 1855-1858

- * *C. fresvillensis* Lambert, 1909d
 - C. gigas* Schlüter, 1892
 - * *C. hagenowi* Desor, 1855-1858
 - C. husseini* Cotteau & Gauthier, 1895
 - C. jeani* Savin, 1902
 - * *C. lingualis* Desor, 1855-1858
 - * *C. mamillata* Cotteau, 1862-1867
 - * *C. minuta* "
 - * *C. mountainvillensis* Lambert, 1892
 - * *C. nigelliensis* "
 - * *C. numidicus* Lambert, 1909d
 - * *C. pennetieri* Bucaille, 1882-1883
 - C. pteracanthoides* Schlüter, 1897b
 - * *C. pseudohirudo* Cotteau, 1862-1867
 - * *C. pseudosceptrifera* "
 - * *C. ratisbonnensis* Gumbel, 1868
 - * *C. rejaudryi* Cotteau, 1882-1893
 - * *C. rennensis* Lambert, 1911f
 - * *C. rholfsi* Wanner, 1902
 - * *C. serrifera* Cotteau, 1862-1867
 - * *C. spinosissima* "
 - * *C. splendens* Clark, 1893b
 - C. squamifera* Schlüter, 1897b
 - * *C. subpyriformis* Bucaille, 1882-1883
 - C. venulosoides* Schlüter, 1897b
 - * *C. vibraye* Cotteau, 1862-1867
 - * *C. walcotti* Clark & Twitchell, 1915
- Montien (Danian)
- * *C. distincta* Cotteau, 1862-1867
 - * *C. forchammeri* "
 - C. valettei* Lambert, 1908c
- Eocene
- * *C. acanthica* Fritsch, 1877
 - * *C. alabamensis* Clark & Twitchell, 1915
 - C. attenuata* Cotteau, 1858-1880
 - * *C. blancherei* Cotteau, 1889-1894
 - * *C. belgica* Cotteau, 1880a
 - C. bielzi* Koch, 1885
 - * *C. blandus* De Gregorio, 1890
 - C. cervicornis* Schauder, 1865
 - C. daguini* Castex & Lambert, 1919-1920
 - C. dubaleni* (Bartonian) Castex, 1947a
 - C. eugeniae* Castex & Lambert, 1919-1920
 - * *C. feliciae* Cotteau, 1882-1893
 - * *C. foveata* Jackson, 1922
 - * *C. grolanus* Oppenheim, 1902b
 - * *C. grossouvrei* Cotteau, 1889-1894
 - * *C. gymnozona* Arnold & Clark, 1927
 - C. handiensis* Castex & Lambert, 1919-1920
 - * *C. hemispinosa* (Lutetian) Lambert, 1933d
 - C. hungarica* Pavay, 1874
 - * *C. interlineata* Cotteau, 1889-1894

<i>C. isnardi</i> (Bartonian)	Lambert, 1924a
* <i>C. janus</i>	Fritsch, 1877
* <i>C. leptacantha</i>	Cotteau, 1889-1894
* <i>C. longicollis</i>	Fritsch, 1877
* <i>C. lorioli</i>	Cotteau, 1889-1894
* <i>C. matronensis</i>	Quenstedt, 1875
* <i>C. merriami</i>	Kew, 1920
* <i>C. modestus</i>	De Gregorio, 1890
* <i>C. moerens</i>	"
* <i>C. mortoni</i>	Conrad, 1850
* <i>C. ordinatus</i>	De Gregorio, 1890
<i>C. pannoniae</i>	Pavay, 1874
* <i>C. perdubius</i>	De Gregorio, 1890
* <i>C. pomeli</i>	Cotteau, 1889-1894
* <i>C. pratti</i>	Clark & Twitchell, 1915
* <i>C. prionata</i>	"
* <i>C. rossii</i>	Oppenheim, 1901
* <i>C. sabaratensis</i>	Cotteau, 1889-1894
<i>C. scampicii</i>	Taramelli, 1874
* <i>C. sigillum</i>	Lambert, 1931c
* <i>C. spileccensis</i>	Dames, 1878
* <i>C. spinigera</i>	Cotteau, 1889-1894
* <i>C. subacicularis</i>	Pavay, 1873
* <i>C. subprionata</i>	Cotteau, 1889-1894
* <i>C. subularis</i>	"
* <i>C. striatogranosa</i>	"
* <i>C. taramellii</i>	"
<i>C. tuberculosa</i>	Taramelli, 1874
<i>C. van den heckei</i>	Lambert, 1907-1909
* <i>C. veronensis</i>	Quenstedt, 1875
* <i>C. vincenti</i>	Cotteau, 1880a
* <i>C. websteriana</i>	Forbes, 1852
Oligocene	
* <i>C. acicularis</i>	Cotteau, 1889-1894
<i>C. assulaeformis</i>	Malaroda, 1951
<i>C. duncani</i>	Socin, 1942
<i>C. lucifera</i>	Castex and Lambert, 1919-1920
<i>C. pelettensis</i>	Castex, 1947a
* <i>C. peloria</i>	Jackson, 1922
* <i>C. lorenzanus</i>	Kew, 1920
* <i>C. söllengensis</i>	Ebert, 1889
* <i>C. subcylindrica</i>	Cotteau, 1889-1894
* <i>C. vepres</i>	Lambert, 1931c
Paleogene	
<i>C. bielzi</i>	Koch, 1885
<i>C. potserdisensis</i>	"
Miocene	
<i>C. aculeata</i>	Jeannet & Martin, 1937
* <i>C. anguillae</i>	Cotteau, 1875
<i>C. canavarii</i>	Loriol, 1882a
* <i>C. clevei</i>	Cotteau, 1875

* <i>C. cojimarensis</i>	Sanchez Roig, 1926b
* <i>C. cubensis</i>	Lambert & Thiéry, 1909-1924
<i>C. eliae</i>	Lambert, 1907-1909
<i>C. hollandei</i>	Cotteau, 1877
<i>C. jullianensis</i>	Loriol, 1902
* <i>C. melitensis</i>	Wright, 1855a
<i>C. pungens</i>	Pomel, 1887
* <i>C. rugata</i>	Herklots, 1854
<i>C. sardica</i>	Lambert, 1907-1909
* <i>C. schwabenau</i>	Laube, 1871
<i>C. tournoueri</i>	Cotteau, 1858-1880
 Pliocene	
* <i>C. desmoulinsi</i>	Desor, 1855-1858
 Genus: <i>Dorocidaris</i>	
Unknown	
<i>D. schweinfurthi</i>	Fourtau, 1914b
Cretaceous	
* <i>D. demujiensis</i>	Sanchez Roig, 1949
<i>D. garciai</i>	Sanchez Roig, 1952a
* <i>D. madrugensis</i>	Sanchez Roig, 1949
* <i>D. molineti</i>	Lambert, 1931
* <i>D. rohlfsi</i>	Wanner, 1902
 Hauterivian	
<i>D. urcustensis</i>	Weber, 1934
 Urgonian (Barremian)	
* <i>D. pyrenaica</i>	Cotteau, 1862-1867
 Barremian	
<i>D. bitakensis</i>	Weber, 1934
 Aptian	
<i>D. julieni</i>	Cotteau, Peron & Gauthier, 1876
 Cenomanian	
<i>D. ciryi</i>	Lambert, 1935f
<i>D. eybrumensis</i>	Dacqué, 1939
* <i>D. nomadicus</i>	Duncan, 1886
* <i>D. rhotomagensis</i>	Cotteau, 1862-1867
* <i>D. taouzensis</i>	Lambert, 1933b
* <i>D. thieryi</i>	Lambert, 1909d
 Turonian	
* <i>D. besseae</i>	Besairie & Lambert, 1930
* <i>D. granulostriata</i>	Cotteau, 1862-1867
* <i>D. othensis</i>	"
* <i>D. perornata</i>	"
 Campanian	
* <i>D. besairiei</i>	Lambert, 1936c

Senonian

- | | |
|------------------------------|-----------------------------|
| * <i>D. africanus</i> | Lambert, 1909a |
| * <i>D. arnaudi</i> | " |
| * <i>D. brasili</i> | Lambert, 1909d |
| * <i>D. cornutus</i> | Cotteau, 1862-1867 |
| * <i>D. defrancei</i> | Lambert & Thiéry, 1909-1924 |
| * <i>D. faujasi</i> | Desor, 1855-1858 |
| * <i>D. faurai</i> | Lambert, 1924b |
| <i>D. herthae</i> | Schlüter, 1892 |
| <i>D. hureae</i> | Valette, 1911 |
| * <i>D. longispinosa</i> | Lambert, 1909a |
| <i>D. malheiroi</i> | Loriol, 1888a |
| * <i>D. periatambonensis</i> | Steinmann, 1881a |
| * <i>D. perlata</i> | Cotteau, 1862-1867 |
| <i>D. persica</i> | Cotteau & Gauthier, 1895 |
| * <i>D. perornata</i> | Forbes, 1850 |
| * <i>D. petrocoriensis</i> | Lambert, 1909a |
| * <i>D. regalis</i> | Goldfuss, 1826-1844 |
| * <i>D. turonensis</i> | Cotteau, 1862-1867 |
| * <i>D. vendocinensis</i> | " |

Montien (Danian)

- | | |
|-----------------------|----------------|
| * <i>D. bazerquei</i> | Lambert, 1908a |
|-----------------------|----------------|

Eocene

- | | |
|---------------------|-----------------------------|
| * <i>D. excelsa</i> | Duncan & Sladen, 1882-1886 |
| * <i>D. opipara</i> | " |
| * <i>D. staadi</i> | Lambert & Thiéry, 1909-1925 |

Oligocene

- | | |
|-----------------------|-----------------------------|
| <i>D. ederae</i> | Castex & Lambert, 1919-1920 |
| * <i>D. exilis</i> | Lambert, 1931 |
| * <i>D. georgiana</i> | Clark & Twitchell, 1915 |
| * <i>D. smithi</i> | " |

Miocene

- | | |
|-------------------------|--------------------|
| * <i>D. allardi</i> | Lambert, 1910-1916 |
| * <i>D. balearis</i> | Lambert, 1907 |
| * <i>D. deydieri</i> | Lambert, 1910-1916 |
| * <i>D. mariae</i> | Lambert, 1907-1909 |
| * <i>D. mazzettii</i> | Stefanini, 1909 |
| <i>D. gattungae</i> | Lambert, 1907-1909 |
| * <i>D. henjamensis</i> | Clegg, 1933 |
| <i>D. saheliensis</i> | Pomel, 1887 |

Pliocene

- | | |
|---------------------------|------------------------|
| <i>D. cerulli</i> | Woods, 1908 |
| * <i>D. margaritifera</i> | Checchia-Rispoli, 1907 |

Genus: *Balanocidaris*

Ladinian

- | | |
|------------------------|--------------|
| * <i>B. migliorini</i> | Venzo, 1934b |
|------------------------|--------------|

Carnian	
<i>B. bronni</i>	Klipstein, 1843
* <i>B. dorsata</i>	Laube, 1864
<i>B. globifera</i>	Klipstein, 1843
* <i>B. hausmanni</i>	Laube, 1864
* <i>B. scrobiculata</i>	"
* <i>B. subdorsata</i>	Venzo, 1934b
Jurassic	
* <i>B. californica</i>	Clark & Twitchell, 1915
Bajocian	
* <i>B. besairie</i>	Lambert, 1933a
* <i>B. cucumifera</i>	Cotteau, 1875-1880
* <i>B. roysii</i>	"
Bathonian	
* <i>B. episcopalis</i>	Cotteau, 1875-1880
* <i>B. euthymei</i>	"
* <i>B. meandrina</i>	"
* <i>B. michaleti</i>	"
Callovian	
* <i>B. japonica</i>	Nisiyama, 1966
Rauracian (M. Jur.)	
* <i>B. icaunensis</i>	Cotteau, 1875-1880
<i>B. glandifera</i>	"
* <i>B. sturi</i>	Cotteau, 1884
Sequanian (M. Jur.)	
<i>B. strambergensis</i>	Cotteau, 1884
Tithonian	
<i>B. azyensis</i>	Loriol, 1902
Cretaceous	
* <i>B. tehamaensis</i>	Kew, 1920
Valangian	
* <i>B. tingitana</i>	Lambert, 1933b
Neocomian	
<i>B. cerioi</i>	Airaghi, 1905d
* <i>B. ryzacantha</i>	Cotteau, 1862-1867
Aptian	
* <i>B. darderi</i>	Lambert, 1935b
Albian	
<i>B. deserti</i>	El-Din Mahmoud, 1955
* <i>B. pilum</i>	Cotteau, 1862-1867
* <i>B. rebouli</i>	Lambert, 1920f

- Cenomanian
B. glandaria
B. velifera
 Loriol, 1902
 Cotteau, 1865b
- Senonian
B. miqueli
 * *B. gibberula*
 * *B. pteracantha*
 * *B. schlüteri*
 Lambert, 1911c
 Cotteau, 1862-1867
 "
 Lambert, 1911f
- Genus: *Alpicidaris*
 Hauterivian
 * *A. cureti*
 Lambert & Thiéry, 1909-1925
- Genus: *Cyathocidaris*
 Senonian
 * *C. cyathifera*
C. erebus
C. nordenskjoldi
C. ortmanni
C. patera
 * *C. pistillum*
C. septemtrionalis
 Cotteau, 1862-1867
 Lambert, 1910a
 "
 Loriol, 1902
 Lambert, 1910a
 Cotteau, 1862-1867
 Schmitz, 1970
- Eocene
 * *C. crateriformis*
 Cotteau, 1889-1894
- Miocene
 * *C. avenionensis*
 Loriol, 1875a
- Genus: *Eucidaris*
 Eocene
 * *E. strobilata*
 Fell, 1954
- Oligocene
 * *E. coralloides*
 Fell, 1954
- Miocene
 * *E. strombilata felli* (Janjukian)
 Philip, 1963d
- Genus: *Paracidaris*
 Rhaetian
 * *P. jeanneti*
 * *P. toucasi*
 Lambert, 1924c
 Cotteau, 1875-1880
- Sinemurian
 * *P. crossei*
 Cotteau, 1875-1880

Bajocian	
* <i>P. bajocensis</i>	Cotteau, 1875-1880
* <i>P. bouchardi</i>	Wright, 1855-1860
* <i>P. caumonti</i>	Cotteau, 1875-1880
* <i>P. spinulosa</i>	"
* <i>P. varusensis</i>	"
* <i>P. zschokkei</i>	"
Bathonian	
* <i>P. babeau</i>	Cotteau, 1875-1880
* <i>P. sublaeris</i>	"
Callovian	
<i>P. lagorgettei</i>	Lambert, 1933c
Argovian (M. Jur.)	
* <i>P. nunlisti</i>	Jeannet, 1927
Rauracian (M. Jur.)	
* <i>P. florigemma</i>	Cotteau, 1875-1880
* <i>P. moeschi</i>	Desor & Loriol, 1872
Sequanian (M. Jur.)	
<i>P. loppei</i>	Castex, 1947a
* <i>P. suevica</i>	Desor & Loriol, 1872
Oxfordian	
* <i>P. alpina</i>	Cotteau, 1875-1880
* <i>P. smithi</i>	Wright, 1855-1860
* <i>P. spinosa</i>	Cotteau, 1875-1880
<i>P. vallata</i>	Quenstedt, 1858
Kimmeridgian	
* <i>P. poucheti</i>	Cotteau, 1875-1880
Portlandian (U. Jur.)	
* <i>P. legayi</i>	Cotteau, 1875-1880
Genus: <i>Plegiocidaris</i>	
Triassic	
* <i>P. dilleri</i>	Clark & Twitchell, 1915
Carnian	
* <i>P. biforis</i>	Laube, 1864
* <i>P. decorata</i>	"
* <i>P. fasciculata</i>	"
* <i>P. flexuosa</i>	"
* <i>P. linearis</i>	"
* <i>P. raiblana rhodiensis</i>	Venzo, 1934b
* <i>P. wissmanni</i>	Laube, 1864

Norian	
<i>P. lanceolata</i>	Schafhauetl, 1859
Rhaetian	
<i>P. cornaliae</i>	Stoppanni, 1860-1865
<i>P. curionii</i>	"
<i>P. fumagalli</i>	"
<i>P. ombonii</i>	"
<i>P. senex</i>	Lambert, 1899b
* <i>P. stoppanii</i>	Desor & Loriol, 1872a
Hettangian	
* <i>P. angulatus</i>	Quenstedt, 1875
* <i>P. falsani</i>	Cotteau, 1875-1880
Sinemurian	
* <i>P. armata</i>	Cotteau, 1875-1880
* <i>P. domeriensis</i>	Meneghini, 1867-1881
* <i>P. pellati</i>	Cotteau, 1875-1880
Pliensbachian	
* <i>P. marizensis</i>	Lambert, 1973b
* <i>P. termieri</i>	"
Charmouthian (Pliensbachian)	
* <i>P. caraboeufi</i>	Cotteau, 1875-1880
* <i>P. striatula</i>	"
* <i>P. subundulosa</i>	"
Toarcian	
* <i>P. ilmensterensis</i>	Wright, 1855-1860
* <i>P. jurensis</i>	Quenstedt, 1875
* <i>P. moorei</i>	Cotteau, 1875-1880
* <i>P. morieri</i>	"
* <i>P. morieri nodosa</i>	Mercier, 1937c
* <i>P. telrhemtensis</i>	Lambert, 1937b
Aalenian	
* <i>P. tingitana</i>	Lambert, 1933b
Domerian (L. Jur.)	
* <i>P. bigoti</i>	Lambert & Thiéry, 1909-1925
* <i>P. pichaurisensis</i>	"
* <i>P. valabrequei</i>	"
Bajocian	
* <i>P. bradfordensis</i>	Wright, 1855-1860
* <i>P. chanterei</i>	Cotteau, 1875-1880
* <i>P. charmassei</i>	"
<i>P. cymosa</i>	Loriol, 1890-1891
* <i>P. dumortieri</i>	Cotteau, 1875-1880
* <i>P. gingensis</i>	Desor & Loriol, 1872a
* <i>P. locardi</i>	Cotteau, 1875-1880

* <i>P. munieri</i>	"
<i>P. palliata</i>	Loriol, 1890-1891
<i>P. penichensis</i>	"
* <i>P. pacomei</i>	Cotteau, 1880-1885
* <i>P. prae nobilis</i>	Quenstedt, 1875
* <i>P. saemanni</i>	Cotteau, 1875-1880
* <i>P. welschi</i>	Lambert, 1935a
<i>P. wrighti</i>	Wright, 1851a
Bathonian	
* <i>P. babeau granulos a</i>	Mercier, 1932
* <i>P. bathonica</i>	Cotteau, 1875-1880
* <i>P. bifrons</i>	Lambert, 1936c
* <i>P. caeuliculus</i>	"
* <i>P. cellensis</i>	"
* <i>P. daroustiana</i>	"
* <i>P. desori</i>	"
* <i>P. koechlini</i>	"
* <i>P. langrunensis</i>	"
* <i>P. microstoma</i>	"
* <i>P. mercieri</i>	Lambert, 1933
* <i>P. minor</i>	Lambert & Thiéry, 1909-1925
* <i>P. pseudohorrida</i>	Lambert, 1936c
* <i>P. noyensis</i>	Cotteau, 1875-1880
<i>P. payebini</i>	Lissajous, 1903-1904
Callovian	
<i>P. ardesica</i>	Thiéry, Lambert & Collignon,
1928	
* <i>P. briconensis</i>	Cotteau, 1875-1880
* <i>P. calloviensis</i>	"
* <i>P. claviceps</i>	Quenstedt, 1875
* <i>P. desnoyersi</i>	Cotteau, 1875-1880
* <i>P. jacodi</i>	Lambert, 1936c
* <i>P. ornata</i>	Quenstedt, 1875
Rauracian (M. Jur.)	
* <i>P. blumenbachi</i>	Desor & Loriol, 1872a
* <i>P. cervicalis</i>	Cotteau, 1875-1880
* <i>P. coronata</i>	Cotteau, 1875-1880
* <i>P. elegantulus</i>	Valette, 1898
* <i>P. granulata</i>	Cotteau, 1875-1880
* <i>P. houllefortensis</i>	"
<i>P. kuchkaensis</i>	Weber, 1934
* <i>P. liesbergensis</i>	Loriol, 1885
<i>P. lineata</i>	Cotteau, 1849-1856
* <i>P. monilifera</i>	Cotteau, 1875-1880
* <i>P. propinqua</i>	"
* <i>P. pseudospina</i>	Valette, 1907-1908
* <i>P. valfinensis</i>	Cotteau, 1875-1880
<i>P. vogdti</i>	Weber, 1934
Sequanian (M. Jur.)	
* <i>P. beltremieuxi</i>	Cotteau, 1875-1880

* <i>P. carinifera</i>	"
* <i>P. constricta</i>	Cotteau, 1880-1885
<i>P. cucumis</i>	Quenstedt, 1858
<i>P. dagordaensis</i>	Loriol, 1902
* <i>P. depicta</i>	Quenstedt, 1875
* <i>P. ducreti</i>	Cotteau, 1875-1880
* <i>P. flabellata</i>	Quenstedt, 1875
<i>P. gibbosa</i>	Cotteau, 1884a
<i>P. guimaraesi</i>	Loriol, 1890-1891
* <i>P. guirandi</i>	Cotteau, 1875-1880
<i>P. louleensis</i>	Loriol, 1890-1891
<i>P. nevesensis</i>	"
<i>P. panasqueirensis</i>	"
<i>P. pasquieri</i>	Loriol, 1902
* <i>P. perlata</i>	Quenstedt, 1875
* <i>P. pilleti</i>	Cotteau, 1875-1880
* <i>P. platyspina</i>	"
* <i>P. pseudocervicalis</i>	Lambert & Thiéry, 1908
* <i>P. subteres</i>	Quenstedt, 1852-1885
<i>P. thyrsiger</i>	Loriol, 1890-1891
<i>P. tithonia</i>	Cotteau, 1884a
* <i>P. tuberculosa</i>	Quenstedt, 1875
* <i>P. taybrensis</i>	Clark, 1893b
Oxfordian	
* <i>P. abichi</i>	Desor & Loriol, 1872a
<i>P. bruni</i>	Lambert, 1909c
* <i>P. chalmasi</i>	Cotteau, 1875-1880
* <i>P. elegans</i>	"
* <i>P. escheri</i>	Desor & Loriol, 1872a
* <i>P. filograna</i>	Cotteau, 1875-1880
* <i>P. laeviuscula</i>	"
* <i>P. marioni</i>	"
* <i>P. matheyi</i>	"
* <i>P. monusteriensis</i>	Desor & Loriol, 1872a
* <i>P. oppeli</i>	"
* <i>P. schlönbachi</i>	Cotteau, 1875-1880
<i>P. segrini</i>	Lambert, 1909c
* <i>P. subhistricoides</i>	Quenstedt, 1875
Kimmeridgian	
* <i>P. beaugrandi</i>	Cotteau, 1875-1880
* <i>P. kimmeridgiensis</i>	"
Tithonian	
<i>P. chomeracensis</i>	Loriol, 1902
* <i>P. helviorum</i>	Lambert, 1932
<i>P. noyarezensis</i>	Loriol, 1902
<i>P. mauritanicus</i>	"
* <i>P. remesi</i>	Loriol, 1901
Hauterivian	
<i>P. lamberti</i>	Weber, 1934
<i>P. lemoinei</i>	Démoly, 1928

Neocomian

- | | |
|--------------------------|-----------------------|
| * <i>P. friburgensis</i> | Loriol, 1873a |
| <i>P. gevreyi</i> | Savin, 1905 |
| * <i>P. gillieron</i> | Loriol, 1873a |
| <i>P. gourdonensis</i> | Lambert & Savin, 1906 |
| * <i>P. lineolata</i> | Cotteau, 1862-1867 |
| * <i>P. loryi</i> | " |
| * <i>P. meridanensis</i> | " |
| <i>P. muricata</i> | Schlüter, 1892 |
| * <i>P. punctata</i> | Loriol, 1873a |
| * <i>P. pustulosa</i> | Cotteau, 1862-1867 |
| * <i>P. spinigera</i> | " |

Barremian

- | | |
|------------------------|----------------|
| <i>P. biassalensis</i> | Weber, 1934 |
| * <i>P. huguenini</i> | Lambert, 1931c |

Aptian

- | | |
|------------------------|--------------------|
| * <i>P. amalecitae</i> | Fourtau, 1921 |
| * <i>P. kiliani</i> | Cotteau, 1882-1893 |

Albian

- | | |
|----------------------|---------------------------------|
| * <i>P. baculina</i> | Cotteau, Peron & Gauthier, 1876 |
| <i>P. delatourei</i> | Cotteau, 1858-1880 |
| <i>P. orientalis</i> | El-Din Mahmoud, 1955 |

Cenomanian

- | | |
|------------------------|---------------------|
| * <i>P. dissimilis</i> | Wright, 1864-1882 |
| * <i>P. heva</i> | Bucaille, 1882-1883 |
| * <i>P. uniformis</i> | Cotteau, 1862-1867 |

Senonian

- | | |
|---------------------------|--------------------|
| <i>P. antarctica</i> | Loriol, 1902 |
| * <i>P. beaussetensis</i> | Cotteau, 1882-1893 |
| * <i>P. nahakalensis</i> | Loriol, 1887 |
| * <i>P. ramoneti</i> | Cotteau, 1883 |
| * <i>P. teilhardi</i> | Lambert, 1909a |

Eocene

- | | |
|----------------------------|--------------------|
| <i>P. einsiedelensis</i> | Ooster, 1865 |
| * <i>P. infratertiarus</i> | Quenstedt, 1875 |
| * <i>P. oosteri</i> | Laube, 1868 |
| <i>P. porcsesdensis</i> | Koch, 1885 |
| * <i>P. suberrata</i> | Cotteau, 1889-1894 |
| * <i>P. unterbachensis</i> | Loriol, 1875a |

Miocene

- | | |
|------------------|--------------------|
| <i>P. cureti</i> | |
| <i>P. peroni</i> | Lambert, 1907-1909 |

Pliocene

- | | |
|--------------------|--------------------|
| <i>P. zea-mays</i> | Lambert, 1907-1909 |
|--------------------|--------------------|

Genus: *Stylocidaris*
 Tertiary
 * *S. chapmani*

Philip, 1963d

Genus: *Menocidaris*
 * *M. compta*

Philip, 1964

Family Echinometridae

Genus: *Echinometra*
 Miocene
 * *E. handoana*

Nisiyama, 1966

Genus: *Ellipsechinus*
 Cretaceous
 * *E. palmeri*

Sanchez Roig, 1949

Miocene
E. miocenicus

Loriol, 1902

Genus: *Echinostrephus*
 Unknown
 * *E. pentagonus*

Yoshiwara, 1898a

Miocene
 * *E. saipanicum*

Cooke, 1957a

Genus: *Evechinus*
 Pliocene
 * *E. palatus*

Philip, 1969

Genus: *Heliocidaris*
 Miocene
 * *H. variolosa*
 * *H. ludbrookae*

Herklots, 1854
 Philip, 1965b

Genus: *Zenocentrotus*
 Miocene
 * *Z. peregrinus*

Philip, 1965b

Family ToxopneustidaeGenus: *Lytechinus*

Miocene

- * *L. coreyi* Grant & Hertlein, 1938b
- L. lovisatoi* Lambert, 1907-1909
- * *L. milleri* Grant & Hertlein, 1938b

Pliocene

- L. afer* Pomel, 1887
- * *L. crassus* Clark, 1945
- * *L. okinawa* Cooke, 1954

Pleistocene

- * *L. variegatus plurituberculatus* Clark, 1945

Genus: *Mirechinus*

Eocene

- * *M. mirabilis* Nisiyama, 1966

Genus: *Oligophyma*

Miocene (Tortonian)

- O. oranense* Pomel, 1887

Helvetian (Pleistocene)

- O. cellense* Pomel, 1887

Genus: *Pseudocentrotus*

Miocene

- * *P. stenoporus* Nisiyama, 1966

Genus: *Schizechinus*

Miocene

- S. balestrai* Oppenheim, 1902
- S. burdigalensis* Lambert, 1912a
- * *S. duciei* Wright, 1855a
- * *S. hungaricus* Laube, 1871
- S. maurus* Pomel, 1887
- * *S. mortenseni* Lambert, 1906b
- * *S. pentagonus* (Burdigalian) Kier, 1972
- S. sahelensis* Pomel, 1887

Pliocene

- S. angulosus* Pomel, 1887
- * *S. bazini* Cotteau, 1882-1893
- * *S. chateleti* Lambert, 1910-1916
- S. serialis* Pomel, 1887
- * *S. candeli* Lambert, 1931c

Genus: *Scoliechinus*

Oligocene

- * *S. dallonii*

Lambert & Thiéry, 1909-1925

Eocene

- * *S. axiologus*

Arnold & Clark, 1927

Genus: *Sphaerechinus*

Eocene

- * *S. leymeriei*

Cotteau, 1889-1894

Miocene (Aquitanian)

- * *S. burdigalensis*

Lambert, 1928b

Genus: *Tripneustes*

Miocene

- * *T. antiquus*
- T. californicus*
- * *T. gahardensis*
- * *T. magnificus*
- * *T. parkinsoni*
- * *T. planus*
- * *T. proavia*
- T. schneideri*
- * *T. tobleri*
- T. ventricosus austriacus*

Duncan & Sladen, 1882-1886

Pomel, 1888b

Lambert, 1906b

Nisiyama, 1966

Lambert, 1910-1916

"

Duncan & Sladen, 1882-1886

Boehm, 1882

Jeannet, 1928a

Tauber, 1951

Appendix II: Tumbling Data

Raw data obtained from the tumbling experiments are presented in this appendix. All weights are given in grams. Data entered for skeletal elements present in each size fraction are listed as number of elements followed by their weight in parentheses. In most instances, spines in the 500 μ - 1 mm size fraction were weighed without being counted. This method was also used for undifferentiated skeletal elements.

A. *Diadema antillarum*, 1 hour of tumbling

Trial	1	2	3	4	5
Wt. >2 mm fraction	27.87	15.58	17.05	17.35	19.69
Wt. 1-2 mm fraction	1.59	1.18	2.21	1.56	1.93
Wt. 500 μ - 1 mm fraction	0.19	0.21	0.34	0.21	0.37
Wt. 125 μ - 500 μ fraction	0.14	0.06	0.67	0.50	0.44
Wt. <125 μ fraction	0.91	0.91	0.52	1.05	1.51
>2 mm Fraction					
Spines	507(16.62)	416(6.80)	485(10.33)	438(11.58)	512(11.28)
Corona	164(7.40)	127(3.38)	118(4.34)	181(3.55)	77(5.57)
Lantern	34(3.85)	30(5.40)	30(2.38)	31(2.22)	31(2.84)
Undif.	0	0	0	0	0
1-2 mm Fraction					
Spines	166(1.39)	252(1.10)	766(1.94)	371(1.12)	379(1.81)
Corona	26(0.05)	26(.08)	44(0.07)	117(0.44)	46(0.09)
Lantern	9(0.11)	6(<.01)	13(0.04)	14(0.07)	13(0.03)
Undif.	16(0.01)	0	.16 g	0	0
500 μ - 1 mm Fraction					
Spines	419 (0.19)	230(0.21)	.14 g	281(0.21)	449(0.30)
Corona	12 (<.01)	70 (<.01)	5(<.01)	12(<.01)	8(<.01)
Lantern	1 (<.01)	7(<.01)	3(<.01)	4(<.01)	12(<.01)
Undif.	7(<.01)	6(<.01)	23(<.01)	.20 g	.14 g

B. *Diadema antillarum*, 10 hours of tumbling

Trial	1	2	3	4	5
Wt. >2 mm fraction	8.18	22.51	29.05	21.37	34.32
Wt. 1-2 mm fraction	0.99	1.69	3.27	1.71	2.97
Wt. 500 μ - 1 mm fraction	0.21	0.40	0.43	0.20	0.29
Wt. 125 μ - 500 μ fraction	0.15	0.15	0.16	0.41	0.32
Wt. <125 μ fraction	0.61	0.79	0.68	1.13	1.14
>2 mm Fraction					
Spines	287(4.07)	454(13.52)	632(16.63)	529(13.06)	628(21.05)
Corona	120(2.28)	212(6.03)	267(8.02)	98(5.36)	216(9.31)
Lantern	31(1.83)	29(2.96)	34(4.40)	31(2.95)	30(3.90)
Undif.	0	0	0	0	0.06 g
1-2 mm Fraction					
Spines	184(0.58)	315(1.48)	1199(2.56)	558(1.60)	899(2.53)
Corona	132(0.41)	40(0.11)	73(0.34)	22(0.03)	61(0.15)
Lantern	0	11(0.10)	12(0.03)	13(0.04)	16(0.11)
Undif.	4(<.01)	0	.34 g	0.04 g	0.18 g
500 μ - 1 mm Fraction					
Spines	419 (0.19)	453(.40)	464(0.32)	0.11 g	0.23 g
Corona	12 (<.01)	13(<.01)	6(<.01)	7(<.01)	1(<.01)
Lantern	1 (<.01)	10(<.01)	6(<.01)	8(<.01)	9(<.01)
Undif.	76 (<.01)	16(<.01)	.09 g	.07 g	0.04 g

C. Diadema antillarum, 100 hours of tumbling

Trial	1	2	3	4	5
Wt. >2 mm fraction	13.49	5.55	31.86	21.62	19.64
Wt. 1-2 mm fraction	1.37	0.95	1.35	2.60	1.54
Wt. 500 μ - 1 mm fraction	0.19	0.01	0.31	0.24	0.23
Wt. 125 μ - 500 μ fraction	0.06	0.11	0.23	0.28	0.11
Wt. <125 μ fraction	1.19	0.46	4.27	1.12	1.17
>2 mm Fraction					
Spines	312(618)	220(3.25)	663(21.03)	579(13.13)	527(11.34)
Corona	211(4.25)	92(1.24)	285(6.89)	203(5.62)	228(5.48)
Lantern	30(3.06)	29(0.96)	29(3.94)	31(2.87)	29(2.82)
Undif.	0	0	0	0	0
1-2 mm Fraction					
Spines	181(0.92)	133(0.58)	945(0.94)	826(2.31)	449(1.23)
Corona	108(0.36)	148(0.37)	64(0.27)	74(0.25)	63(0.24)
Lantern	7(0.09)	5(<.01)	12(0.10)	10(0.04)	6(0.07)
Undif.	0	0	.04 g	0	0
500 μ - 1 mm Fraction					
Spines	279(0.19)	152(0.10)	0.26 g	0.18 g	0.20 g
Corona	13 (<.01)	18(<.01)	3(<.01)	3(<.01)	7(<.01)
Lantern	8 (<.01)	8(<.01)	9(<.01)	1(<.01)	4(<.01)
Undif.	16 (<.01)	10(<.01)	.03 g	.04 g	0.01 g

D. *Echinometra lucunter*, 1 hour of tumbling

Trial	1	2	3	4	5
Wt. >2 mm fraction	2.16	4.43	5.00	12.98	5.79
Wt. 1-2 mm fraction	0.49	0.60	0.58	1.37	1.01
Wt. 500 μ - 1 mm fraction	0.13	0.18	0.12	0.43	0.16
Wt. 125 μ - 500 μ fraction	0.10	0.16	0.07	0.20	0.11
Wt. <125 μ fraction	0.02	0.09	0.08	0.16	0
>2 mm Fraction					
Spines	91(0.85)	147(1.50)	47(2.21)	264(4.29)	159(2.18)
Corona	1(1.02)	1(2.25)	10(2.10)	3(6.40)	8(2.77)
Lantern	17(0.29)	25(0.68)	24(0.69)	30(2.29)	24(0.84)
Undif.	0	0	0	0	0
1-2 mm Fraction					
Spines	173(0.43)	203(0.55)	157(0.56)	352(1.33)	513(0.90)
Corona	5(<.01)	5(<.01)	7(<.01)	18(0.03)	16(0.02)
Lantern	11(0.06)	6(<.01)	5(<.01)	4(0.01)	11(0.09)
Undif.	0	0	0	0	0
500 μ - 1 mm Fraction					
Spines	302(0.11)	191(0.10)	191(0.10)	0.41 g	0.15 g
Corona	19 (0.01)	4(<.01)	4(<.01)	6(<.01)	9(<.01)
Lantern	8(0.01)	1(<.01)	1(<.01)	5(<.01)	5(<.01)
Undif.	0	0	0	0	0

E. Echinometra lucunter, 10 hours of tumbling

Trial	1	2	3	4	5
Wt. >2 mm fraction	2.15	1.02	3.50	7.27	2.89
Wt. 1-2 mm fraction	0.40	0.28	0.84	0.96	0.62
Wt. 500 μ - 1 mm fraction	0.11	0.09	0.14	0.19	0.10
Wt. 125 μ - 500 μ fraction	0.20	0.13	0.06	0.10	0.08
Wt. <125 μ fraction	0	0	0.12	0	0.07
>2 mm Fraction					
Spines	95(0.82)	46(0.37)	109(1.18)	152(2.40)	105(1.20)
Corona	1(1.10)	1(0.53)	1(1.78)	2(3.18)	5(1.28)
Lantern	14(0.23)	13(0.12)	24(0.54)	28(1.69)	18(0.41)
Undif.	0	0	0	0	0
1-2 mm Fraction					
Spines	139(0.33)	111(0.25)	274(0.80)	303(0.91)	295(0.54)
Corona	5(<.01)	4(<.01)	5(<.01)	12(0.01)	7(0.01)
Lantern	16(0.07)	15(0.03)	8(0.04)	8(0.04)	11(0.07)
Undif.	0	0	0	0	0
500 μ - 1 mm Fraction					
Spines	254(0.11)	219(0.09)	0.13 g	0.18 g	0.10 g
Corona	18(<.01)	13(<.01)	16(0.01)	10(0.01)	20(<.01)
Lantern	5(<.01)	5(<.01)	4(<.01)	7(<.01)	6(<.01)
Undif.	0	0	0	0	0

F. *Echinometra lucunter*, 100 hours of tumbling

Trial	1	2	3	4	5
Wt. >2 mm fraction	1.91	1.12	2.64	4.08	3.03
Wt. 1-2 mm fraction	0.51	0.41	0.93	0.81	0.77
Wt. 500 μ - 1 mm fraction	0.11	0.09	0.09	0.16	0.13
Wt. 125 μ - 500 μ fraction	0.13	0.10	0.12	0.17	0.08
Wt. <125 μ fraction	0.32	0	0.24	0.31	0.12
>2 mm Fraction					
Spines	69(0.82)	38(0.32)	98(1.01)	93(1.32)	82(1.08)
Corona	1(0.94)	1(0.60)	1(1.31)	1(2.12)	7(1.63)
Lantern	9(0.15)	15(0.20)	15(0.32)	20(0.64)	15(0.32)
Undif.	0	0	0	0	0
1-2 mm Fraction					
Spines	166(0.45)	143(0.36)	254(0.82)	222(0.70)	226(0.68)
Corona	5(<.01)	6(<.01)	5(0.06)	4(<.01)	6(<.01)
Lantern	15(0.06)	17(0.05)	17(0.10)	13(0.11)	15(0.09)
Undif.	0	0	0	0	0
500 μ - 1 mm Fraction					
Spines	170(0.11)	203(0.09)	0.09 g	0.14 g	0.12 g
Corona	17(<.01)	29(<.01)	17(<.01)	18(0.01)	18(<.01)
Lantern	6(<.01)	4(<.01)	7(<.01)	7(0.01)	8(<.01)
Undif.	0	0	0	0	0

G. Eucidaris tribuloides, 1 hour of tumbling

Trial	1	2	3	4	5
Wt. >2 mm fraction	5.32	7.29	2.17	4.52	2.83
Wt. 1-2 mm fraction	0.61	1.05	0.12	0.40	0.32
Wt. 500 μ - 1 mm fraction	0.42	0.38	0.21	0.38	0.26
Wt. 125 μ - 500 μ fraction	0.15	0.17	0.08	0.08	0.12
Wt. <125 μ fraction	0.18	0	0.04	0	0.05
>2 mm Fraction					
Spines	50(3.46)	62(3.86)	39(1.43)	46(3.01)	32(1.87)
Corona	14(1.56)	16(2.54)	6(0.59)	19(1.18)	15(0.77)
Lantern	12(0.30)	24(0.89)	15(0.15)	14(0.33)	14(0.19)
Undif.	0	0	0	0	0
1-2 mm Fraction					
Spines	192(0.36)	478(0.72)	64(0.08)	145(0.28)	80(0.22)
Corona	7(0.02)	16(0.05)	8(0.02)	16(0.05)	9(0.02)
Lantern	20(0.08)	10(0.09)	13(0.02)	18(0.07)	14(0.03)
Undif.	0	0	0	0	0.05 g
500 μ - 1 mm Fraction					
Spines	192(0.36)	0.26 g	0.18 g	0.32 g	0.22 g
Corona	7(0.02)	12(<.01)	0	33(0.02)	18(<.01)
Lantern	20(0.08)	5(<.01)	5(<.01)	7(0.01)	6(<.01)
Undif.	0.15 g	0.19 g	0.03 g	0.03 g	0.04 g

H. Eucidaris tribuloides, 10 hours of tumbling

Trial	1	2	3	4	5
Wt. >2 mm fraction	4.00	3.38	1.55	1.97	1.76
Wt. 1-2 mm fraction	0.28	0.12	0.14	0.08	0.11
Wt. 500 μ - 1 mm fraction	0.39	0.30	0.13	0.15	0.13
Wt. 125 μ - 500 μ fraction	0.09	0.07	0.07	0.06	0.07
Wt. <125 μ fraction	0.20	0.17	0.11	0.06	0.13
>2 mm Fraction					
Spines	43(2.62)	38(2.45)	26(1.02)	38(1.47)	30(1.29)
Corona	7(1.09)	22(0.77)	7(0.43)	5(0.39)	10(0.37)
Lantern	15(0.29)	13(0.16)	11(0.10)	15(0.11)	14(0.10)
Undif.	0	0	0	0	0
1-2 mm Fraction					
Spines	108(0.22)	30(0.08)	25(0.12)	17(0.04)	20(0.06)
Corona	6(0.01)	15(0.02)	11(0.01)	12(0.02)	11(0.02)
Lantern	15(0.04)	16(0.02)	12(0.01)	14(0.02)	12(0.01)
Undif.	0.01 g	0	0	0	0.02 g
500 μ - 1 mm Fraction					
Spines	0.36 g	0.28 g	0.12 g	0.13 g	0.10 g
Corona	1(0.01)	27(<.01)	1(<.01)	1(<.01)	10(<.01)
Lantern	7(<.01)	5(<.01)	10(<.01)	8(0.01)	6(<.01)
Undif.	0.03 g	0.02 g	0.01g	0.02 g	0.03 g

I. *Eucidaris tribuloides*, 100 hours of tumbling

Trial	1	2	3	4	5
Wt. >2 mm fraction	1.69	1.69	1.53	2.06	2.55
Wt. 1-2 mm fraction	0.18	0.13	0.28	0.14	0.21
Wt. 500 μ - 1 mm fraction	0.28	0.24	0.22	0.24	0.36
Wt. 125 μ - 500 μ fraction	0.11	0.05	0.06	0.04	0.08
Wt. <125 μ fraction	0.08	0.11	0.05	0.08	0.09
>2 mm Fraction					
Spines	35(0.93)	29(1.00)	25(1.00)	30(1.42)	43(1.72)
Corona	6(0.60)	5(0.53)	11(0.41)	7(0.52)	7(0.67)
Lantern	13(0.16)	13(0.16)	13(0.12)	13(0.12)	13(0.16)
Undif.	0	0	0	0	0
1-2 mm Fraction					
Spines	22(0.12)	24(0.09)	40(.21)	37(0.11)	34(0.11)
Corona	16(0.03)	3(0.01)	13(0.04)	5(0.01)	8(0.03)
Lantern	17(0.03)	15(0.03)	18(0.03)	12(0.02)	17(0.03)
Undif.	0	0	0	0	0.04 g
500 μ - 1 mm Fraction					
Spines	0.25 g	0.21 g	0.18 g	0.20 g	0.31 g
Corona	0	64(0.01)	23(0.01)	8(0.01)	5(<.01)
Lantern	6(<.01)	6(0.01)	5(0.01)	7(0.01)	7(0.01)
Undif.	0.03 g	0.01 g	0.02g	0.02 g	0.04 g

J. Tripneustes ventricosus, 1 hour of tumbling

Trial	1	2	3	4	5
Wt. >2 mm fraction	3.04	1.59	1.54	1.32	1.01
Wt. 1-2 mm fraction	0.66	0.76	0.70	0.36	0.38
Wt. 500 μ - 1 mm fraction	0.57	0.22	0.23	0.20	0.18
Wt. 125 μ - 500 μ fraction	0.43	0.22	0.30	0.13	0.16
Wt. <125 μ fraction	0.03	0.07	0	0	0
>2 mm Fraction					
Spines	150(0.45)	73(0.18)	47(0.11)	70(0.14)	5(0.01)
Corona	2(2.33)	1(1.28)	18(1.27)	1(1.04)	1(0.88)
Lantern	17(0.26)	11(0.13)	16(0.16)	15(0.14)	14(0.12)
Undif.	0	0	0	0	0
1-2 mm Fraction					
Spines	312(0.54)	532(0.68)	606(0.61)	332(0.28)	456(0.31)
Corona	12(0.03)	5(<.01)	12(0.02)	6(0.01)	12(0.02)
Lantern	18(0.09)	23(0.08)	18(0.07)	17(0.07)	17(0.05)
Undif.	0	0	0	0	0
500 μ - 1 mm Fraction					
Spines	0.55 g	0.19 g	0.19 g	0.17 g	0.15 g
Corona	19(0.03)	16(0.01)	13(0.01)	23(0.01)	12(0.01)
Lantern	5(<.01)	6(0.01)	7(0.01)	9(0.01)	8(0.01)
Undif.	0.01 g	0.01 g	0.02g	0.01 g	0.01 g

K. Tripneustes ventricosus, 10 hours of tumbling

Trial	1	2	3	4	5
Wt. >2 mm fraction	0.93	1.82	1.32	1.54	0.56
Wt. 1-2 mm fraction	0.25	0.54	0.38	0.48	0.25
Wt. 500 μ - 1 mm fraction	0.18	0.22	0.24	0.34	0.13
Wt. 125 μ - 500 μ fraction	0.15	0.21	0.13	0.33	0.15
Wt. <125 μ fraction	0	0	0.03	0.01	0.01
>2 mm Fraction					
Spines	36(0.05)	116(0.28)	103(0.17)	66(0.13)	5(0.01)
Corona	2(0.78)	1(1.34)	1(1.00)	1(1.23)	10(0.48)
Lantern	14(0.10)	17(0.20)	17(0.15)	16(0.18)	12(0.07)
Undif.	0	0	0	0	0
1-2 mm Fraction					
Spines	329(0.20)	498(0.44)	348(0.32)	483(0.40)	271(0.15)
Corona	9(0.01)	11(0.02)	9(0.01)	6(0.01)	42(0.06)
Lantern	13(0.04)	18(0.08)	13(0.05)	18(0.07)	20(0.04)
Undif.	0	0	0	0	0
500 μ - 1 mm Fraction					
Spines	0.15 g	0.19 g	0.21g	0.28 g	0.11 g
Corona	17(0.01)	17(0.01)	24(0.01)	20(0.01)	26(0.01)
Lantern	11(0.01)	7(0.01)	10(0.01)	10(0.01)	7(0.01)
Undif.	0.01 g	0.01 g	0.01g	0.04 g	0

L. Tripneustes ventricosus, 100 hours of tumbling

Trial	1	2	3	4	5
Wt. >2 mm fraction	1.25	2.82	1.09	0.79	0.64
Wt. 1-2 mm fraction	0.61	0.99	0.55	0.31	0.40
Wt. 500 μ - 1 mm fraction	0.26	0.43	0.23	0.17	0.15
Wt. 125 μ - 500 μ fraction	0.19	0.19	0.18	0.08	0.07
Wt. <125 μ fraction	0.15	0.07	0	0.01	0.07
>2 mm Fraction					
Spines	72(0.14)	173(0.52)	49(0.09)	32(0.04)	39(0.06)
Corona	36(0.98)	68(2.04)	3(0.90)	46(0.70)	23(0.51)
Lantern	13(0.13)	20(0.26)	10(0.10)	13(0.05)	12(0.07)
Undif.	0	0	0	0	0
1-2 mm Fraction					
Spines	522(0.43)	593(0.77)	56(0.35)	321(0.21)	335(0.20)
Corona	56(0.11)	63(0.15)	11(0.08)	34(0.05)	86(0.15)
Lantern	20(0.07)	12(0.07)	20(0.12)	22(0.05)	21(0.05)
Undif.	0	0	0	0	0
500 μ - 1 mm Fraction					
Spines	0.22 g	0.38 g	0.22 g	0.15 g	0.13 g
Corona	45(0.02)	38(0.02)	3(0.01)	40(0.02)	52(0.01)
Lantern	7(0.01)	12(0.02)	10(<.01)	9(<.01)	8(0.01)
Undif.	0.01 g	0.01 g	0	0	0

APPENDIX III: Transect Data

A. Smuggler's Cove Data

Station	(m)	Substrate	Echinoid	Quadrat #									
				1	2	3	4	5	6	7	8	9	10
0		Dense seagrass	<i>E. lucunter</i>						3	1	2	4	3
60		Dense seagrass	No echinoids										
120		Sparse seagrass	No echinoids										
180		Dense seagrass	No echinoids										
240		Dense seagrass	No echinoids										
300		Mod. seagrass	No echinoids										
360		Patch reef	No echinoids										
420		Bare sand	No echinoids										
480		Sparse seagrass	No echinoids										
540		Reef Tract (sand/rubble)	<i>E. lucunter</i> <i>T. ventricosus</i>	10	4	9	10	9	1	1 1	4		

A. Smuggler's Cove Data -cont-

Station (m)	Substrate	Echinoid	Quadrat #									
			1	2	3	4	5	6	7	8	9	10
600	Fore-reef (bare sand)	<i>D. antillarum</i>	4	1								
		<i>E. lucunter</i>				5	5	4	2	2	1	2
		<i>E. tribuloides</i>					2	2	1	2		
660	Bare sand	No echinoids										
720	Bare sand	No echinoids										

B. Rod Bay Data

Station	(m)	Substrate	Echinoid	Quadrat #									
				1	2	3	4	5	6	7	8	9	10
0		Rubbly pavement	<i>E. lucunter</i> <i>T. ventricosus</i>	59	28	26	32	17	48	30	33 1	3	5
10		Dense seagrass	No echinoids										
20		Dense seagrass	No echinoids										
30		Dense seagrass	No echinoids										
40		Coral rubble	<i>E. lucunter</i> <i>T. ventricosus</i>	13				2	1	1			2 2
50		Patch reef (coral rubble)	<i>E. lucunter</i> <i>E. tribuloides</i>		2				4 2	5 2	4		2

C. Graham's Harbour Data

T. ventricosus was the only regular echinoid observed along the transect. Therefore, the taphonomic condition is recorded.

Station (m)	Substrate	Taph. Condition	Quadrat #									
			1	2	3	4	5	6	7	8	9	10
0	Beach rock	No echinoids										
100	Sparse seagrass	No echinoids										
200	Sparse seagrass	No echinoids										
300	Sparse seagrass	Intact corona Fresh kill	1									1
400	Sparse seagrass	Alive encrusted corona coronal fragments	1			1		1				
500	Dense seagrass	fragments					1					1
600	Dense seagrass	No echinoids										
700	Sparse seagrass	fragments						1			1	

APPENDIX IV: Multivariate Data

Listed below are the number of cidarid type species characterized with each taphonomic code from each geologic series from the Middle Triassic through the Pleistocene.

<u>Series</u>	<u>Code 1</u>	<u>Code 2</u>	<u>Code 3</u>	<u>Code 4</u>	<u>Code 5</u>	<u>Code 6</u>	<u>Code 7</u>
Pleistocene						1	2
Pliocene						2	6
Miocene		2	2	3		6	22
Oligocene	1	4				3	17
Eocene		20	1	3		12	45
Paleocene						1	2
U. Cretaceous	1	36	1	3	1	13	67
L. Cretaceous	1	15		1	1	2	38
U. Jurassic	1	14	2	1	1	5	31
M. Jurassic	2	35	2	2	3	9	73
L. Jurassic		2		1		4	30
U. Triassic		1		1			46
M. Triassic		1		1		3	23