To the Graduate Council:

I am submitting herewith a thesis written by Stacy B. Howard entitled "Relating Geographic Range, Abundance, and Species Richness in Living and Fossil Echinoids." I have examined the final copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Geological Sciences.

Michael L. McKinney, Major Professor

We have read this thesis and recommend its acceptance:

Accepted for the Council:

Associate Vice Chancellor and
Dean of the Graduate School

RELATING GEOGRAPHIC RANGE, ABUNDANCE, AND SPECIES RICHNESS IN LIVING AND FOSSIL ECHINOIDS

A Thesis
Presented for the
Master of Science
Degree
The University of Tennessee, Knoxville

Stacy B. Howard
May 1997

DEDICATION

This thesis is dedicated to my parents

Mr. Roger D. Butler

and

Mrs. Judy B. Jones,

and to my husband

Skip

ACKNOWLEDGMENTS

I am grateful to many people for making my graduate career at the University of Tennessee a successful and rewarding one. The faculty and my fellow graduate students in the Department of Geological Sciences have shared their knowledge and encouragement. I would like to thank the members of my Thesis Committee, Tom Broadhead and Jim Drake for their assistance and cooperation in this research project. In particular I would like to thank my Committee Chairman, Mike McKinney for his patience, support, and suggestions. This volume would not have been possible without him.

Numerous other individuals were instrumental in the preparation of this thesis. Burt Carter of Georgia Southwestern College has given me much advice, as well as given instruction in the field. He also has generously allowed my use of his personal collection. Gray Dean of the University of Tennessee was gracious enough to let me borrow some of his echinoid samples. Chris Helms also of the University of Tennessee aided in some of the data collection. The Geology office staff of Melody Branch, Cindy Turner, and Denise Stansberry made my life much easier with their help and friendship. I would also like to thank the Department of Geological Sciences and the Graduate School for their financial support.

Lastly, the greatest debt is owed to my husband, Skip. Without his love and understanding I never could have accomplished this dream.

ABSTRACT

Irregular echinoids are a widespread and diverse group of organisms. Members of modern irregular groups possess varies distributions that reflect biogeographic factors and ecological factors. Recently it has been suggested that species characteristics including body size, local abundances, species richness, and geographic range may exhibit genetic influence over these parameters. These characteristics often determine a taxon's extinction selectivity. The purpose of this project is to examine possible taxonomic influence over these species characteristics by examining an Eocene fossil assemblage and the modern irregular echinoid fauna.

The upper Ocala Limestone (Late Eocene) of panhandle Florida contains a well-preserved echinoid fauna. Samples were collected "*in situ* " and the resultant specimens were identified, counted, and measured. The most species rich group, the clypeasteroids, is also the most abundant. Body size versus abundance plots are constructed that show the classic "hollow curve" pattern with the smallest echinoid, *Fibularia vaughni* being the most abundant. Further, analysis of 38 fossil species from late Eocene and early Oligocene collections suggests that there is no correlation between large body size and the rarity of a species.

The modern irregular fauna is examined by using known geographic distributions. Measurements compiled include geographic range, species richness, and latitudinal occurrence (maximum, absolute minimum, range, northern-, and southern-most). Correlation analysis showed these variables are largely independent. Binomial analysis reveals that geographic range is randomly distributed within genera except for three cases: *Echinocardium* (unusually localized) and *Fibularia* and *Spatangus* (unusually widespread). Chi-square analysis shows that species of species-poor taxa are no more likely to be widespread than species of species-rich taxa. Also discerned from statistical

analysis are (1) most irregular echinoid species have relatively small geographic ranges, (2) most genera are species-poor, and (3) irregular echinoids do not follow Rapoport's rule.

Geographic range, species richness, species abundance, and body size are often considered in ecological and evolutionary studies. There is no doubt that these characteristics play an important role in the extinction selectivity of a taxon. There is little evidence in this study that genera tend to stack the deck with species that are extinction resistant.

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CHAPTER I

INTRODUCTION

Paleontology has long been a valuable tool for understanding large scale features in the evolution of life. The modern distribution of organisms has been shown to provide valuable information regarding possible ecological time scale phylogenetic effects on such parameters as range size, body size, and abundance (Harvey 1996). Similar distributions of ancient organisms might demonstrate that these phylogenetic effects also act on an evolutionary time scale with respect to the same parameters.

Research Objectives

Irregular echinoids are a widespread and diverse group of organisms that have a rich evolutionary history. The modern groups possess varied distributions that have likely been shaped by millions of years of evolutionary process such as extinction resistance and speciation rates. Analysis of the modern patterns of geographic distribution may delineate taxonomic affinity. Statistical clustering of distribution patterns among certain groups would be a strong indication of genetic influence in biogeography.

Results of a modern analysis of geographic distribution will be compared to examples from the fossil record to see if similar patterns are present in the ancestral groups. The modern-ancient comparison will be difficult to achieve primarily because there is not a single time frame of the past that provides the equivalent of the distribution data available for the present. Application of ecological ideas such as body size patterns, local abundance,

and geographic range will aid in the comparison of distribution of irregular echinoids from the present to those of the past.

This comparison between modern and fossil echinoids will provide some idea as to the presence or lack of genetic control over distribution patterns. This will, in turn, help identify which groups of echinoids have been in the past, and may be in the future, most susceptible to extinction events. This knowledge could prove useful in the conservation of species and maintenance of diversity.

General Ecology

Geographic Range - For several decades scientists have explored the relationships between the distribution and abundance of organisms. As early as 1922 Willis recognized that localized species were often rare within their geographic ranges. He further noted that most species in a taxon have small ranges and only very few species are very widespread. This long-standing observation is discussed by Jablonski (1986) and Gaston (1994). Within most taxonomic groups analyzed by earlier workers, species that have large geographic ranges tend to have greater local abundances than more geographically restricted species (Lawton 1993; Brown 1995).

The strong positive correlation between geographic range size and local species abundance has several possible explanations. According to Brown's hypothesis (1984), species that have broad niches are capable of exploiting a wide range of resources, and so become both geographically widespread and locally abundant. Similarly, species that have small ranges are limited by their narrow tolerances for the existing abiotic and biotic conditions. Niche breadths are extremely difficult to measure which makes Brown's hypothesis nearly impossible to test directly. There is evidence, however, that demonstrates

the general relationship among abundance, niche diversity and range. When closely related organisms are examined, species with the highest local population densities tend to occupy a greater proportion of sites within a region and have larger geographic ranges. This argument is supported by Hanski (1982), who found strong positive correlation between the average density within a sample site and the number of local sites where his target species (terrestrial arthropods) were found. In addition, Bock and Ricklefs (1983) observed a similar pattern in North American birds. On a much larger geographic scale, they found a strong positive correlation between average local abundance and geographic range.

New evidence suggests that geographic range and abundance are inherent species characteristics (Lawton 1993; McKinney 1995). This evidence could support Brown's idea of evolutionary control of niche breadths. Evolved characteristics would be passed to new species and, thus, be preserved in the lineage. Lawton cites evidence for phylogenetic effects on distribution and geographic ranges for both plants and animals. Studies discussed by Lawton imply that, at least in some taxa, local abundance and range are phylogenetically controlled.

Body Size - Another interesting ecological phenomenon is the apparent relationship between body size and population density in animals (Cotgreave 1993). For instance, studies of rocky shore invertebrate community studies (with little taxonomic restriction) have shown negative relationships between body size and local abundance. May (1988) and Dial and Marzluff (1988) have revealed this "hollow curve" pattern in modern organisms in which the smaller sized individuals are more common. The fossil record has also revealed hollow curve patterns of body size distributions in such organisms as foraminifera (Murray 1991) and echinoids (McKinney 1986).

Positive correlations exist, however, for some animal groups that are closely related. Cotgreave (1993) cites an example of bird tribes (including owls, ducks, woodpeckers, and crows) with the species containing the largest individuals being the most abundant. The reason for this correlation is unclear. It may be related to the overlap in niche space between the species. Closely related species have more similar resource needs which may create competition for food or living space. It might, therefore, be advantageous to be larger than members of a competing species. This of course would have no effect if resources were so plentiful that species did not need to compete for them.

Latitudinal Gradient - Wallace (1878) was the first to notice a latitudinal gradient in species diversity. There are far more species at the equatorial regions than there are in the higher latitudes. After several decades of study this pattern is still relatively poorly understood. A more newly discovered pattern of latitudinal distribution has become known as Rapoport's Rule (Stevens 1989). This gradient, first reported by Rapoport (1982), demonstrates that species with ranges centered at higher latitudes tend to have larger ranges than those at the equator. Two hypotheses help explain this observation. The first hypothesis is climatic variability pointed out by Dobzhansky (1950), Stevens (1989) and others. Animals near the poles must endure a wider range of climatic conditions, both seasonally and diurnally, than their equatorial counterparts. The polar species could be considered generalists with large ranges and tolerance of widely varying environmental conditions. Tropical species, on the other hand, are specialists that are adapted to narrow sets of environmental conditions.

The second hypothesis explaining latitudinal gradients in range size is the fact that range size and species diversity show opposite latitudinal trends. Range size decreases from the poles toward the equator while species diversity increases. Dobzhansky (1950)

and MacArthur (1972) suggest that at lower latitudes species ranges may be limited by interactions with an increasing number of other species.

Recent studies have shown that Rapoport's rule does not hold true for some marine animals. Roy et al. (1994) examined the latitudinal ranges of marine molluscan species which failed to show trends that followed Rapoport's rule. Instead, they found that diversity gradients and range magnitudes of the molluscs vary independently according to influence of oceanic barriers. Rohde and Heap (1996) have also found evidence in marine teleost fish that contradicts Rapoport's rule.

Echinoids

The Class Echinoidea of the Phylum Echinodermata is a diverse and abundant group of organisms. Echinoids arose in the Ordovician as a result of the development of a new bottom-feeding technique for the echinoderms. Species diversity rose through the first part of the Paleozoic (Smith 1984). Species numbers diminished through the Pennsylvanian and Permian. The drastic Permian extinction wiped out all echinoid taxa except the genus *Miocidaris* (Smith 1984). By the end of the Triassic, the miocidarids had experienced very successful radiation establishing all the major Post-Paleozoic lineages. Today the Echinoidea is represented by over 900 extant species that inhabit a spectrum of marine environments from polar to tropical and from the littoral zone to more than 5,000 meters in depth.

Morphology - Many general references are excellent sources for basic echinoid morphology (Smith 1984; Clarkson 1993). The following morphology review draws upon these sources. For the sake of convenience, echinoids will hereafter be divided into two

informal groups, the "regulars" and the "irregulars" as discussed by Smith (1984) and Clarkson (1993).

The echinoid skeleton, or test, is structurally complex, consisting of tens to hundreds of high magnesium calcite plates (Mg = 5 to 15%) (Weber 1969). Each plate has an assortment of spines and/or pincer-like pedicillariae which articulate on tubercules. This thermodynamically metastable calcite makes up the skeletal network known as stereom. The resulting structure is a feature that enhances preservation in the entire echinoid group.

In the Post-Paleozoic echinoids the corona forms the greater part of the test. It is composed of twenty columns of plates that are arranged in pairs. The ambulacra are biserial columns of plates with ambulacral pore perforations. The interambulacra are biserial columns of plates that lie between ambulacra. Coronal plates are commonly interlocked and sutured together to provide test rigidity. The extent to which the plates are interlocked is a taxonomic trait. The irregular echinoids often have very intricate complex networks which render their tests especially durable and rigid. Regular echinoids, on the other hand, have less rigidly bound skeletal plates.

Regular echinoid tests have an apical system that is located on the dorsal surface. This system consists of five genital plates arranged in a ring. Each genital plate has a genital pore that serves for the release of gametes. There are also five occular plates (which are actually the terminal ambulacral plates). Each occular plate contains a pore that allows for the extrusion of the radial water vessel. This system encloses the periproct which is covered by a flexible membrane with embedded plates that contains the anus.

The peristome is a membrane-covered opening on the ventral surface that contains the mouth. Sometimes present are buccal slits which are notches on the terminal interambulacral plates. A lantern, or complex dental apparatus, lies internal to the mouth

and within the test. Internal processes on the inside edge of the corona provide attachments for muscles that move the five teeth of the lantern.

Irregular echinoid tests have a bilateral symmetry superimposed on the original radial symmetry. The periproct has migrated out of the apical system and posteriorly or, in some cases, to the oral surface. Some irregular echinoids have completely lost their lantern structures. Figure 1 illustrates generalized echinoid test morphologies.

The echinoid test interior is mostly fluid-filled and contains the soft tissues of the organism. (The soft tissues are not preserved and will only be generally described here for completeness.) Sac-like gonads are positioned interradially and are suspended by connective tissue from the corona. The digestive system is made of the pharynx (which lies within the lantern), a long esophagus that leads to the double U-shaped intestine, and the rectum leading to the anal opening in the periproct.

Echinoids have a water-vascular system that consists of a central ring vessel situated just above the lantern. The stone canal leads from the central ring to the madreporite which is a modified genital plate. The madreporite is the only opening to the water vascular system. Radial water vessels branch from the central ring vessel and lie near the middle of each ambulacrum. Branches of the radial water vessels go to tube feet (connected to internal ampullae and to the rest of the water vascular system by ambulacral pores) and ampullae (fluid-filled reservoirs that allow tube feet to function independently of one another).

The nervous system lies close to the water vascular system. The nerve ring surrounds the esophagus and branches into five radial nerves. Radial nerves, in turn, branch and run through each associated ambulacral pore into the exterior of the test. The nerve divides with part going to the tips of tube feet and part going beneath the epidermis of the plates. Here it forms a nerve plexus which innervates the spines and pedicellariae (Smith 1984).

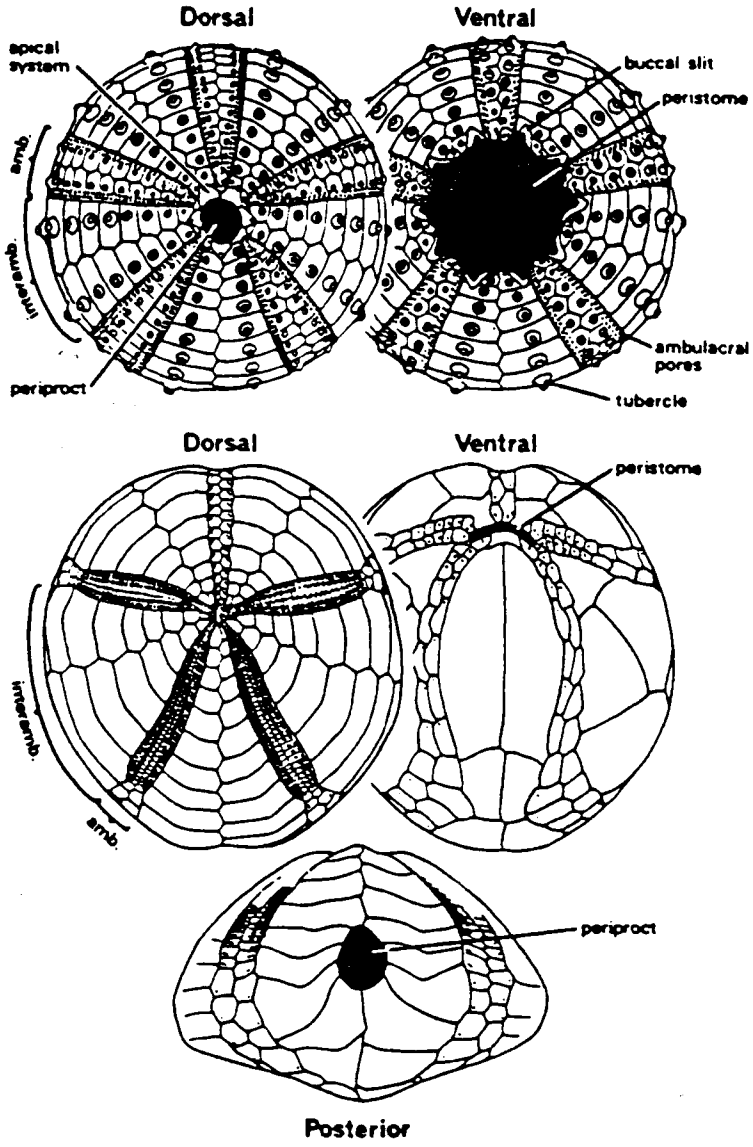

Figure 1. Generalized illustrations of regular (upper) and irregular (lower) test morphologies. Illustration from Smith, 1984.

Ecology - There are over 900 extant species of echinoids (Smith, 1984). All these species are both benthic and marine. As a group they live in every possible depth range from the coast to depths of over 7,000 meters. The most concentrated areas of occupancy are the littoral tropical and subtropical zones (Lehmann and Hillmer, 1983).

Specific habitats of echinoids are taxon dependent. Regular echinoids often live in rocky shore areas or in other hard substrate areas. Here they graze on algae and other plants, bryozoans, corals, or sponges. Deep sea species are detritus feeders.

In contrast, irregular echinoids most often live infaunally. Some are very shallow burrowers, such as the sand dollars. Others, like some heart urchins, burrow more deeply. Irregular echinoids primarily obtain their nutrition by swallowing bulk sediment and removing usable organic material from it. There is at least one case of suspension feeding in the sand dollar genus *Dendraster.*

It has long been thought that the life strategy (epi- or infaunal) directly affects preservation potential of echinoids (Kier 1977). In general, regular echinoids are less well-preserved than irregulars. There are possible structural reasons for this preservation bias. Irregular echinoids have more intricate interlocking stereom which enhances skeletal rigidity and thus enhances preservation potential. While this no doubt plays an important part in preservation, Kier (1977) attributed the poor fossil record of regular echinoids to their epifaunal life mode. Not only are regulars exposed to currents, storms, and scavengers but they tend to live in environments of active erosion. Most irregular echinoids live infaunally and often inhabit environments of active deposition. There is evidence for this preservational bias in fossil assemblages from the southeast United States (Cooke 1959). Cooke describes 144 species or subspecies of echinoids from the Atlantic and Gulf Coastal Plains and the adjacent waters. These species represent 60 genera and 4

subgenera; 44 genera are irregulars (73%). Irregular echinoids also dominate with numerical abundance.

Classification - Echinoid classification is still a topic for heated discussion among echinoid workers. In 1925 (Lambert and Thiery, 1909-1925) there was a classification system whereby the class Echinoidea was divided into Regularia and Irregularia (Clarkson, 1993). This system was not a true phyletic classification but it served as a convenient way to distinguish groups. Later schemes by Durham and Melville (1957) and Durham (1966) were based on morphological similarity of several structural characters. Jensen (1981) and Smith (1981) used schemes based on cladistics. Smith's 1984 revision is partly cladistic and takes the much-debated view that irregular echinoids are monophyletic. This classification scheme will be used in this work and is summarized here:

Subclass: Perischoechinoidea
Subclass: Cidaroidea
Subclass: Euechinoidea
- **Infraclass**: Echinothuroidea
- **Infraclass**: Acroechinoidea
  - **Cohort**: Diadematacea
  - **Cohort**: Echinacea
  - **Cohort**: Irregularia
    - **Superorder**: Eognathostomata
      - **Order**: Pygasteroidea
      - **Order**: Holectypoidea
    - **Superorder**: Microstomata
      - **Order**: Cassiduloidea
      - **Order**: Clypeasteroidea
      - **Order**: Disasteroidea
      - **Order**: Holasteroidea
      - **Order**: Spatangoidea

Evolutionary History - The echinoids arose in the Ordovician as an epifaunal deposit-feeding group of animals. By the Silurian the lantern structure had developed from a "scoop" into an effective biting apparatus (Smith, 1984). This allowed for the exploitation

of new food resources. Diversity slowly grew until the Lower Carboniferous. By this time there were four main groups that were each adapted for specific niches.

The Upper Carboniferous brought a reduction in both species numbers within taxa and complete lineages. By Permian times there were only six species left (Smith 1984). All but the genus *Miocidaris* were extinct as a result of the drastic environmental changes at the end of the Permian. This single genus possibly saved the entire group from extinction. Descendents of *Miocidaris* slowly began to diversify in the Triassic. As environmental conditions became more favorable in the Upper Triassic, diversification rates increased (Smith 1984). By the end of the Triassic all the major post-Paleozoic regular echinoid lineages had been established.

The Early Jurassic brought the beginning of one of the most cited adaptive radiation examples in paleontology-the evolution of the irregular echinoids. Kier (1982) discusses the possible reasons for such an explosion in evolution. Because of changes in skeletal structure, the irregulars were able to exploit a habitat that had previously been unavailable to them. This habitat was subsurface in the loose sediment where much organic material existed. An infaunal lifestyle was made possible by a more streamlined profile. The elongate and flattened test made it easier to burrow into the sediment. The newly evolved periproct position at the posterior of the animal allowed for waste discharge in the trail rather than in the path. Broader tube feet allowed for greater surface area for oxygen gathering (very much needed in the stifling subsurface environment). These enlarged dorsal tube feet resulted in the formation of the distinct petals characteristic in most irregulars. Sediment-collecting perioral tube feet became larger and more abundant. Finally, the many shortened spines allowed for the forward thrust into the sediment and the excavation of the sediment as the animal burrowed. So the irregulars have several morphological features that enable them to exploit habitat not available to the regular group.

The first appearance of irregular echinoids occurred suddenly in the Early Jurassic (Kier 1982). *Plesiechinus hawkinsi* , a pygasteroid, is the earliest recognized species of echinoid to have an "asymmetrical test with small tuberculation, short and numerous spines, differential pores with the adapical pores larger than the adoral ones, posteriorly eccentric periproct, and presumably keeled teeth" (Kier 1982). These characteristics are diagnostic of most subsequent irregular echinoids, with the exception of teeth. Most irregular echinoids have no teeth at all.

The last great echinoid evolutionary event was the Tertiary appearance of *Togocyamus*, the first sand dollar. This clypeasteroid arose in the Paleocene and had obtained world wide distribution by the Middle Eocene. The rapid evolution of the clypeasteroids is an often-cited classic example of adaptive radiation.

Lehmann and Hillmer (1983) described the five characteristics that summarize the evolution of echinoids since their beginning in the Ordovician. These five characteristics are (1) development of a rigid test, (2) development of preferred direction of locomotion and the corresponding orientation, (3) improvement of the water-vascular system, (4) modification of the tube feet for special functions and (5) specialized feeding habits. Because of these developments, echinoids have a rich phylogenetic history that has led to many hundreds of extant species that exploit a variety of marine habitats and food sources.

CHAPTER 2

FOSSIL ECHINOIDS

Introduction

In general, echinoids are abundant in the fossil record, especially since the Mesozoic. This is when the group evolved a rigid, mineralized skeleton or test. The echinoid test is composed of complex, pentamerally arranged, high magnesium calcite. This thermodynamically metastable calcite makes up the skeletal network known as stereom (Smith 1984). The resulting rigid structure is a feature that enhances preservation in both regular and irregular echinoids.

Fossil echinoids are often best represented by the group Irregularia (the irregulars) (Smith 1984). Smith, believing the irregulars to be monophyletic, used a cladistic scheme to classify this group (see Chapter 1 this compilation). His classification is widely recognized in the field of paleontology, and, for the most part, will be utilized in this work.

The irregular echinoids contribute much to the fossil record because of their preservation potential. This potential exists because of two primary factors distinguishing the preservation of the irregulars from the regulars. First, the internal mesodermal skeletons of irregulars remain intact far easier than those of their regular cousins because of differences in skeletal structure between the two groups. In irregulars the skeletons have a connective tissue covering binding the high-Mg calcite plates together. After death this tissue decays. The test remains intact because the corona, or main part of the test, is cemented together by the interdigitation of the stereom across the sutures (Smith 1984). In

contrast, the regulars generally lack significant amounts of this interdigitating stereom and so collapses upon death-induced decay of the connective tissue.

The second factor contributing to the superior preservation potential of the irregulars is their lifestyles. Irregular echinoids live infaunally and so, in a sense, are pre-buried. Kier (1977) noted, however, that many irregular individuals died at or very near the sediment surface instead of in life position within the sediment. These individuals apparently came to the surface when stressed. The advantage of irregular over regular is not infaunal over epifaunal, but rather sediment preference. Regular echinoids enjoy life as grazers on firm substrates. These substrates are usually areas of active erosion and disturbance. The deposit-feeding irregulars, on the other hand, inhabit unconsolidated sediments in areas of active sedimentation. Thus they have greater preservation potential.

Fossil Distribution

There are numerous Cenozoic deposits in the Southeastern United States that boast large echinoid faunas. These faunas were examined by Cooke (1959) and, more recently, Carter (1987) and McKinney *et al.* (1992). McKinney and Oyen (1989) documented 183 Cenozoic species of echinoids in the Gulf Coastal Plain area. Forty-five of these were regulars (24.6%). The remaining 138 irregular species (75.4%) represent six orders: holectypoids, holasteroids, oligopygoids, cassiduloids, clypeasteroids, and spatangoids.

Species diversity within each group can be broken down as percentages of the entire irregular population. Holectypoids are represented by 3 species (2.2%). Holasteroids are represented by 2 species (1.4%). Oligopygoids are represented by 5 species (3.6%). Cassiduloids are represented by 19 species (13.8%). Clypeasteroids are represented by 56 species (40.6%). Spatangoids are represented by 53 species (38.4%). (See Table 1).

Table 1. Species diversity of the irregular echinoid fauna of the Gulf Coastal Plain. (Data from McKinney and Oyen, 1989.)

Group	**# Species**	**% of Irregular Species**
Holectypoids	3	2.2
Holasteroids	2	1.4
Oligopygoids	5	3.6
Cassiduloids	19	13.8
Clypeasteroids	56	40.6
Spatangoids	53	38.4
Totals	138	100

A look at global diversity of echinoids (McKinney and Oyen 1989) shows 4614 total echinoid species with 3259 (70.6%0 of these being irregulars). Individual groups of global irregulars break down similarly to the Gulf Coastal Plain examples. The holectypoids are represented by 88 species (2.7%). The holasteroids are represented by 56 species (1.7%). The cassiduloids are represented by 741 species (22.7%). The clypeasteroids are represented by 1049 species (32.2%). The spatangoids are represented by 1314 species (40.3%). The pourtelasesoids are represented by 8 species (0.2%). The neolampadoids are represented by 3 species (0.09%). (Table 2).

The stratigraphic position of echinoid faunas has also been well studied (e.g. Cooke 1959, Carter and Hammack 1989, McKinney and Zachos 1986, and Toulmin 1977). Most striking is the extremely high levels of echinoid diversity during the Eocene. This peak of echinoids has been strongly correlated with mean annual temperature (McKinney and Oyen 1989). Diversity drastically dropped off following the Eocene-Oligocene extinction event and never fully recovered to its Eocene heyday. Overall stratigraphic percentages of the Cenozoic irregular fauna are as follows: Paleocene 3.6%, Eocene 58.0%, Oligocene 7.2%, Miocene 7.2%, Pliocene 10.9%, and Pleistocene-Recent 13.0% (Table 3).

Because of the great diversity in the Eocene, this time interval has been most thoroughly explored by paleontologists (Croft and Shaak 1985). There has also been great interest in the effect of the extinction at the Eocene-Oligocene boundary on the diversity of echinoid groups, especially the irregulars. Other relevant studies using echinoids from the Gulf Coastal Plain include echinoid biostratigraphy (Zachos and Schaak 1978), substrate preferences (Carter *et al.* 1989), and echinoid biofacies (Carter 1990).

Table 2. Species diversity of the entire global irregular echinoid fauna. (Data from McKinney and Oyen, 1989.)

Group	# Species	% of Irregular Species
Holectypoids	88	2.7
Holasteroids	56	1.7
Cassiduloids	741	22.7
Clypeasteroids	1049	32.2
Spatangoids	1314	40.3
Pourtelasesoids	8	0.2
Neolampadoids	3	0.1
Totals	3259	100

Table 3. Stratigraphic diversity of the Cenozoic irregular fauna. (data from McKinney and Oyen, 1989.)

	% in GCP	% Global
Paleocene	3.6	2.8
Eocene	58.0	32.5
Oligocene	7.2	10.4
Miocene	7.2	29.8
Pliocene	10.9	6.4
Pleistocene-Recent	13.0	18.2
Totals	99.9	100.1

Geological Setting: The Ocala Limestone

Stratigraphy - Stratigraphic descriptions of the Eocene limestones of Florida are not uniform among workers of these units. Dall and Harris (1892) used the term "Ocala Limestone" to describe all Jackson Stage limestones of Florida. Cooke (1915) recognized the Ocala Limestone as Upper Eocene because it is overlain by the Oligocene Marianna Limestone. Applin and Applin (1944) subdivided the Ocala Limestone into Lower and Upper Members based on both lithologic and paleontologic characteristics. The classifications of Applin and Applin were modified by Vernon (1951). The Upper Member became the Ocala Limestone (restricted) and the Lower Member became the Moodys Branch Formation. The Moodys Branch was further divided into an upper Williston Member and a lower Inglis Member. Puri's (1957) Ocala Limestone consisted of all the Jackson stage calcareous sediments in Florida. He proposed a three member Ocala consisting of Vernon's Inglis and Williston formations (but dropping the Moodys Branch designation) and a "new" Crystal River Formation (the equivalent of the restricted Ocala Limestone of Vernon). These stratigraphic divisions of the Ocala Limestone are depicted in Figure 2.

Most lithostratigraphic terminology of the Upper Eocene rocks of Florida since Vernon and Puri (1951) has been based on fossil characteristics rather than lithological ones. This is a technical violation of the *North American Stratigraphic Code* (NACSN 1983). The history of the Eocene stratigraphic nomenclature precedes the rules of naming stratigraphic units as defined by the first *Code of Stratigraphic Nomenclature* (ACSN 1961), the *North American Stratigraphic Code* (NACSN 1983), and others. Most workers today use either Applin and Applin's (1944) nomenclature or that of Puri (1957) (see Carter 1987; 1990; Carter *et al. 1989* ; and Carter and McKinney 1992 for examples).

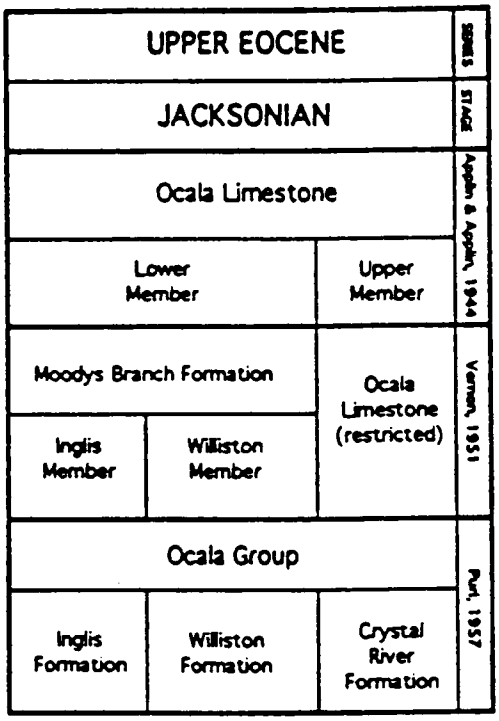

Figure 2. Stratigraphic nomenclature used for the "Ocala Limestone" as illustrated by Oyen (1996).

Lithology - Lithologic characteristics vary throughout Florida's Upper Eocene strata. The Lower Ocala is a light tan to cream, chalky, soft to crystalline, porous, fossiliferous packstone to grainstone (Oyen 1995). Average fossil content has been reported as 33.7% by volume reaching 60% in some facies (Randazzo and Saroop 1976). The dominant biota is foraminifera (miliolids) with significant amounts of algae, mollusks, echinoids, bryozoans, and ostrocodes. Chen (1965) identified finely crystalline dolomite and quartz (< 10%) as accessory minerals.

The Upper Ocala lithology has more variable facies. Generally it is cream to white, chalky, soft and granular to dense and crystalline, porous, fossiliferous wackestone to grainstone (Oyen 1995). Mud-rich wackestones are more abundant in the Upper Eocene than in the Lower Eocene as noted by Fenk (1979). The dominant biota is, again, foraminifera with appreciable amounts of mollusks, echinoids, algae, corals, and crustaceans. Faunal diversity overall is higher in the Upper Ocala than in the Lower Ocala. Fossil material is so concentrated in some locales than Puri (1957) was prompted to call these rocks coquinas. Non-carbonate grain content is very low (less than 5% insoluble residue, Oyen unpublished data).

Paleoenvironment - The Late Eocene sediments of Florida represent warm, shallow, carbonate shelf environments. Many facies can be identified in the Ocala Limestone that reflect the transgression (high energy) and regressive (low energy) conditions on the Florida platform. The mud-free Lower Ocala lithologies are indicative of high energy shallow subtidal environments that existed during the early Jacksonian (Randazzo and Saroop 1976). The muddier lithologies of the Upper Ocala generally indicate lower energy, deeper subtidal conditions of the late Jacksonian (Fenk 1979). Environmental interpretations by Randazzo and Saroop (1976) and Fenk (1979) were in

agreement with observations by Cheetham (1963). Cheetham used fossil cheilostome bryozoans to reconstruct the environmental conditions of the Florida Platform during the Upper Eocene.

Methods

Sample Collection - Approximately 77 kilograms of bulk rock samples were collected from a limestone quarry approximately 3 miles south of Mayo, Florida (Figure 3). Samples were removed from the quarry walls with a hammer and chisel. Samples were labeled with respect to *Oligopygus* zone (Figure 4) (see Zachos and Schaak 1978; McKinney and Zachos 1986), locality information, and date, and packaged for transport to the laboratory. Approximately 55 kilograms of the bulk rock were from the *Oligopygus wetherbyi* zone and approximately 22 kilograms were from the *Oligopygus haldemani* zone. Samples were also collected from the quarry floor and notation was made regarding collection date and locality. These float samples were also labeled and packaged for transport.

Sample Preparation - Echinoid samples and bulk rock samples were returned to the laboratory for preparation. The echinoid samples collected as float material were cleaned of calcium carbonate matrix first by mechanical methods such as hammers, picks, scrapers, files, and tweezers. The samples were then treated with a weak (5%) solution of acetic acid to remove attached debris. Treatment with acid lasted from 30 minutes to over 24 hours depending on the degree of sediment adherence. Additional cleaning of the echinoids was done with picks, brushes, and tweezers.

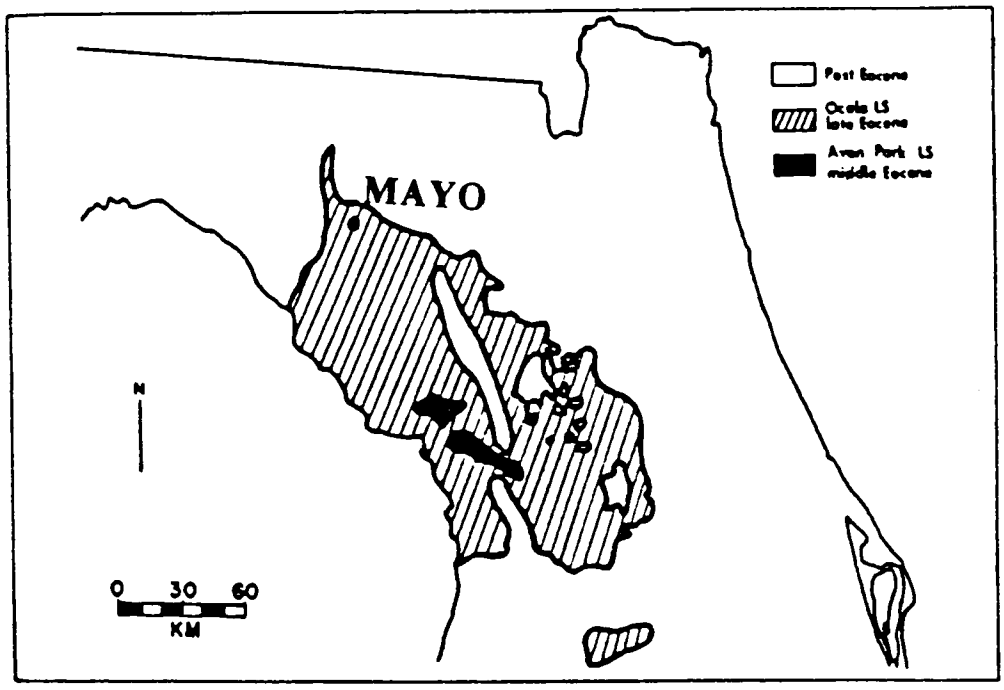

Figure 3. Locality map of fossil collection site showing surface exposures of the Ocala Limestone in northwest peninsular Florida (modified from Puri and Vernon, 1964). Mayo is depicted by the enclosed circle.

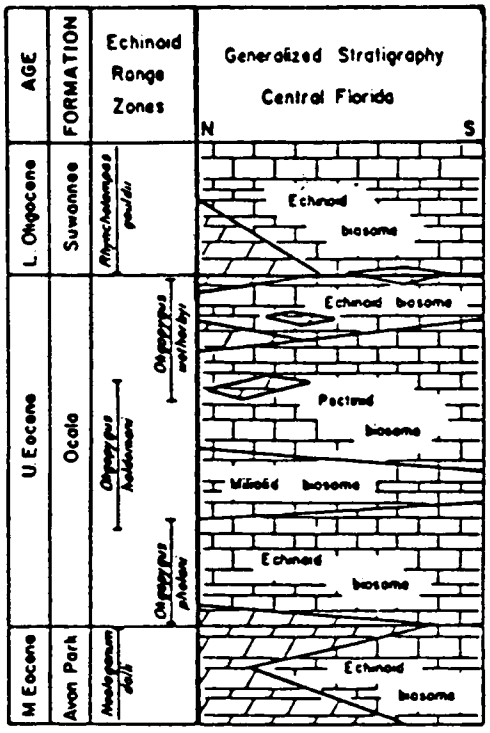

Figure 4. Echinoid biozones of the Ocala Limestone as interpreted by Zachos and Shaak (1978).

Bulk rock samples were reduced by hammer into 6-10 kg. blocks. All smaller pieces were retained for later sieving. As the bulk samples were being mechanically reduced they were also examined for evidence of echinoid test remains on the freshly exposed surfaces. This helped insure that no obvious echinoid tests would be destroyed by hammering. The calcium carbonate blocks were broken down until all pieces were approximately 5 cm. or smaller. Echinoids were constantly removed from the carbonate material as they were found.

The loosened sediment and the 5 cm. pieces were wet sieved in a set of sieves of decreasing size (2 mm-.25 mm). Carbonate pieces larger than 2 mm were soaked in 5% acetic acid from 1 to 24 hours to help break up the matrix material and release any fossils. This soaked material was wet sieved again, and, echinoids tests were removed when found. This procedure was followed until all the material had been reduced and sieved. All echinoids removed from the bulk rock samples were air dried and stored with pertinent labels. For the sake of stratigraphic integrity, all samples were categorized as either "float", *Oligopygus haldemani* zone, or *Oligopygus wetherbyi* zone. The specimens were identified to the level of species with the aid of monographs by Cooke (1959) and Toulmin (1977).

Data Collection - Whole specimens of each species were counted and the total number entered into a spreadsheet. Fragments were noted separately when they could be identified confidently at the species level. Specimens from each category (above) were grouped together for the sake of analysis.

Measurements of test morphology for each specimen were taken using calipers with accuracy to 0.01 mm. Test length, width, height, and volume were the measured variables. Length, as used here, is simply the maximum distance between the anterior and posterior margins. Likewise, width is the maximum distance between the lateral margins. Test height is harder to measure because of the concavity of some of the species (especially

the oligopygoids). As used in this work, height is defined as the distance between the apical system and the ventral plane containing the lowest points of the anterior and posterior margins (Figure 5). The total volume for each test was estimated by multiplying length **x** width **x** height. Many of the "flat" species (from the genera *Durhamella*, *Weisbordella*, and *Wythella*) were missing the central portion of the test from both the aboral and adoral planes, making it virtually impossible to accurately measure test height. For all specimens of these species height measurements were taken from the few samples of each species that were preserved in their entirety. All values were recorded in millimeters and are contained in Appendix A.

Statistical Analysis - Abundance counts were performed and documented for each species within a specific biostratigraphic zone and for the float samples. The abundance counts reflect complete specimens and identifiable fragments (Table 4). This was accomplished by assigning a morphological feature to be representative of a complete individual. For example, the presence of a single madreporite equals the presence of a single individual. Also the presence of "right-sided" petal structures (or "left-sided" petal structures) suggests a corresponding number of individuals (since each individual contains only one right or left side). An average volume was determined for each species within each category (Table 4). A bivariate graph was constructed for the *O. wetherbyi* Zone by plotting average volume (mm^3) versus species abundance (Figure 6).

Results

Oligopygus haldemani Zone - The approximately 22 kilograms of bulk rock sample from this echinoid biozone yielded only 23 identifiable irregular echinoid

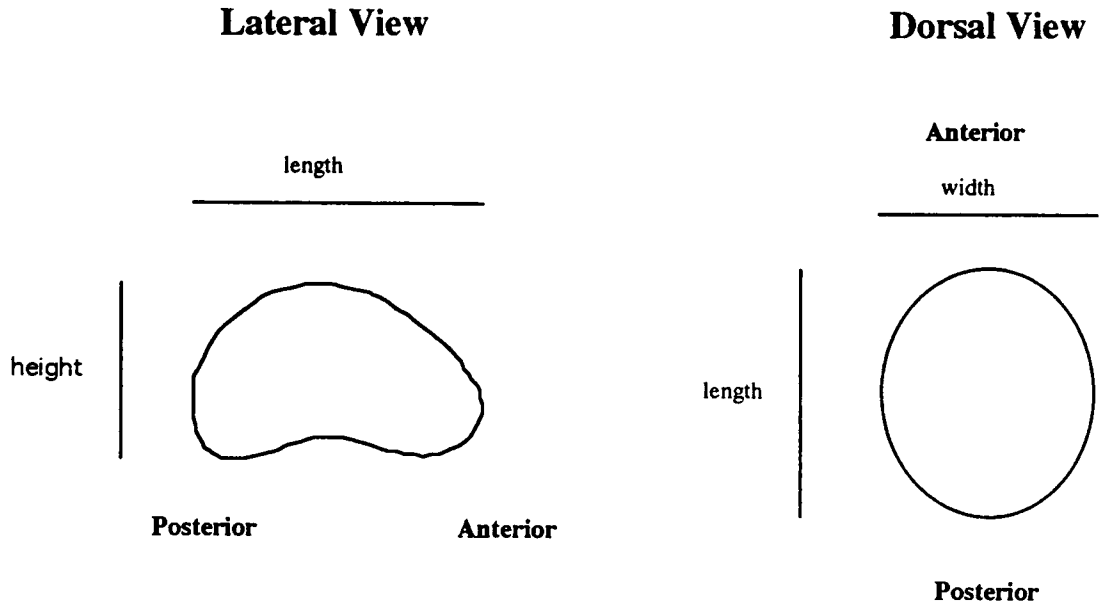

Figure 5. Parameters for test measurements.

Table 4. Fossil abundances and average species volumes. Volumes are reported as mm^3. Asterices indicate lack of data.

Oligopygus wetherbyi Zone		
Species	**Average volume (mm^3)**	**Abundance**
Agassizia floridana	520.89	1
Durhamella ocalana	385.31	6
Weisbordella cubae	110.98	19
Wythella eldridgei	264.01	6
Oligopygus haldemani	497.22	4
Oligopygus wetherbyi	15767.80	10
Fibularia vaughni	46.07	227
Total		**273**

Oligopygus haldemani Zone		
Durhamella floridana	*	2
Fibularia vaughni	36.49	6
Oligopygus haldemani	726.33	15
Total		**23**

Float Material		
Fibularia vaughni	135.39	4
Agassizia floridana	897.96	2
Durhamella floridana	2307.42	3
Rhyncholampas conrad	16744.01	2
Weisbordella cubae	2189.44	30
Wythella eldridgei	257.14	5
Oligopygus haldemani	2370.66	24
Oligopygus wetherbyi	29816.28	31
Schizaster armiger	77446.02	1
Schizaster ocalanus	7448.45	1
Total		**103**

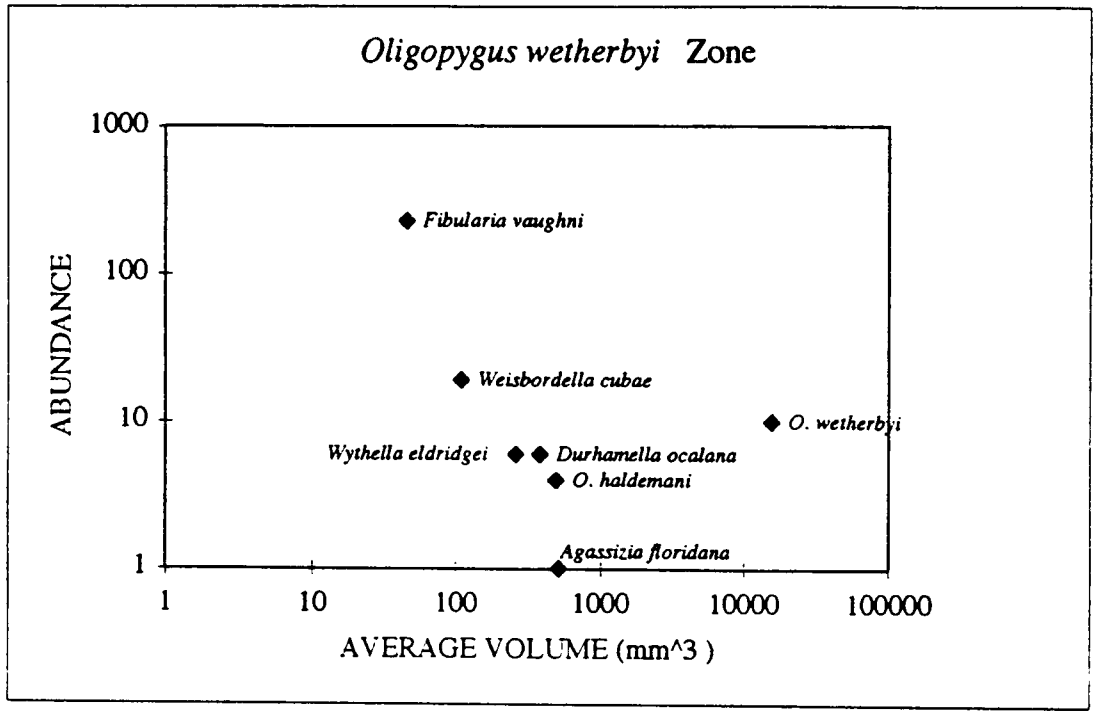

Figure 6. Bivariate plot of average test volume (mm^3) versus species abundance for the *Oligopygus wetherbyi* zone.

specimens. Three species were present: *Durhamella floridana*, *Fibularia vaughni*, and *Oligopygus haldemani*. These three genera represent different families: Neolaganidae (*Durhamella*) and Fibularidae (*Fibularia*), which are both clypeasteroids, and Oligopygidae (*Oligopygus*) which is an oligopygoid. The *O. haldemani* zone fauna corresponds to the Middle Ocala Association of McKinney and Zachos (1986) which represents a stable, deep subtidal (>60 meters) (McKinney and Zachos 1986) environment. Further, these species have been shown to occur primarily in sandy substrates (Carter *et al.* 1989).

The echinoid fauna present in the *O. haldemani* zone is very species poor compared to the *O.wetherbyi* zone fauna in this study. The disparity in bulk rock sample size of the two echinoid biozones may play some roll in the species richness difference. There was simply more *O.wetherbyi* zone collected than *O. haldemani* zone and therefore a greater chance for more species to be found within the *O.wetherbyi* zone sample. However, the difference in species richness between echinoid biozones is a real phenomenon that has been previously reported (McKinney and Zachos 1986).

Even at such low species richness it is expected that all species not be from the same higher taxa. Fox (1989) showed that in animal communities each different genus tends to be represented by one species before a second species of any genus is added. This type of community structure allows for filling of all niche spaces. As new or more resources become available more species can be added to genera already represented. Interspecific competition ultimately determines the community structure (Brown 1995). Consistent with this idea, the *O. haldemani* zone fauna consists of three different species belonging to three different genera and three different families.

The most abundant species in this biozone is *Oligopygus haldemani* with 15 specimens. Six specimens of *Fibularia vaughni* were identified as were 2 specimens of *Durhamella floridana*. In the *O. haldemani* zone the smallest echinoid is not the most

abundant (Figure 6) as would be expected (May 1988). The sample size for this biozone is only 23 specimens and, therefore, this may be statistically invalid.

Oligopygus wetherbyi Zone - The *O.wetherbyi* zone sample consisted of approximately 55 kilograms of bulk rock sample that yielded 273 total identifiable specimens. Represented in this sample were 7 species: *Agassizia floridana*, *Durhamella ocalana*, *Fibularia vaughni*, *Oligopygus haldemani*, *O.wetherbyi*, *Weisbordella cubae*, and *Wythella eldridgei*. These 7 species are representative of 5 families: Schizasteridae (*Agassizia*), Oligopygidae (*Oligopygus*), and Laganidae (*Durhamella*), Neolaganidae (*Weisbordella* and *Wythella*), and Fibularidae (*Fibularia*). The O.wetherbyi zone fauna is best described by the Late Ocala Deep Association of McKinney and Zachos (1986). This Association is also suggestive of a stable, subtidal deep (> 60 meters) environment. However, unlike the Middle Ocala Association of the *O. haldemani* zone, the Late Ocala Deep Association fauna is indicative of a more mud-rich environment. *Wythella eldridgei* is associated with a more shallow mud-rich environment and, therefore, its presence may suggest that the Mayo collection site was a transition area where deep and shallow fauna may have been mixed (Carter and McKinney 1992).

Species-richness in the *O.wetherbyi* zone (7 species) is higher than in the *O.haldemani* zone (3 species) in this study. Again this could partially be due to the size difference in sample removed with respect to each biozone. The most abundant species by far in the *O.wetherbyi* zone is *Fibularia vaughni*, which is also at least an order of magnitude smaller than any other species in this biozone. The sample size in this case (273 total specimens) is sufficiently large to satisfactorily correlate small size with abundance.

As with the *O. haldemani* zone, faunal composition is limited to one species per genus with the exception of *Oligopygus* as inferred from the co-occurrence of

O.haldemani and *O. wetherbyi* . The bulk sample for this biozone was extracted from the lowest part of the *O.wetherbyi* zone approximately 0.5 meters above the biozone boundary. According to Zachos and Shaak (1978) these two species have a small transition zone where both species may occur. The overall increased diversity of the *O.wetherbyi* zone may indicate greater resources, which could lead to more niche space to be used by more echinoid species. That con-generic species are able to live together within the same environment also suggests abundant resources (Fox 1989). The paleoenvironment was apparently well-suited for clypeasteroids because 4 of 7 species belong to this group and with the exception of *O.wetherbyi,* the clypeasteroids are the most abundant of all the species.

Float Material - Ten species and 103 total specimens were identified from the float material collected from the quarry floor. There is possibility of mixing between biozones in this material but useful observations can be made because the samples from the ground are at least partly representative of the quarry wall fauna. Indeed all but three species of the float material was found in one or the other biozones (or both). The three species not collected from the biozone samples are *Rhyncholampas conradi*, *Schizaster armiger*, and *Schizaster ocalanus*. These species are indicative of transition from Late Ocala Deep Association to Late Ocala Shallow Association (McKinney and Zachos 1986).

A body size versus abundance analysis of the float material was not performed. The validity of this type of analysis was questionable for two primary reasons. First, the float material is probably composed of more than one biozone. Secondly, there is inherent sampling bias when collecting loose material from the ground. Larger, more robust specimens are much easier to see and are, therefore, much more likely to be picked up by the collector.

Discussion

The faunal composition dissimilarity between the *O. haldemani* and *O.wetherbyi* zone samples can be correlated with environmental changes occurring in the Late Eocene. There was progression in water depths from the shallow, sandy environments generally represented by the *O. haldemani* zone to the deeper, muddier *O.wetherbyi* zone (Carter and McKinney 1992). Many specimens from both biozones exhibited evidence of taphonomic processes, especially encrustation by bryozoa and foraminifera. This indicates that at least some of the echinoid tests rested on top of the marine substrate for a time before final burial. There was, however, no evidence for significant transport of echinoid tests. Size-sorting was nonexistent and many specimens were very well preserved with little or no fragmentation. Each biozone is a assemblage of echinoids that is preserved in the environment in which it lived.

Samples collected for this study did not yield all the species known to exist at the collection locality. Many of the species not collected are known to be rare in these paleoenvironments. General abundance data collected here does correlate with a previous volumetric abundance study of the Late Eocene echinoids (McKinney 1986). In both studies there are many *Fibularia vaughni*, with other clypeasteroids being generally abundant as well. Also present in samples from both studies are spatangoids and cassiduloids although these are found in much fewer numbers than the clypeasteroids.

Summary

Bulk rock samples of Late Eocene age have yielded individual specimens that provide insight into the echinoid faunal structure and environments of this time.

Observations are summarized in the following.

- The smallest echinoid, *Fibularia vaughni*, is not the most abundant in the *O.haldemani* zone but the sample size may be too small for this to be statistically significant.
- The smallest echinoid, *Fibularia vaughni*, is also the most abundant in the *O.wetherbyi* zone where the sample size is statistically reliable.
- The most species-rich group, the clypeasteroids, also tends to have high species abundance in the *O. wetherbyi* zone.
- The low diversity found in the *O. haldemani* zone and high diversity found in the *O. wetherbyi* zone found in this study are consistent with previous observations for relative species richness for these strata.
- Faunal changes from one stratigraphic interval to the next in the Late Eocene are partially influenced by environmental shift from shallow sandy areas in the *O.haldemani* zone to deeper and muddier areas in the *O. wetherbyi* zone.
- Comparison of bulk samples to float material and to previously documented occurrences for the same locality indicate sampling of only part of the echinoid fauna. Many of the echinoids that were not found in the sampled biozones are known to be rare.

CHAPTER 3

MODERN ECHINOIDS

Introduction - Irregular echinoids are a very diverse group of organisms, having found success in a wide variety of marine habitats since their evolutionary breakthrough at the beginning of the Mesozoic. Modern examples of these animals are found from equatorial to polar regions. They inhabit a spectrum of depths ranging from shallow intertidal areas to those as deep as 7,000 meters (Lehmann and Hillmer 1983).

The Recent fauna of all echinoids (regular and irregular) contains 25% spatangoids, 16% cidaroids, 14% clypeasteroids, 14% temnopleuroids, and 31% less species-rich groups (data from Clarkson 1993). The explosive radiations of irregular echinoids (Jurassic), and, specifically, of clypeasteroids (Tertiary), have led to the modern faunal compositions. Because the irregular echinoids offer the greatest preservation potential and, thus, the most abundant fossil material, they are examined for this study.

Methods

Echinoids are found in virtually every body of marine water. A 1988 study by Ghiold resulted in detailed biogeographic distribution information about extant irregular echinoids. Ghiold used Mortensen's (1948a, 1948b; 1950; 1951) work as the basis for his compilation, updating and supplementing Mortensen's work with regional studies by Clark (1950), Kier (1975), McNamara and Philip (1980), and many others (Ghiold 1988). These data were assembled by Ghiold into 92 maps detailing the distribution of extant irregular echinoid species. Species that were known from only one or two samples or only from

fragments were omitted from Ghiold's data. Also omitted were species that had poor biogeographic records. Ghiold also recognized the possibility of sampling bias due to the non uniformity of the surveying methods from region to region. Nevertheless, his work is the most intensive, exhaustive distribution data set available on these organisms.

Data Collection - Ghiold's distribution maps were created using Goode homolosine projections that correct for latitudinal distortion in a two dimensional depiction. The maps were enlarged by 121% for analysis. Species variables measured for this study include taxonomic affinities (genus, family, and order), species richness, northern- and southern-most latitudinal occurrences, absolute minimum latitudinal occurrence, absolute latitudinal range, and geographic range (Appendix D). Species richness, SPR, as defined here, refers simply to the number of species belonging to a genus.

The northern- and southern-most latitudinal occurrences for each species were located on the maps and estimated. These variables will also be known as NML and SML respectively. The latitudinal increments on Ghiold's maps are 10° each. Enlargement of the maps enabled an estimation to within 1-2°. All measurements of northern- and southern-most latitude were recorded as either positive degree values (northern hemisphere) or negative values (southern hemisphere). The absolute minimum latitudinal occurrence, AMLO, is the absolute value of the lowest latitude a species occupies, in other words how close the range is to the equator? The absolute latitudinal range, ALR, is the total range from the northern most latitude to the southern most latitude. Geographic range variable was measured (in kilometers) by measuring the farthest distance apart two members of the same species could be and the members still be in their mapped distributions. This linear measurement was used instead of an areal measurement because it provides a better indication of extinction resistance. For instance two species could each occupy an areal range of 4000 km^2 but their respective geographic distributions have different shapes. The

species that is able to spread its members out the most will, in effect, be better insulated against environmental disturbances that can cause extinction (see Figure 7).

Statistical Analysis - The numerical values for each of the specified variables: SPR, geographic range, NML, SML, ALR, and AMLO were entered into a spreadsheet for analysis. The descriptive statistics including mean, median, mode, and standard deviation were calculated for each variable (Figure 8). Frequency distributions were plotted for each variable to determine whether mean, median, or mode would be a better representation of the number (Figures 9 ,10 ,11 ,12 ,13 , and 14). This, of course, depended on whether or not the data were normally distributed.

Bivariate analysis was used to explore the relationship between numerical variables. The Pearson correlations were more meaningful for those variables that were normally distributed. Conversely, the Spearmen correlations were more meaningful for those variables that were not normally distributed. Both Spearman and Pearson correlations were calculated for the variables. These correlations are summarized in Table 5.

Chi-square analysis was employed to determine if range patterns were non-randomly distributed within genera. In other words, does each species of a genus have a similar range to other members of the same species. Also examined by the chi-square method was range and species richness. Do species-poor species differ from species-rich species with respect to their ranges? These analyses would help determine whether patterns were random or non-random. For the range versus genus analysis the ranges were first grouped into 5 incremental groups: Group 1: 2,500 km, Group 2: 2,501-5,000 km, Group 3: 5,001-7,500, Group 4: 7,501- 10,000, and Group 5: >10,001. The actual and expected frequencies were calculated for each genus, family, and order. Because there are several species poor genera and families, there were many cells of the chi-square matrix

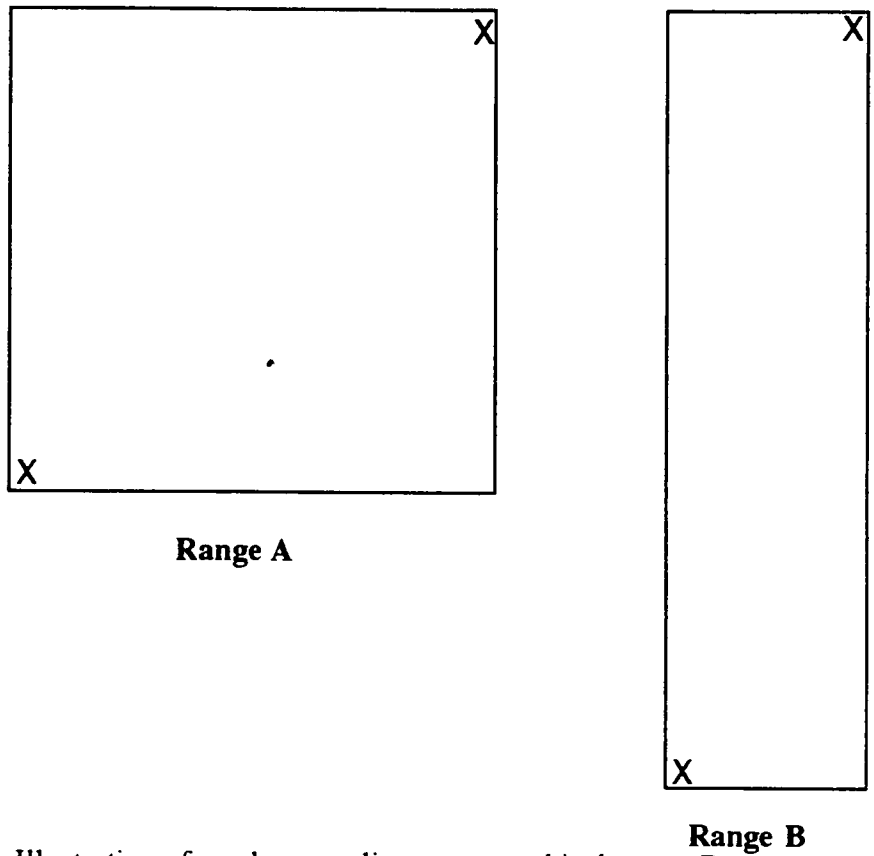

Figure 7. Illustration of areal versus linear geographical range. Ranges **A** and **B** have the same square area but members of species **B** would be able to position themselves further apart. **X** represents an individual of a species.

Geographic Range	
Mean	5179.1
Standard Error	253.7
Median	3366.5
Mode	2000.0
Standard Deviatio	5161.5
Sample Variance	26641432.2
Kurtosis	5.9
Skewness	2.2
Range	34569.0
Minimum	446.0
Maximum	35015.0
Sum	2144146.0
Count	414.0
Confidence Level	498.7

NML	
Mean	13.7
Standard Error	1.5
Median	24.0
Mode	30.0
Standard Deviatio	31.0
Sample Variance	959.1
Kurtosis	-0.1
Skewness	-0.7
Range	159.0
Minimum	-73.0
Maximum	86.0
Sum	5658.5
Count	414.0
Confidence Level	3.0

SML	
Mean	-12.9
Standard Error	1.4
Median	-11.0
Mode	-11.0
Standard Deviatio	28.2
Sample Variance	793.0
Kurtosis	-0.5
Skewness	-0.3
Range	145.0
Minimum	-85.0
Maximum	60.0
Sum	-5334.0
Count	414.0
Confidence Level	2.7

ALR	
Mean	27.3
Standard Error	1.1
Median	19.0
Mode	13.0
Standard Deviatio	22.8
Sample Variance	520.9
Kurtosis	3.0
Skewness	1.6
Range	150.0
Minimum	2.0
Maximum	152.0
Sum	11288.5
Count	414.0
Confidence Level	2.2

AMLO	
Mean	13.8
Standard Error	0.8
Median	7.0
Mode	0.0
Standard Deviatio	16.5
Sample Variance	273.0
Kurtosis	0.9
Skewness	1.3
Range	73.0
Minimum	0.0
Maximum	73.0
Sum	5725.5
Count	414.0
Confidence Level	1.6

Species Richness	
Mean	6.3
Standard Error	2.5
Median	3.0
Mode	1.0
Standard Deviatio	9.9
Sample Variance	97.0
Kurtosis	10.1
Skewness	3.1
Range	39.0
Minimum	1.0
Maximum	40.0
Sum	101.0
Count	16.0
Confidence Level	5.2

Figure 8. Descriptive statistics for the numerical variables. NML is northern-most latitude. SML is southern-most latitude. ALR is absolute latitude range. AMLO is absolute minimum latitudinal occurrence.

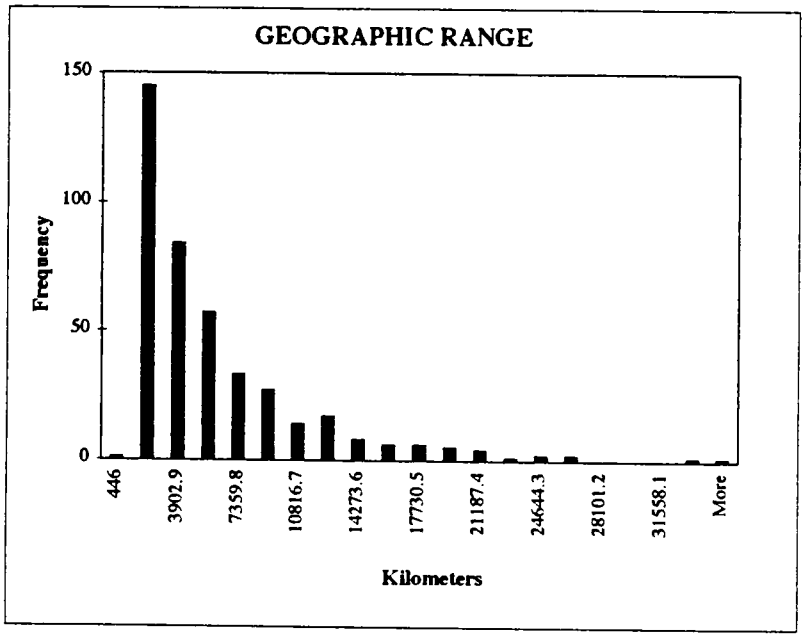

Figure 9. Frequency histogram for geographic range.

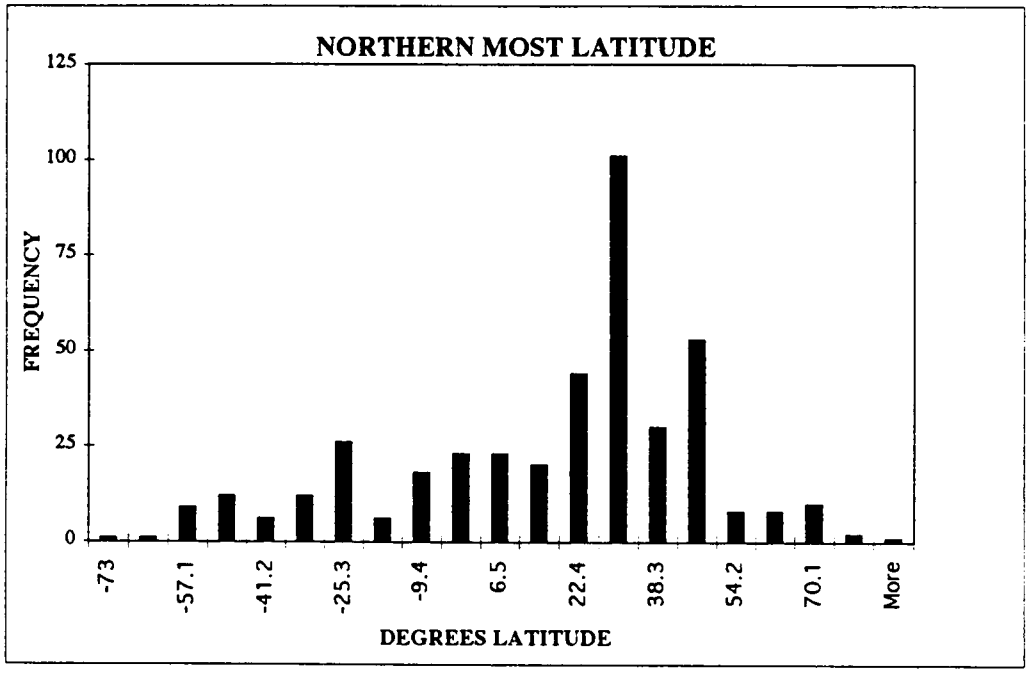

Figure 10. Frequency histogram for NML.

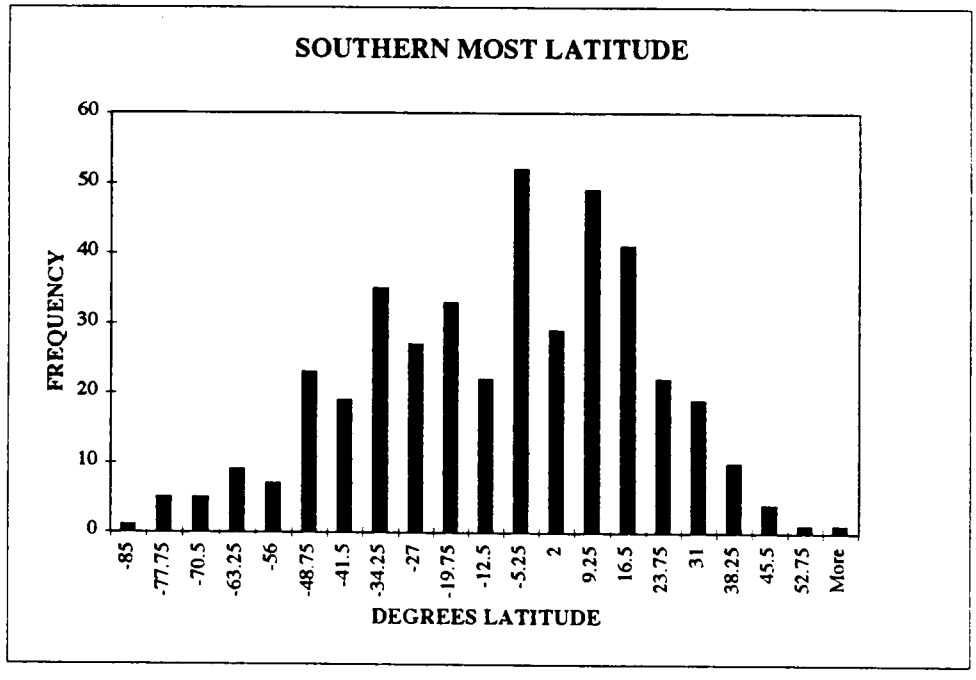

Figure 11. Frequency histogram for SML.

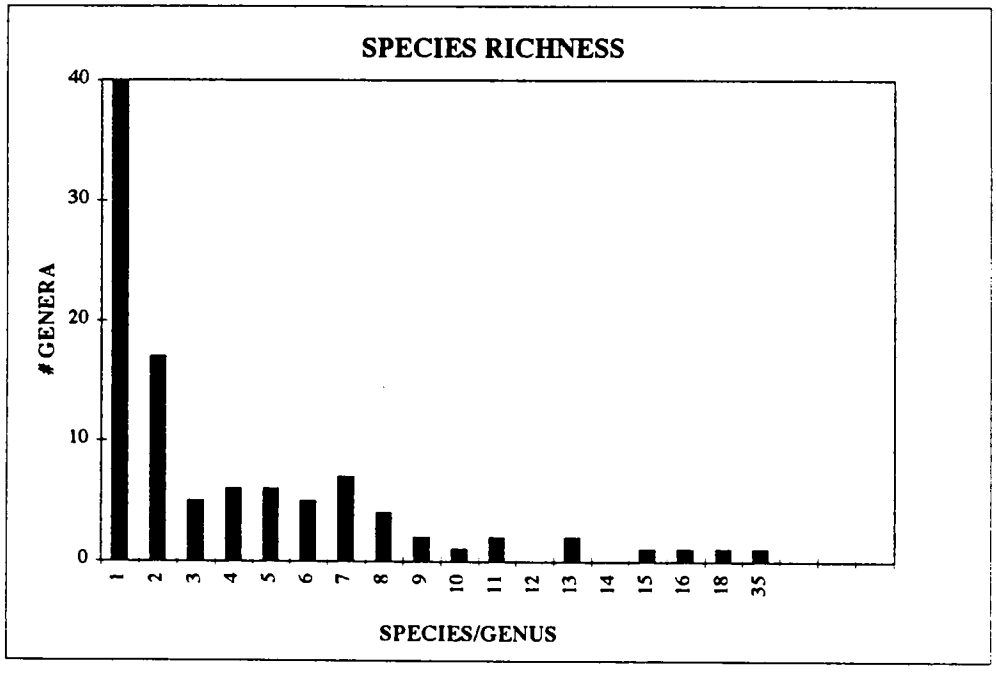

Figure 12. Frequency histogram for SPR.

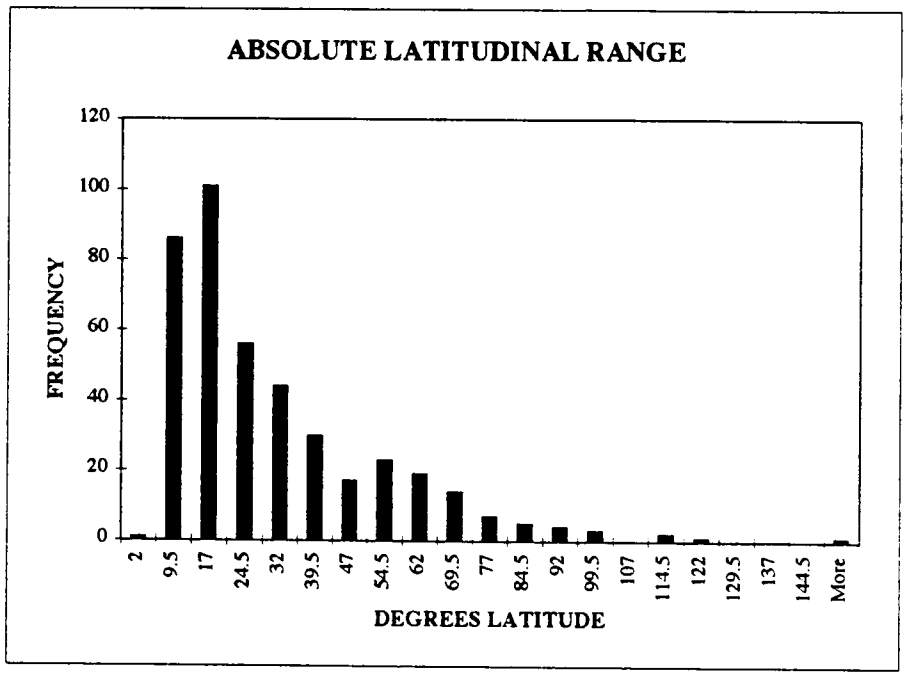

Figure 13. Frequency histogram for ALR.

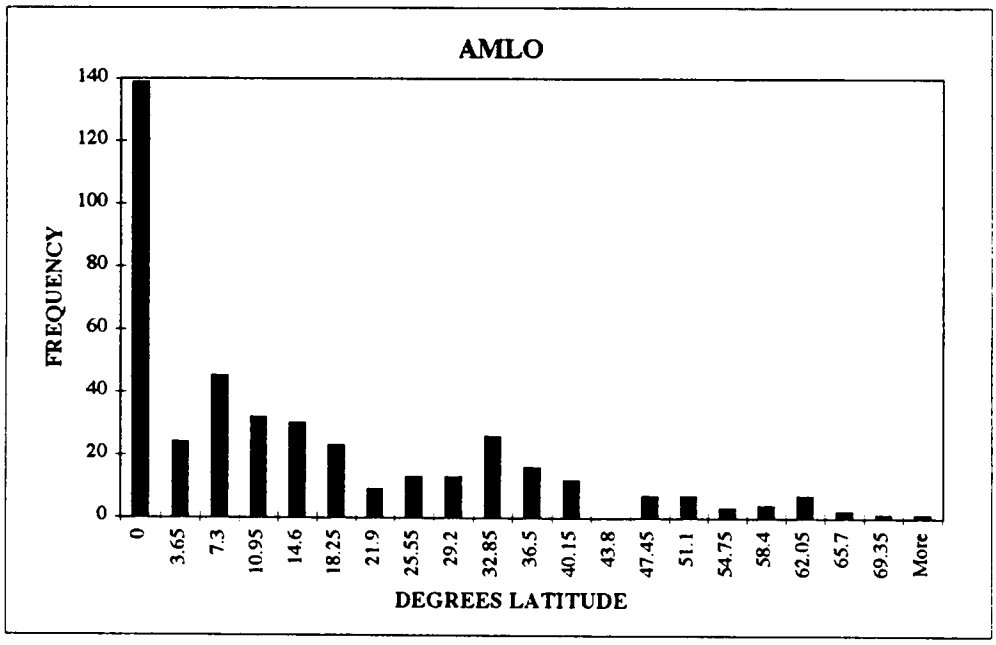

Figure 14. Frequency histogram for AMLO.

Table 5. Pearson and Spearman correlation coefficients for the numerical variables.

PEARSON CORRELATION COEFFICIENTS						
	RANGE	*NML*	*SML*	*ALR*	*AMLO*	*SPR*
RANGE	1					
NML	0.33249	1				
SML	-0.29495	0.68377	1			
ALR	0.79777	0.4879	-0.27615	1		
AMLO	-0.30577	-0.52979	-0.24457	-0.42293	1	
SPR	0.00393	0.11049	0.09599	0.03028	-0.12355	1
SPEARMAN CORRELATION COEFFICIENTS						
	RANGE	*NML*	*SML*	*ALR*	*AMLO*	*SPR*
RANGE	1					
NML	0.36725	1				
SML	-0.31991	0.55847	1			
ALR	0.85422	0.50062	-0.21835	1		
AMLO	-0.47444	-0.30046	-0.04693	-0.56913	1	
SPR	0.00863	0.09532	0.06295	0.07963	-0.08091	1

containing zeroes. This reduced the reliability of the chi-square analysis. Even in the order level analysis, zeroes occupied 57% of the cells. In order to better constrain the data, the range increments were increases so that Group 1: 500-10,500 km, Group 2: 10,501-20,500, Group 3: 20,501-30,000, and Group 4: >30,001. For these data the actual and expected frequencies were calculated for the 9 most species rich families (these 9 of 29 total families contain 78.5% of all species). Also the frequencies were calculated for the two most species rich orders, the Clypesteroida and Spatangoida. These orders contain 88.4% of all modern species. These additional constraints provided more meaningful results (Tables 6 and 7).

The SPR versus range chi-square analysis began by creating two groups of species richness. The species that belonged to a genus with 5 or fewer species are considered "species-poor", while the species that belong to genera with more than 5 species are "species-rich". Range was likewise grouped into "widespread" (greater than the approximate mean range of 3370 km) or "localized" (range larger than 3370 km). A second trial was performed with the species-richness designations the same and ranges redefined as "widespread" having greater than 10,000 km and "localized" having less than 10,000 km. The 10,000 km was more or less arbitrarily chosen. These results are summarized in Tables 8 and 9.

The randomness (or non-randomness) of range within genera was also examined by binomial analysis. The range median of 3,366.5 km was used to divide ranges into two possible groups. Widespread species had ranges greater than 3,366.5 km, while localized species had ranges smaller than 3,366.5 km. Only those genera containing 5 or more species were used to keep the sample size statistically significant. Thirty-three of the 101 genera met this criteria. Binomial calculations were made for each of these 33 genera to obtain the expected number of species occurring within a specific group (widespread or localized) if the number were indeed random at the 95% confidence level. The numerical

Table 6. Statistic matrix for chi-square analysis of **Family** by **Range** groups. Chi-square value is 41.59 with 24 degrees of freedom. The probability value is 0.015.

Frequency **Expected** **Percent** **Row %** **Col %**	**Range (km)** 500-10,500	**Range (km)** 10,500-20,500	**Range (km)** 20,500-30,500	**Range (km)** >30,500	**Total**
Asterostomatidae	16 13.686 4.92 50.00 11.51	11 8.3692 3.38 34.38 12.94	4 3.9385 1.23 12.50 10.00	1 6.0062 0.31 3.13 1.64	32 9.85
Brissidae	28 28.228 8.62 42.42 20.14	17 17.262 5.23 25.76 20.00	8 8.1231 2.46 12.12 20.00	13 12.388 4.00 19.70 21.31	66 20.31
Clypeasteridae	14 14.969 4.31 40.00 10.07	12 9.1538 3.69 34.29 14.12	1 4.3077 0.31 2.86 2.50	8 6.5692 2.46 22.86 13.11	35 10.77
Fibularidae	5 10.265 1.54 20.83 3.60	3 6.2769 0.92 12.50 3.53	7 2.9538 2.15 29.17 17.50	9 4.5046 2.77 37.50 14.75	24 7.38
Lovenidae	17 14.114 5.23 51.52 12.23	8 8.6308 2.46 24.24 9.41	3 4.0615 0.92 9.09 7.50	5 6.1938 1.54 15.15 8.20	33 10.15
Laganidae	5 8.5538 1.54 25.00 3.60	4 5.2308 1.23 20.00 4.71	3 2.4615 0.92 15.00 7.50	8 3.7538 2.46 40.00 13.11	20 6.15
Mellitidae	12 9.8369 3.69 52.17 8.63	4 6.0154 1.23 17.39 4.71	4 2.8308 1.23 17.39 10.00	3 4.3169 0.92 13.04 4.92	23 7.08
Spatangidae	17 11.975 5.23 60.71 12.23	6 7.3231 1.85 21.43 7.06	0 3.4462 0.00 0.00 0.00	5 5.2554 1.54 17.86 8.20	28 8.62
Schizasteridae	25 27.372 7.69 39.06 17.99	20 16.738 6.15 31.25 23.53	10 7.8769 3.08 15.63 25.00	9 12.012 2.77 14.06 14.75	64 19.69
Total	139 42.77	85 26.15	40 12.31	61 18.77	325 100.00

Table 7. Statistic matrix for chi-square analysis of **Order** by **Range** groups. Chi-square statistic is 9.117 with 3 degrees of freedom. The probability value is 0.028.

Frequency **Expected** **Percent** **Row %** **Col %**	**Range (km)** 500-10,500	**Range (km)** 10,500-20,500	**Range (km)** 20,500-30,500	**Range (km)** >30,500	 **Total**
Clypeasteroida	41 50.721 11.20 34.45 26.28	28 30.238 7.65 23.53 30.11	17 14.306 4.64 14.29 38.64	33 23.735 9.02 27.73 45.21	119 32.51
Spatangoida	115 105.28 31.42 46.56 73.72	65 62.762 17.76 26.32 69.89	27 29.694 7.38 10.93 61.36	40 49.265 10.93 16.19 54.79	247 67.49
Total	156 42.62	93 25.41	44 12.02	73 19.95	366 100.00

Table 8. Statistic matrix for chi-square analysis of **Species Richness** by **Range 1.** (**Species rich** = more than 5 species per genus. **Species poor** = 5 or fewer species per genus. **Widespread** = >3370 km. **Localized** = <3370 km.) Chi-square value is 0.096 with 1 degree of freedom. The probability value is 0.757.

Frequency **Expected** **Percent** **Row %** **Column %**	**Localized**	**Widespread**	**Total**
Species-Poor	70 71.5 16.91 48.95 33.82	73 71.5 17.63 51.05 35.27	143 34.54
Species-Rich	137 135.5 33.09 50.55 66.18	134 135.5 32.37 49.45 64.73	271 65.46
Total	207 50.00	207 50.00	414 100.00

Table 9. Statistic matrix for chi-square analysis of **Species Richness** by **Range 2.** (**Species rich** = more than 5 species per genus. **Species poor** = 5 or fewer spevies per genus. **Widespread** = >10,000 km. **Localized** = <10,000 km.) Chi-square value is 1.395 with 1 degree of freedom. The probability value is 0.238.

Frequency **Expected** **Percent** **Row %** **Col %**	**Range (km)** <10,000	**Range (km)** >10,000	**Total**
Species-poor	119 122.97 28.74 83.22 33.43	24 20.034 5.80 16.78 41.38	143 34.54
Species-rich	237 233.03 57.25 87.45 66.57	34 37.966 8.21 12.55 58.62	271 65.46
Total	356 85.99	58 14.01	414 100.00

ranges of number of species within a group explained by randomness were obtained by taking the expected number of species and adding and subtracting the standard deviation. Any number of species falling outside these ranges indicated a statistically non-random pattern.

Results

Four-hundred fourteen species of extant irregular echinoids have been recognized for this study (see Ghiold 1988). These species comprise six orders: Cassiduloida, Clypeasteroida, Holasteroida, Holectypoida, Neolampadoida, and Spatangoida. Twenty-eight families and one-hundred one genera are represented in these six orders. The Cassiduloids are represented by 4 families (14.3% of the total families), 7 genera (7% of the total genera), and 17 species (4.1% of the total species). The Clypeasteroids are represented by 9 families (32.1%), 16 genera (16%), and 119 species (28.7%). The Holasteroids are represented by 3 families (10.7%), 12 genera (12%), and 25 species (6.0%). The Holectypoids are represented by 1 family (3.6%), 2 genera (2.0%), and 3 species (0.7%). The Neolampadoids are represented by 1 family (3.6%), 3 genera (3.0%), and 3 species (0.7%). The Spatangoids are represented by 10 families (35.2%), 60 genera (60.0%), and 247 species (59.7%). These results are summarized in Table 10.

Descriptive Statistics - The normality of the distribution of each variable was determined by examining the descriptive statistics. The NML and SML had barely negatively skewed distributions and so were nearly normal (Figures 10 and 11). The NML distribution was skewed approximately -0.708 and the SML distribution was skewed approximately -0.274. Range (skewed $\approx$ 2.164), ALR (skewed $\approx$ 1.563), AMLO (skewed $\approx$ 1.273), and SPR (skewed $\approx$ 3.065) had non-normally distributed data (Figure 12).

Table 10. Taxonomic diversity of the modern irregular echinoids.

ORDER	# FAMILIES	% FAMILIES	# GENERA	% GENERA	# SPECIES	% SPECIES
Cassiduloida	4	14.3	7	6.9	17	4.1
Clypeasteroida	9	32.1	16	15.8	119	28.7
Holasteroida	3	10.7	12	11.9	25	6
Holectypoida	1	3.6	2	2	3	0.7
Neolampadoida	1	3.6	3	3	3	0.7
Spatangoida	10	35.2	61	60.4	247	59.7
TOTALS	**28**	**99.5**	**101**	**100**	**414**	**99.9**

Histograms - Of particular interest here are the non-normally distributed variables. Although the data range for "range" is 446 to 35,015 km., almost 70% of the ranges are smaller than 5,600 km. About 87% of the ranges are less than 10,850 km. Fewer than 3% of the species have ranges greater than 20,000 km (Figure 9). A similar situation occurs for the other non-normal variables. Almost half of all species had ALR of 17° or less. Almost 77% had ALR of less than 40°. Only about 6% of species had ALR of greater than 70°. The ALR data ranges from 2° to 152° (Figure 13). The AMLO values ranged from 0° to 73°. However, over a third of species had geographic ranges that crossed the equator. Almost 71% had ranges that came within about 18° of the equator. Only about 6% of the species get no closer than 50° from the equator (Figure 14). Finally, species richness ranges from genera with only a single species to a genus with 35 species. Almost 40% of all genera contained only a single species, while over 70% of the genera contained 5 or fewer species. Only about 9% of genera contained at least 10 species (Figure 12).

Correlations - Correlation matrices were constructed for the Pearson and Spearman correlations (Table 5). Most correlations were very weak. SPR showed virtually no correlation with any of the other variables, and SML had virtually no correlation with ALR and AMLO. Range showed moderate correlation with AMLO (negative), SML (negative), and NML (positive). Other moderate correlations include northern-most latitude with ALR (positive) and AMLO (negative), and ALR with AMLO (negative). The only strong correlations are range and ALR, NML and SML (positive). This implies that ranges are oriented north-south and are linear in shape reflecting the coastline.

Chi-square - Initial analysis of the complete data set of 101 genera and 414 species yielded unreliable results when examining range and genus because there were too few

non-zero cells. When range was constrained to only four groups (as discussed above) and the taxa limited to the 9 most species rich families, the chi-square test became a valid test of independence. The null hypothesis is that range and taxonomic affinity (family level) are independent or unrelated. The value of chi-square allowed for rejection of the null hypothesis (Tables 6 and 7). In other words, range is related to family membership.

Also examined were the ranges (again the four groups as discussed previously) and the two most species-rich orders, Clypeasteroida and Spatangoida. The chi-square value allowed rejection of the null hypothesis. In other words, species range and taxonomic affinity at the ordinal level are unrelated. These chi-square results show that, statistically speaking, species ranges are dependent upon the taxonomic affinity of the species (Tables 8 and 9).

The relationship between species richness and range were then analyzed. Do species-rich genera have different ranges than species-poor genera? Simple chi-square results of species-poor (5 or fewer species) and species-rich (more than 5 species) species versus localized (3370 km or fewer) and widespread (greater than 3370 km) ranges indicated that there is no statistically significant difference between species-rich species and species-poor species with respect to their ranges. The same result was obtained when the ranges were redefined using 10,000 km as the division. In other words, range does not correlate with SPR.

Binomial analysis - Species richness ranges from 1 species per genus (several genera) to 35 species per genus (*Clypeaster*) . The "range" values ranged from 446 km (*Echinocardium mortenseni*) to 35,015 km (*Echinoneus cyclostomus*). There were 33 genera that met the 5 species minimum requirement. Binomial calculations of these 33 genera revealed only three genera falling outside the expected range of species richness for randomness. These genera are *Echinocardium*, *Fibularia*, and *Spatangus*. *Echinocardium*

exhibited geographic ranges that are unusually localized statistically while *Fibularia* and *Spatangus* exhibited ranges that are unusually widespread. These results are summarized in Table 11.

Discussion

Examination and analysis of Ghiold's (1988) maps has provided important information about the distribution patterns of irregular echinoid taxa. Many of the important results of this research involve the geographic range of the 414 species recognized for this study. The range frequency histogram (Figure 9) displays the classic "hollow curve" distribution of the data. Most irregular echinoids have relatively small ranges. This finding is certainly supportive of previous work (see Brown, 1995 p.102). The "hollow curve" frequency distribution pattern may imply that irregular echinoids differ widely in their ecological requirements, both biotic and abiotic. Species with small ranges may have more restricted tolerances for ecological conditions whereas more widespread species may have greater tolerance for the same conditions.

Do species of the same genus have similar ranges? The chi-square analysis revealed that the means of ranges within genera were significantly different at the 95% confidence level from the means of ranges between genera. This means that a species is more likely to have a geographic range similar to members of its own genus rather than to members of a different genus. Further, this relationship held true at the level of family and order. Yet this still does not fully answer the question. Binomial analysis showed that geographic range was indeed random within all analyzed genera except *Echinocardium*, *Fibularia*, and *Spatangus*. All other genera contain species that are equally likely to be widespread or localized.

Table 11. Results for genera that exhibit nonrandom geographic range. **# Obs. SP** = number of observed species. **#TS** = total species for the genus explained by randomness plus/minus the standard deviations at 95% confidence level. **Exp** = expected range of random number of species within either group (Large or Small range) with standard deviation at 95% confidence interval. Numbers smaller than the expected range represent nonrandom localization. Numbers larger than the expected range represent nonrandom widespreadedness.

GENUS	# OBS. SP	#TS	EXP
Echinocardium	11	5.5+/-3.25	2.25-8.75
Fibularia	8	4.0+/-2.8	1.2-6.8
Spatangus	13	6.5+/-3.5	3.0-10

A very important question addressed in this study is how do species-poor and species-rich genera compare with respect to their frequency distributions? Most genera are species-poor (Figure 12). Over 70% of all genera contain 5 or fewer species while 40% contain only a single species. With respect to extinction selectivity, it is generally understood that the more species contained within a taxon the greater the chance of that taxon surviving an extinction event. If a negative correlation could be demonstrated between species richness and geographic range, this may imply that it is beneficial for a species-poor genus to contain species that have large ranges. Both correlation and chi-square analysis showed that this relationship does not exist. Statistically, a species-poor genus is no more likely to have a large geographic range than a species belonging to a species-rich taxa.

The frequency plot for the absolute minimum latitudinal occurrence for the 414 species in the study is also a classic hollow curve (Figure 14). In fact over a third of the species have geographic ranges that cross the equator. Over two-thirds of the species have ranges that lie within about 18° the equator. This finding is consistent with many previous studies summarized by Rosenzweig (1996, p. 25). "The tropics, if not the seat of life, are the center of its richest display."

There is evidence from the correlation analysis that irregular echinoids do not follow Rapoport's rule. A moderately strong negative correlation (-0.47444) between range and AMLO means that individual ranges tend to get larger as they occur nearer the equator. This finding is consistent with recent studies of other marine organisms which also fail to support Rapoport's rule (Roy *et al.* 1994; Rohde and Heap 1996).

Very good correlation also exists between geographic range and the absolute latitudinal range. This indicates that geographic ranges are generally positioned across latitude rather than across longitude. This is a simple reflection of the position of the coastlines of the continents. In modern configuration the continents tend to lie north-south more so than east-west. By default there are more north-south oriented coastlines than east-

west oriented ones. Lehmann and Hillmer (1983) stated that most echinoids inhabit the littoral zone. These organisms thus tend to inhabit the coastal margins which renders a north-south orientation to their ranges.

Summary

Modern irregular echinoids have exhibited specific patterns of occurrence with respect to range and latitudinal gradients. There was, however, a surprising lack of correlation for species-richness and the other variables. The following is a summary of the most important findings.

- Most irregular echinoid species have relatively small geographic ranges.
- Geographic range seem to be randomly distributed within genera except for three cases : *Echinocardium*, *Fibularia*, and *Spatangus*.
- Most genera are species-poor.
- Species of species-poor taxa are no more likely to be widespread than species of species-rich taxa.
- Most irregular echinoids have ranges that cross the equator or approach it.
- Irregular echinoids do not follow Rapoport's rule.
- Ranges of irregular echinoids tend to lie in a north-south orientation most likely due to the orientation of the continents.

CHAPTER 4

MODERN AND ANCIENT COMPARISONS

Irregular echinoids are a prominent group in both modern and post-Triassic ancient marine assemblages. There is no doubt that the structure of the modern echinoid fauna has been shaped by the origination from and extinction of faunas of the past. Today's lower taxa are a reflection of which groups were extinction-resistant and/or were able to exploit new and different resources. It is impossible to do a one-to-one comparison of modern species and species from earlier in the Cenozoic because the faunal compositions have changed drastically at this level. There are, however, modern representatives of genera that existed in the past. By examining groups that are common to both past and present one can come to understand how extinction selectivity relates to taxonomic membership. Are some groups more prone become extinct? If so, are these groups nested or clustered within higher taxa?

McKinney (1995) showed that species extinction for echinoids was not a random event. He found that reverse rarefaction of past species overestimates genus extinction rates by as much as 6%-15%. In his discussion of possible causes of this observation, McKinney suggests that a clustering of large-bodied, rare or narrowly distributed species within genera might make these genera more extinction prone.

Species Richness

The species diversity of echinoids in the North American Gulf Coast area has declined for every major group from the Late Eocene to Pleistocene-Recent (see Table 2 in

McKinney and Oyen 1989). This is somewhat misleading, however, since the Pleistocene-Recent fauna is more diverse than that of the Early Pliocene. This means that since the Early Eocene there has been fluctuation in echinoid diversity in the Gulf Coast area.

The spatangoids and clypeasteroids have historically made up most of the echinoid fauna in every stage of the Cenozoic. This is certainly the case for both the Upper Eocene samples and the modern species examined for this study. These two groups are very different morphologically and ecologically. The clypeasteroids are surface dwellers or shallow burrowers inhabiting the sandier sublittoral or littoral zones. Their tests are generally ovoid or discoid in shape to allow for streamlined shallow burial. Spatangoids, on the other hand, are usually deeper burrowers that inhabit the muddier neritic and abyssal zones. Their globular shapes allow for more powerful burrowing into deeper sediments.

Range/Abundance

Binomial analysis of the modern irregular echinoid species has shown that geographic range within genera is randomly distributed. In other words, species of any genus are equally likely to have widespread or localized ranges. There are three genera that did show a specifically non-random pattern of distribution. These three genera are *Echinocardium* and *Spatangus* (spatangoids) and *Fibularia* (a clypeasteroid). Modern *Echinocardium* are geographically localized while *Spatangus* and *Fibularia* are geographically widespread. Have these three genera always possessed ranges of these magnitudes? *Echinocardium* has experienced a drastic reduction in range from the Oligocene where it was cosmopolitan in occurrence to the Recent where it is found only in the English Channel (Durham *et al.*1966). *Fibularia* is presently found only in the Indo-Pacific Ocean, which is also a range reduction. It was cosmopolitan as a fossil (Mooi

1989). In contrast, *Spatangus* has had a cosmopolitan distribution both as a fossil and as a living genus.

Body Size

Large body size can be at least loosely correlated with species rarity in a sample of fossil echinoids (Chapter 2 this volume). Does this association hold true for a larger collection of fossil groups? Table 12 is a compilation of the relative abundances and body sizes for 38 fossil echinoid species from the late Eocene and Early Oligocene of modern Florida and Georgia (relative abundances taken from Carter 1990, McKinney and Zachos 1986, and Carter personal communication. The relative body sizes were compiled using the length of the largest available specimen in the extensive personal collection of Burt Carter).

By examining the 10 largest species it can be determined if body size is strongly correlated to rarity. Only two of the ten largest species were categorized as rare. The others were either moderately abundant (3 of 10) or very abundant (5 of 10). This would certainly suggest that there is no relationship between large body size and how rare an echinoid is.

Discussion

Range, species abundance, body size, and species richness are variables often considered in ecological and evolutionary studies. Characteristic traits of certain groups can be passed on to new species and, thus be persistent in the lineage. The relationships between these variables can, therefore, lend important insight into the phylogenetic histories of organisms. Once a relationship between parameters for modern organisms has been determined, then this same relationship can be examined in the ancient ancestors. Comparison of such parameters of fossil groups and their modern counterparts can help

Table 12. Echinoid species in the study. Relative abundance data modified from Carter (1990). **A**= found at all localities. **M**= found in most locations. **R**= occasionally found at one or a few localities. Body size measurements are test length of largest specimen sampled. The ten largest species are marked with an * .

Species	Abundance	Body Size (mm)	
Agassizia clevei	A	29.0	
Agassizia floridana	M	36.2	
Cassidulus conradi	R	41.4	
Cassidulus trojanus	A	25.4	
Durhamella floridana	R	20.1	
Durhamella ocalana	M	24.0	
Eupatagus antillarum	A	70.0	*
Eupatagus clevei	M	129.0	*
Eupatagus gardnerae	R	40.0	
Eupatagus ocalanus	M	75.5	*
Eurhodia patelliformis	R	26.2	
Eurhodia rugosa	A	37.3	
Eurhodia trojana	A	47.2	*
Fibularia alabamanensis	M	7.4	
Fibularia vaughni	A	12.3	
Oligopygus haldemani	A	35.8	
Oligopygus phelani	M	15.2	
Oligopygus wetherbyi	A	57.9	*
Plagiobrissus curvus	R	58.0	*
Plagiobrissus dixie	A	80.2	*
Rhyncholampas ericsoni	R	45.5	
Rhyncholampas georgiensis	R	50.0	*
Schizaster armiger	A	58.0	*
Schizaster beckeri	R	33.0	
Schizaster ocalanus	M	37.0	
Weisbordella cubae	A	44.6	
Weisbordella johnsoni	M	54.5	*

delineate the random or non random occurrence of traits. For example, are the same genera that are species-rich also the ones with the widest ranges? Non random patterns might suggest phylogenetic control on these traits. If there is evidence for phylogenetic control of the range, abundance, body size, and species-richness of echinoid taxa this could be an indication that extinction resistance may evolve to be concentrated in certain genera. While no doubt range, abundance, and species richness play an important role in the extinction selectivity of a taxon, there is little evidence that genera tend stack the deck with species that are extinction resistant. Important observations in this argument are included in the following.

Conclusions

- Species richness for all echinoids has fluctuated during the Cenozoic.
- The clypeasteroids and the spatangoids have been the most prolific groups of the Cenozoic even though they are often very different morphologically and ecologically.
- Range within genera of modern echinoids is randomly distributed except in *Echinocardium*, *Spatangus*, and *Fibularia*. The ranges of *Echinocardium* and *Fibularia* have experienced declines from ancient times to the Recent. *Spatangus* remains cosmopolitan.
- Large body size is not strongly correlated with abundance for 38 fossil species.
- Genera do not tend to accumulate species that are similar in their extinction resistance.

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Appendices

Appendix A. Species list and test measurements for the *Oligopygus haldemani* zone.

***Oligopygus haldemani* Zone**				
Species	**Length (mm)**	**Width (mm)**	**Height (mm)**	**Volume (mm^3)**
Durhamella floridana	12.93	*	*	*
	5.98	*	*	*
Fibularia vaughni	6.39	4.26	3.05	83.03
	3.23	2.44	1.86	14.66
	4.26	2.93	2.25	28.08
	2.84	2.00	1.64	9.32
	4.85	3.45	2.83	47.35
Oligopygus haldemani	11.77	10.22	6.39	768.65
	3.29	2.84	2.01	18.78
	14.84	13.17	7.12	1391.55

Appendix B. Species list and test measurements for the *Oligopygus wetherbyi* zone.

Oligopygus wetherbyi Zone

Species	Length (mm)	Width (mm)	Height (mm)	Volume (mm^3)
Agassizia floridana	9.20	7.44	7.61	520.89
Durhamella ocalana	16.13	14.39	2.99	694.01
	17.55	15.76	2.47	683.17
	14.23	12.85	2.50	457.14
	8.00	6.87	1.71	93.98
	12.17	10.94	2.47	328.86
	6.13	5.19	1.72	54.72
Fibularia vaughni	8.09	5.50	3.76	167.30
	6.75	4.45	3.05	91.61
	6.64	4.37	2.52	73.12
	7.87	5.14	3.64	147.24
	4.50	3.43	3.16	48.77
	4.44	3.40	2.84	42.87
	4.68	3.27	2.52	38.57
	3.95	3.09	2.53	30.88
	7.40	5.14	3.65	138.83
	4.34	3.51	2.61	39.76
	6.19	4.35	3.24	87.24
	8.04	5.83	3.79	177.65
	4.17	2.88	2.64	31.71
	4.82	3.39	2.46	40.20
	3.44	2.67	2.09	19.20
	3.92	2.79	2.31	25.26
	4.29	3.30	3.12	44.17
	5.56	3.63	2.52	50.86
	3.73	2.90	2.27	24.55
	3.64	2.76	1.90	19.09
	6.54	4.37	3.01	86.03
	2.89	2.15	1.90	11.81
	5.20	3.84	3.35	66.89
	4.82	3.67	2.92	51.65
	4.00	3.02	2.80	33.82
	7.56	5.05	3.84	146.60
	3.66	2.70	2.28	22.53
	4.74	3.64	2.90	50.04
	4.51	3.25	2.81	41.19
	3.46	2.34	1.94	15.71
	2.49	1.78	1.23	5.45
	3.70	2.70	2.14	21.38
	5.90	4.12	2.97	72.19
	4.64	3.10	2.26	32.51

Appendix B. (continued)

Oligopygus wetherbyi Zone

Species	Length (mm)	Width (mm)	Height (mm)	Volume (mm^3)
	4.10	3.06	2.54	31.87
	5.85	3.86	2.64	59.61
	6.14	4.02	2.64	65.16
	4.47	3.52	2.82	44.37
	5.86	3.84	2.71	60.98
	3.35	2.46	1.73	14.26
	3.27	2.48	1.80	14.60
	3.17	2.30	1.80	13.12
	3.09	2.26	1.93	13.48
	3.06	2.33	1.66	11.84
	4.41	3.14	2.35	32.54
	2.73	2.12	1.48	8.57
	3.02	2.18	1.74	11.46
	6.72	4.57	3.80	116.70
	5.66	3.72	2.40	50.53
	5.15	3.88	3.33	66.54
	3.76	2.89	2.34	25.43
	4.75	3.65	3.03	52.53
	5.20	3.37	2.40	42.06
	5.95	3.94	2.65	62.12
	4.47	3.31	2.64	39.06
	4.01	2.93	2.26	26.55
	4.24	3.28	2.59	36.02
	4.16	3.12	2.52	32.71
	6.13	4.09	2.98	74.71
	7.18	4.70	3.29	111.02
	4.43	3.23	2.68	38.35
	4.61	3.11	1.97	28.24
	5.77	4.05	2.66	62.16
	5.63	3.63	2.46	50.27
	5.43	4.04	3.25	71.30
	4.84	3.10	2.15	32.26
	4.54	3.61	2.85	46.71
	5.39	3.62	2.68	52.29
	6.08	4.12	3.02	75.65
	3.39	2.95	2.05	20.50
	4.56	3.44	2.75	43.14
	4.23	3.16	2.73	36.49
	6.14	4.04	2.83	70.20
	3.84	3.10	2.35	27.97
	4.38	3.32	2.76	40.13

Appendix B. (continued)

Oligopygus wetherbyi Zone

Species	Length (mm)	Width (mm)	Height (mm)	Volume (mm^3)
	6.85	4.61	3.35	105.79
	7.08	4.89	3.23	111.83
	4.64	3.43	2.69	42.81
	5.08	3.35	2.28	38.80
	6.40	4.23	2.99	80.95
	4.57	2.66	3.44	41.82
	4.79	3.30	2.45	38.73
	3.70	2.67	2.19	21.64
	4.71	3.37	2.26	35.87
	6.23	4.11	2.97	76.05
	3.46	2.54	2.07	18.19
	4.70	3.23	2.69	40.84
	5.17	3.48	2.38	42.82
	4.56	3.52	2.91	46.71
	4.88	3.83	2.81	52.52
	4.11	3.29	2.56	34.62
	4.31	3.37	2.79	40.52
	6.34	4.53	3.03	87.02
	4.09	3.00	2.78	34.11
	5.24	3.67	2.69	51.73
	5.65	3.84	2.77	60.10
	5.16	3.88	2.90	58.06
	4.43	3.34	2.93	43.35
	5.25	3.52	2.77	51.19
	5.58	3.63	2.47	50.03
	3.42	2.57	2.56	22.50
	5.50	3.79	2.67	55.66
	3.96	3.00	2.26	26.85
	5.77	3.75	2.57	55.61
	3.70	2.96	2.47	27.05
	5.00	3.34	2.56	42.75
	3.91	3.21	2.57	32.26
	6.05	3.81	2.99	68.92
	4.67	3.57	2.74	45.68
	3.90	2.78	2.18	23.64
	5.26	3.80	3.03	60.56
	4.14	3.27	2.45	33.17
	4.89	3.75	3.29	60.33
	4.61	3.42	2.60	40.99
	3.63	2.76	2.15	21.54
	4.52	3.53	2.84	45.31

Appendix B. (continued)

Oligopygus wetherbyi Zone

Species	Length (mm)	Width (mm)	Height (mm)	Volume (mm^3)
	3.57	2.75	2.28	22.38
	4.60	3.54	2.81	45.76
	4.65	3.35	2.57	40.03
	4.05	2.68	2.17	23.55
	4.04	3.03	2.25	27.54
	3.88	2.87	2.27	25.28
	3.95	3.10	2.68	32.82
	3.97	3.06	2.40	29.16
	3.62	2.53	2.23	20.42
	5.42	3.52	2.43	46.36
	4.36	3.09	2.84	38.26
	3.61	2.77	2.50	25.00
	4.35	3.21	2.27	31.70
	3.84	2.85	2.07	22.65
	6.03	4.24	2.81	71.84
	5.50	3.66	2.54	51.13
	4.26	3.39	2.48	35.81
	5.00	3.61	2.80	50.54
	4.15	3.10	2.68	34.48
	4.17	3.19	2.48	32.99
	3.89	2.92	2.51	28.51
	3.25	2.54	2.07	17.09
	3.86	2.72	2.26	23.73
	4.21	2.93	2.07	25.53
	5.98	4.17	2.89	72.07
	3.94	2.78	1.96	21.47
	4.47	3.34	2.54	37.92
	4.17	3.27	2.63	35.86
	4.87	3.50	2.59	44.15
	5.75	3.57	2.72	55.83
	5.90	4.03	2.82	67.05
	4.11	3.01	2.57	31.79
	5.28	3.56	2.48	46.62
	3.72	2.81	2.26	23.62
	4.15	2.96	2.44	29.97
	4.83	3.67	3.16	56.01
	3.75	2.86	2.16	23.17
	3.93	3.01	2.49	29.45
	3.57	2.63	2.32	21.78
	6.39	4.36	3.24	90.27
	4.20	3.36	2.60	36.69

Appendix B. (continued)

Oligopygus wetherbyi Zone

Species	Length (mm)	Width (mm)	Height (mm)	Volume (mm^3)
	4.40	3.37	2.73	40.48
	4.07	2.98	2.48	30.08
	4.42	2.86	2.42	30.59
	4.66	3.67	2.85	48.74
	4.69	3.64	2.84	48.48
	4.42	2.86	2.11	26.67
	4.65	3.51	2.83	46.19
	3.99	2.60	1.81	18.78
	4.68	3.19	2.18	32.55
	3.83	2.89	2.31	25.57
	5.93	4.07	2.81	67.82
	4.98	3.68	2.73	50.03
	5.38	3.61	2.70	52.44
	7.61	4.89	3.49	129.87
	4.28	3.30	2.81	39.69
	6.26	4.27	3.15	84.20
	6.10	3.98	2.78	67.49
	6.18	4.10	2.73	69.17
	5.53	3.72	2.42	49.78
	3.39	2.49	2.04	17.22
	4.87	3.70	2.69	48.47
	4.50	3.43	3.04	46.92
	3.88	3.02	2.27	26.60
	4.48	3.44	2.68	41.30
	5.38	3.50	2.59	48.77
	4.22	3.37	2.70	38.40
	3.73	2.78	2.17	22.50
	5.12	3.67	3.14	59.00
	3.59	2.82	1.98	20.05
	3.29	2.57	1.90	16.07
	4.01	3.03	2.48	30.13
	3.96	3.03	2.77	33.24
	5.13	3.37	2.34	40.45
	5.10	3.18	*	*
	2.70	*	1.43	*
	*	4.33	3.08	
	*	3.67	2.43	
	*	*	1.74	*
Oligupygus haldemani	9.70	8.64	5.37	450.05
	8.39	7.34	8.84	544.39
Oligopygus wetherbyi	40.81	31.41	16.94	21714.41

Appendix B. (continued)

Oligopygus wetherbyi Zone

Species	Length (mm)	Width (mm)	Height (mm)	Volume (mm^3)
	31.71	26.15	15.30	12687.01
	44.00	35.98	21.43	33926.26
	29.58	24.26	13.57	9737.98
	35.67	28.9	15.98	16473.19
	5.48	4.51	2.75	67.97
Weisbordella cubae	9.73	8.22	3.15	251.94
	9.50	8.02	2.48	188.95
	5.42	4.83	1.56	40.84
	7.03	6.16	1.83	79.25
	6.49	5.34	2.19	75.90
	8.05	6.83	2.48	136.35
	4.44	3.83	1.01	17.18
	7.50	6.62	2.07	102.78
	8.26	7.40	1.91	116.75
	3.86	3.21	1.38	17.10
	4.50	4.07	1.42	26.01
	10.51	9.05	2.93	278.69
	8.93	*	*	*
	*	7.57	3.52	*
	7.38	6.28		*
	6.42		1.70	*
Wythella eldridgei	10.40	9.51	1.82	180.01
	10.84	9.90	1.82	195.32
	8.90	7.87	2.18	152.69
	7.12	6.32	*	*
	12.43	10.68	*	*

Appendix C. Species list and test measurements for the float material.

Float Material Measurements

Species	Length (mm)	Width (mm)	Height (mm)	Volume (mm^3)
Agassizia floridana	9.76	8.70	8.07	685.24
	11.75	10.89	8.68	1110.67
Durhamella ocalana	21.44	1.94	3.37	140.17
	26.28	22.73	3.04	1815.93
	31.13	27.27	5.85	4966.15
Fibularia vaughni	4.31	3.17	2.54	34.70
	5.76	4.42	3.62	92.16
	9.32	6.83	5.21	331.65
	5.29	4.22	3.72	83.04
Oligopygus haldemani	9.33	8.19	4.48	342.33
	17.40	15.81	8.42	2316.29
	17.95	15.60	9.13	2556.58
	24.45	20.34	10.78	5361.03
	17.90	15.53	8.49	2360.11
	10.77	9.05	5.53	539.00
	17.06	14.83	8.07	2041.71
	18.54	16.17	9.53	2857.02
	19.68	16.92	8.69	2893.64
	12.30	10.59	7.18	935.25
	13.77	12.23	6.96	1172.11
	18.51	16.76	9.53	2956.47
	7.75	6.71	3.77	196.05
	22.99	20.92	10.35	4977.84
	17.30	15.02	8.09	2102.15
	16.69	14.37	8.14	1952.26
	17.27	15.35	*	*
	12.56	11.23	*	*
	28.24	23.39	*	*
Oligopygus wetherbyi	46.14	39.41	23.09	41986.33
	42.73	35.53	19.24	29210.11
	54.28	44.49	26.07	62956.89
	41.63	35.80	19.97	29762.37
	43.02	36.24	19.00	29621.85
	40.15	32.54	18.19	23764.89
	44.76	37.88	19.67	33350.66
	46.84	36.09	21.26	35939.09
	42.03	36.66	20.10	30970.48
	40.52	31.78	15.27	19663.57
	48.69	39.23	21.87	41774.08
	31.20	23.47	19.40	14205.92
	37.89	31.82	16.81	20267.14

Appendix C. (continued)

Float Material Measurements

Species	Length (mm)	Width (mm)	Height (mm)	Volume (mm^3)
	26.84	21.76	12.31	7189.51
	34.59	29.36	17.73	18005.92
	46.02	38.64	21.59	38391.61
	37.83	32.21	*	*
	34.59	29.12	*	*
	38.07	32.58	*	*
	*	32.45	17.19	*
Rhyncholampas conrad	27.32	24.36	13.91	9257.32
	36.91	31.93	20.56	24230.71
Schizaster armiger	52.38	49.17	30.07	77446.02
Schizaster ocalanus	20.73	20.89	17.20	7448.45
Weisbordella cubae	36.70	31.96	9.40	11025.56
	12.35	10.82	3.06	408.90
	21.42	19.74	5.43	2295.97
	22.34	18.99	5.60	2375.72
	7.65	6.57	2.02	101.53
	23.07	20.17	5.55	2582.54
	13.79	11.64	3.57	573.04
	17.34	14.52	5.34	1344.49
	24.96	22.78	6.52	3707.20
	29.12	25.25	6.93	5095.49
	13.41	11.68	3.27	512.18
	9.28	8.22	2.23	170.11
	11.13	8.99	2.99	299.18
	14.25	11.82	3.34	562.57
	26.36	24.02	6.03	3818.00
	16.32	14.75	4.28	1030.28
	16.14	15.24	3.69	907.64
	8.85	7.40	2.26	148.01
	9.88	8.77	2.32	201.02
	30.67	27.30	7.87	6589.48
	14.76	13.09	4.56	881.03
	13.67	11.92	4.31	702.30
	29.05	25.40	6.81	5024.89
	6.50	5.76	*	*
Wythella eldridgei	11.27	9.73	1.66	182.03
	8.56	7.61	1.81	117.91
	14.18	12.33	2.26	395.14
	14.72	12.90	2.14	406.36
	9.94	8.87	2.09	184.27

Appendix D. Species list and variable measurements for the modern irregular echinoids.

GENUS	SPECIES	RANGE	NML	SML	ALR	AMLO	SPR	FMLY	ORD
Abatus	*agassizia*	1047	-50	-55	5	50	9	SC	SP
Abatus	*cavernosus*	5083	-40	-70	30	40	9	SC	SP
Abatus	*cordatus*	1346	-45	-53	8	45	9	SC	SP
Abatus	*curvidens*	1495	-60	-68	8	60	9	SC	SP
Abatus	*elongatus*	897	-60	-64	4	60	9	SC	SP
Abatus	*ingens*	12708	-33	-50	17	33	9	SC	SP
Abatus	*nimrodi*	2392	-73	-80	7	73	9	SC	SP
Abatus	*philipii*	5083	-40	-70	30	40	9	SC	SP
Abatus	*schackletoni*	8372	-63	-85	22	63	9	SC	SP
Aceste	*bellidifera*	12000	42	-55	97	0	3	AE	SP
Aceste	*ovata*	25818	44	-24	68	0	3	AE	SP
Aceste	*weberi*	1364	-6	-14	8	6	3	AE	SP
Aeropsis	*fulva*	16662	6	-18	24	5	2	AE	SP
Aeropsis	*rostrata*	12160	60	-36	96	0	2	AE	SP
Agassizia	*excentrica*	2778	28	10	18	10	2	SC	SP
Agassizia	*scribicularia*	5370	20	-20	40	0	2	SC	SP
Ammotrophus	*cyclius*	1786	-36	-48	12	36	1	AR	CL
Amphipneustes	*bifidus*	8364	-55	-65	10	55	8	SC	SP
Amphipneustes	*brevisternalis*	11406	-47	-55	8	47	8	SC	SP
Amphipneustes	*koehleri*	1141	-52	-57	5	52	8	SC	SP
Amphipneustes	*lorioli*	3422	-60	-70	10	60	8	SC	SP
Amphipneustes	*marsupialis*	4753	-51	-65	14	51	8	SC	SP
Amphipneustes	*rostratus*	3232	-50	-55	5	50	8	SC	SP
Amphipneustes	*similus*	3422	-63	-77	14	63	8	SC	SP
Amphipneustes	*tumescens*	3232	-50	-55	5	50	8	SC	SP
Anabrissus	*damesi*	4167	6	-28	34	0	1	B	SP
Anametalia	*grandis*	2635	16	7	9	7	3	B	SP
Anametalia	*regularis*	2635	-7	-12	5	7	3	B	SP
Anametalia	*sternaloides*	4286	24	-9	33	0	3	B	SP
Apatopygus	*recens*	2400	-32	-51	19	32	1	AP	CA
Arachnoides	*placenta*	12800	31	-48	79	0	3	AR	CL
Arachnoides	*tenuis*	2200	-10	-21	11	10	3	AR	CL
Arachnoides	*zelandiae*	1900	-34	-48	14	34	3	AR	CL
Araeolampas	*atlantica*	8960	38	0	38	0	1	L	SP
Argopatagus	*aculeata*	571	-6	-11	5	6	4	AS	SP
Argopatagus	*multispinus*	1905	29	16	13	16	4	AS	SP
Argopatagus	*planus*	1524	44	30	14	30	4	AS	SP
Argopatagus	*vitreus*	14476	42	-12	54	2	4	AS	SP
Astriclypeus	*manni*	2700	41	24	17	24	1	A	CL
Breynia	*australasiae*	2917	-5	-38	33	5	5	L	SP
Breynia	*desorii*	2000	-13	-24	11	13	5	L	SP
Breynia	*elegans*	5000	21	-11	32	0	5	L	SP
Breynia	*neanika*	2500	-9	-17	8	9	5	L	SP
Breynia	*vredenburgi*	3333	25	7	18	7	5	L	SP
Brisaster	*capensis*	1176	-30	-38	8	30	7	SC	SP
Brisaster	*fragilis*	8137	70	30	40	30	7	SC	SP
Brisaster	*kerguelensis*	1471	-45	-57	12	45	7	SC	SP
Brisaster	*latiformis*	13182	60	15	45	15	7	SC	SP

Appendix D. (continued)

GENUS	SPECIES	RANGE	NML	SML	ALR	AMLO	SPR	FMLY	ORD
Brisaster	*moseleyi*	1078	-52	-62	10	52	7	SC	SP
Brisaster	*owstoni*	1961	48	32	16	32	7	SC	SP
Brisaster	*townsendi*	8529	60	2	58	2	7	SC	SP
Brissopsis	*alta*	1441	28	22	6	22	18	B	SP
Brissopsis	*atlantica*	7928	32	8	24	8	18	B	SP
Brissopsis	*bengalensis*	6036	43	-8	51	0	18	B	SP
Brissopsis	*caparti*	5225	19	-17	36	0	18	B	SP
Brissopsis	*columbaris*	4144	21	-5	26	0	18	B	SP
Brissopsis	*elongata*	3964	26	10	16	10	18	B	SP
Brissopsis	*evanscens*	1250	-30	-39	9	30	18	B	SP
Brissopsis	*luzonica*	17861	43	-27	70	0	18	B	SP
Brissopsis	*lyrifera*	12793	69	-40	109	0	18	B	SP
Brissopsis	*mediterranea*	8750	52	-4	56	0	18	B	SP
Brissopsis	*micropetalus*	3153	22	3	19	3	18	B	SP
Brissopsis	*obliqua*	1802	18	3	15	3	18	B	SP
Brissopsis	*oldhami*	6964	17	-9	26	0	18	B	SP
Brissopsis	*pacifica*	6607	47	-4	51	0	18	B	SP
Brissopsis	*parallela*	3423	25	5	20	5	18	B	SP
Brissopsis	*persica*	1411	30	24	6	24	18	B	SP
Brissopsis	*similis*	3964	20	-10	30	0	18	B	SP
Brissopsis	*zealandiae*	804	-32	-40	8	32	18	B	SP
Brissus	*agassizii*	13373	43	-52	95	29	5	B	SP
Brissus	*gigas*	932	-33	-40	7	33	5	B	SP
Brissus	*latecarinatus*	20521	30	-26	56	0	5	B	SP
Brissus	*obesus*	4068	25	5	20	5	5	B	SP
Brissus	*unicolor*	11864	47	0	47	0	5	B	SP
Calymne	*relicta*	860	39	34	5	34	1	CA	HA
Cassidulus	*caribboearum*	3913	28	7	21	7	4	CS	CA
Cassidulus	*delectus*	4200	3	-32	35	0	4	CS	CA
Cassidulus	*infidus*	4200	3	-32	35	0	4	CS	CA
Cassidulus	*mitis*	4200	3	-32	35	0	4	CS	CA
Ceratophysa	*ceratopyga*	6279	-23	-38	15	23	1	PO	HA
Cionobrissus	*revinctus*	720	-8	-14	6	8	1	B	SP
Clypeaster	*annandalei*	10600	30	-12	42	0	35	CL	CL
Clypeaster	*australasiae*	3261	-23	-43	20	23	35	CL	CL
Clypeaster	*chesheri*	7391	25	-10	35	0	35	CL	CL
Clypeaster	*cyclopilus*	1639	25	16	9	16	35	CL	CL
Clypeaster	*durandi*	850	8	4	4	4	35	CL	CL
Clypeaster	*elongatus*	1967	7	-3	10	0	35	CL	CL
Clypeaster	*euclastus*	1639	25	16	9	16	35	CL	CL
Clypeaster	*europacificus*	5000	24	-4	28	0	35	CL	CL
Clypeaster	*eurychorius*	2400	-5	-30	25	5	35	CL	CL
Clypeaster	*eurypetalus*	2600	28	15	13	15	35	CL	CL
Clypeaster	*fervens*	13000	30	-28	58	0	35	CL	CL
Clypeaster	*humilis*	16304	30	-31	61	0	35	CL	CL
Clypeaster	*isolatus*	870	-24	-29	5	24	35	CL	CL
Clypeaster	*japonicus*	1522	42	30	12	30	35	CL	CL
Clypeaster	*lamprus*	1639	25	1	24	16	35	CL	CL

Appendix D. (continued)

GENUS	SPECIES	RANGE	NML	SML	ALR	AMLO	SPR	FMLY	ORD
Clypeaster	*latissimus*	4200	16	-6	22	0	35	CL	CL
Clypeaster	*luetkeni*	1475	22	16	6	16	35	CL	CL
Clypeaster	*lytopetalus*	2300	29	15	14	15	35	CL	CL
Clypeaster	*miniaceus*	19508	30	-28	58	11	35	CL	CL
Clypeaster	*ochrus*	4600	25	-4	29	0	35	CL	CL
Clypeaster	*oshimensis*	1639	44	31	13	31	35	CL	CL
Clypeaster	*oliveirai*	3000	1	-24	25	0	35	CL	CL
Clypeaster	*pallidus*	1475	16	10	6	10	35	CL	CL
Clypeaster	*pateriformis*	1148	-3	-10	7	3	35	CL	CL
Clypeaster	*prostratus*	3478	35	11	24	11	35	CL	CL
Clypeaster	*rangianus*	4130	24	-2	26	0	35	CL	CL
Clypeaster	*rarispinus*	12400	30	-38	68	0	35	CL	CL
Clypeaster	*ravenellii*	4800	35	7	28	7	35	CL	CL
Clypeaster	*reticulatus*	20000	30	-35	65	0	35	CL	CL
Clypeaster	*rosaceus*	3400	28	8	20	8	35	CL	CL
Clypeaster	*rotundus*	4400	25	0	25	0	35	CL	CL
Clypeaster	*speciosus*	1311	29	16	13	16	35	CL	CL
Clypeaster	*subdepressus*	7800	3	-25	28	0	35	CL	CL
Clypeaster	*telurus*	4800	-9	-34	25	9	35	CL	CL
Clypeaster	*virescens*	12131	35	-51	86	0	35	CL	CL
Conolampus	*malayana*	3800	7	-11	18	3	2	EL	CA
Conolampus	*sigsbei*	3600	2	15	13	15	2	EL	CA
Cyclaster	*recens*	1574	19	7	12	7	2	B	SP
Cyclaster	*regalis*	1157	-33	-43	10	33	2	B	SP
Cystocrepsis	*setigera*	1538	11	0	11	0	1	PO	HA
Delopatagus	*brucei*	947	-51	-57	6	51	1	AS	SP
Dendraster	*excentricus*	4694	61	22	39	22	4	D	CL
Dendraster	*laevis*	3981	37	17	20	17	4	D	CL
Dendraster	*mexicanus*	4694	61	22	39	22	4	D	CI
Dendraster	*rugosus*	816	32	27	5	27	4	D	CI
Echinarachinus	*parma*	15167	60	33	27	33	1	EA	CL
Echinocardium	*capense*	1760	-29	-38	9	29	11	L	SP
Echinocardium	*connectens*	625	17	13	4	13	11	L	SP
Echinocardium	*cordatum*	31611	72	-37	109	0	11	L	SP
Echinocardium	*fenauxi*	640	43	39	4	39	11	L	SP
Echinocardium	*flavascens*	5893	68	33	35	33	11	L	SP
Echinocardium	*keiense*	1360	-2	-10	8	2	11	L	SP
Echinocardium	*laevigaster*	1120	3	21	18	21	11	L	SP
Echinocardium	*lymani*	1600	43	30	13	30	11	L	SP
Echinocardium	*mediterraneum*	3200	46	37	9	37	11	L	SP
Echinocardium	*mortenseni*	446	43	39	4	39	11	L	SP
Echinocardium	*pennatifidum*	2080	64	48	16	48	11	L	SP
Echinocyamus	*apicatus*	1957	-29	-42	13	29	16	F	CL
Echinocyamus	*australis*	7727	14	-35	49	0	16	F	CL
Echinocyamus	*crispus*	18910	36	-27	63	0	16	F	CL
Echinocyamus	*elegans*	7391	30	-28	58	13	16	F	CL
Echinocyamus	*grandiporus*	7627	40	-14	54	0	16	F	CL
Echinocyamus	*grandis*	9576	18	1	17	1	16	F	CL

Appendix D. (continued)

GENUS	SPECIES	RANGE	NML	SML	ALR	AMLO	SPR	FMLY	ORD
Echinocyamus	*incertus*	1957	30	14	16	14	16	F	CL
Echinocyamus	*macrostomus*	5543	40	9	31	9	16	F	CL
Echinocyamus	*megapetalus*	1029	30	-3	33	0	16	F	CL
Echinocyamus	*planissimus*	6957	-10	-51	41	0	16	F	CL
Echinocyamus	*platytatus*	2797	-26	-47	21	26	16	F	CL
Echinocyamus	*polyporus*	6623	-27	-44	17	27	16	F	CL
Echinocyamus	*provectus*	3696	10	-11	21	0	16	F	CL
Echinocyamus	*pusillus*	7391	68	20	48	20	16	F	CL
Echinocyamus	*scaber*	19130	30	-35	65	0	16	F	CL
Echinocyamus	*sollers*	1413	15	3	12	3	16	F	CL
Echinodiscus	*auritis*	14821	42	-38	80	0	3	A	CL
Echinodiscus	*bisperforatus*	15714	42	-37	79	0	3	A	CL
Echinodiscus	*tenuissimus*	11250	35	-24	59	0	3	A	CL
Echinolampas	*alexandri*	21087	30	-24	54	0	7	EL	CA
Echinolampas	*crassa*	1630	-30	-39	9	30	7	EL	CA
Echinolampas	*depressa*	3913	28	7	21	7	7	EL	CA
Echinolampas	*keiensis*	2609	7	-13	20	0	7	EL	CA
Echinolampas	*oviformis*	11522	30	-24	54	0	7	EL	CA
Echinolampas	*rangii*	978	19	12	7	12	7	EL	CA
Echinolampas	*sternopetala*	1739	44	29	15	29	7	EL	CA
Echinoneus	*abnormalis*	21515	30	-30	60	0	2	E	HE
Echinoneus	*cyclostomus*	35015	49	-34	83	0	2	E	HE
Echinosigra	*paradoxa*	879	-59	-66	7	59	2	PO	HA
Echinosigra	*phiale*	10166	-59	-69	10	59	2	PO	HA
Elipneustes	*denudatus*	900	8	3	5	3	2	AS	SP
Elipneustes	*rubens*	1000	13	5	8	5	2	AS	SP
Encope	*aberrans*	2857	38	20	18	20	15	M	CL
Encope	*arcensis*	1714	43	32	11	32	15	M	CL
Encope	*cocosi*	857	6	-1	7	0	15	M	CL
Encope	*ecuadorensis*	857	1	-7	8	0	15	M	CL
Encope	*emarginata*	8000	20	-38	58	0	15	M	CL
Encope	*fragilis*	3333	30	10	20	10	15	M	CL
Encope	*grandis*	1238	29	19	10	19	15	M	CL
Encope	*insularis*	1048	13	7	6	7	15	M	CL
Encope	*irregularis*	1524	10	0	10	0	15	M	CL
Encope	*laevis*	1048	13	7	6	7	15	M	CL
Encope	*michelini*	3619	39	20	19	20	15	M	CL
Encope	*micropora*	5714	31	-11	42	0	15	M	CL
Encope	*perspectiva*	5524	38	5	33	5	15	M	CL
Encope	*stokesii*	5905	28	-11	39	0	15	M	CL
Encope	*wetmori*	5524	34	3	31	3	15	M	CL
Eupatagus	*dyscritus*	926	-40	-46	6	40	8	B	SP
Eupatagus	*lymani*	2222	28	14	14	14	8	B	SP
Eupatagus	*magnus*	5741	43	-6	49	0	8	B	SP
Eupatagus	*micropetalus*	1296	40	30	10	30	8	B	SP
Eupatagus	*obscurus*	2222	28	14	14	14	8	B	SP
Eupatagus	*rubellus*	2222	20	4	16	4	8	B	SP
Eupatagus	*valdiviae*	2407	11	-10	21	0	8	B	SP

Appendix D. (continued)

GENUS	SPECIES	RANGE	NML	SML	ALR	AMLO	SPR	FMLY	ORD
Eupatagus	*valenciennesi*	2222	-26	-42	16	26	8	B	SP
Faorina	*chinensis*	5647	25	-13	38	0	2	SC	SP
Faorina	*kawaguchii*	706	-17	-23	6	17	2	SC	SP
Fibularia	*acuta*	6667	44	-10	54	0	8	F	CL
Fibularia	*angulipora*	3600	15	3	12	3	8	F	CL
Fibularia	*cribellum*	9333	23	-14	37	0	8	F	CL
Fibularia	*nutriens*	5067	0	-44	44	30	8	F	CL
Fibularia	*oblonga*	9600	18	-41	59	0	8	F	CL
Fibularia	*ovulum*	17867	30	-28	58	0	8	F	CL
Fibularia	*plateia*	2133	-32	-40	8	32	8	F	CL
Fibularia	*volva*	16267	30	-20	50	0	8	F	CL
Genicopatagus	*affinis*	1968	-54	-58	4	54	1	AS	SP
Granobrissoides	*hirsutus*	2588	-10	-42	32	10	1	B	SP
Helgocystis	*carinata*	8970	-35	-75	40	35	1	PO	HA
Hemiaster	*clarki*	1389	42	30	12	30	5	H	SP
Hemiaster	*expergitis*	25278	67	-52	119	0	5	H	SP
Hemiaster	*hickmani*	2315	26	16	10	16	5	H	SP
Hemiaster	*tenuis*	2278	0	-20	20	0	5	H	SP
Hemiaster	*vanus*	1852	25	11	14	11	5	H	SP
Hemimaretia	*elavata*	2857	-2	-24	22	2	1	S	SP
Heterobrissus	*hemingi*	1400	21	8	13	8	3	AS	SP
Heterobrissus	*hystrix*	4400	28	9	19	9	3	AS	SP
Heterobrissus	*niasicus*	3200	8	-11	19	0	3	AS	SP
Homolampas	*fragilis*	2952	27	5	22	5	6	L	SP
Homolampas	*fulva*	4762	16	-16	32	0	6	L	SP
Homolampas	*glauca*	1905	27	14	13	14	6	L	SP
Homolampas	*hastata*	1333	7	2	5	2	6	L	SP
Homolampas	*lovenoides*	3619	21	-8	29	0	6	L	SP
Homolampas	*rostrata*	1238	-7	-11	4	7	6	L	SP
Idiobrissus	*sp*	833	3	-3	6	0	1	B	SP
Isopatagus	*obovatus*	3524	24	3	21	3	1	T	SP
Laganum	*boninense*	816	30	25	5	25	7	LA	CL
Laganum	*decagonale*	8571	23	-19	42	0	7	LA	CL
Laganum	*depressum*	17143	30	-25	55	0	7	LA	CL
Laganum	*fudsiyama*	10590	43	-23	66	0	7	LA	CL
Laganum	*joubini*	7143	30	-27	57	0	7	LA	CL
Laganum	*laganum*	10000	24	-45	69	0	7	LA	CL
Laganum	*retinens*	9694	25	-33	58	0	7	LA	CL
Leodia	*sexiesperforata*	8800	35	-37	72	0	1	M	CL
Linopneustes	*brachypetalus*	4909	0	-41	41	0	6	AS	SP
Linopneustes	*excentricus*	818	-4	-9	5	4	6	AS	SP
Linopneustes	*fragilis*	6182	44	-9	53	0	6	AS	SP
Linopneustes	*longispinus*	2000	26	11	15	11	6	AS	SP
Linopneustes	*murrayi*	6000	40	-11	51	0	6	AS	SP
Linopneustes	*spectabilis*	7273	21	-6	27	0	6	AS	SP
Lovenia	*camarota*	1667	-9	-17	8	9	9	L	SP
Lovenia	*cordiformis*	10000	31	-5	36	0	9	L	SP
Lovenia	*doderleini*	4833	22	-12	34	0	9	L	SP

Appendix D. (continued)

GENUS	SPECIES	RANGE	NML	SML	ALR	AMLO	SPR	FMLY	ORD
Lovenia	*elongata*	16800	36	-35	71	0	9	L	SP
Lovenia	*gregalis*	6167	43	-9	52	0	9	L	SP
Lovenia	*grisea*	2000	28	17	11	17	9	L	SP
Lovenia	*hawaiienesis*	2100	28	16	12	16	9	L	SP
Lovenia	*subcarinata*	11810	25	-25	50	0	9	L	SP
Lovenia	*triforis*	6400	39	-11	50	0	9	L	SP
Maretia	*carinata*	11810	19	-26	45	0	5	S	SP
Maretia	*cordata*	4000	21	-11	32	0	5	S	SP
Maretia	*parvituberculata*	3810	-20	-33	13	20	5	S	SP
Maretia	*planulata*	17905	43	-40	83	0	5	S	SP
Maretia	*tuberculata*	1333	41	33	8	33	5	S	SP
Mellita	*eduardobarrosi*	900	16	10	6	10	7	M	CL
Mellita	*grantii*	1800	-5	-15	10	5	7	M	CL
Mellita	*longifissa*	3800	23	4	19	4	7	M	CL
Mellita	*notabilis*	800	14	7	7	7	7	M	CL
Mellita	*pacifica*	2400	0	-19	19	0	7	M	CL
Mellita	*platensis*	2000	-37	-55	18	37	7	M	CL
Mellita	*quinquiesperforata*	8600	-42	-24	18	0	7	M	CL
Meoma	*cadenati*	2000	15	2	13	2	4	B	SP
Meoma	*frangibilis*	800	8	3	5	3	4	B	SP
Meoma	*grandis*	5800	26	-17	43	0	4	B	SP
Meoma	*ventricosa*	4500	28	10	18	10	4	B	SP
Metalia	*dicrana*	15556	23	-25	48	0	7	B	SP
Metalia	*latissima*	1667	18	5	13	5	7	B	SP
Metalia	*noblis*	5636	36	4	32	4	7	B	SP
Metalia	*robillardi*	3889	-10	-28	18	10	7	B	SP
Metalia	*spatangus*	23519	43	-25	68	0	7	B	SP
Metalia	*sternalis*	24273	43	-43	86	0	7	B	SP
Metalia	*townsendi*	1818	31	22	9	22	7	B	SP
Micropetalon	*purpureum*	10682	28	13	15	13	1	E	HE
Moira	*atropos*	5444	35	5	30	5	5	SC	SP
Moira	*clotho*	4667	25	-6	31	0	5	SC	SP
Moira	*lachesis*	1556	42	30	12	30	5	SC	SP
Moira	*lethe*	4667	-11	-43	32	11	5	SC	SP
Moira	*stygia*	10333	30	-22	52	0	5	SC	SP
Nacospatangus	*alta*	11650	43	-24	67	0	7	S	SP
Nacospatangus	*depressus*	1845	35	20	15	20	7	S	SP
Nacospatangus	*gracilis*	728	-32	-36	4	32	7	S	SP
Nacospatangus	*interrupta*	1553	-14	-20	6	14	7	S	SP
Nacospatangus	*leavis*	3689	29	12	17	12	7	S	SP
Nacospatangus	*oblonga*	874	4	-2	6	0	7	S	SP
Nacospatangus	*tylotus*	3883	21	-10	31	0	7	S	SP
Nannolampas	*tenera*	1667	-5	-12	7	5	1	N	NE
Neolampas	*rostellata*	8250	48	14	34	14	1	N	NE
Palaeobrissus	*hilgardi*	3265	29	10	19	10	1	AS	SP
Palaeostoma	*mirabile*	11636	30	-11	41	0	1	PA	SP
Palaeotrema	*loveni*	4737	43	4	39	4	2	AS	SP
Palaeotrema	*ovatum*	6947	24	-9	33	3	2	AS	SP

Appendix D. (continued)

GENUS	SPECIES	RANGE	NML	SML	ALR	AMLO	SPR	FMLY	ORD
Palaeotropus	*josephinae*	3200	48	35	13	35	1	AS	SP
Palaeopneustes	*cristatus*	4421	30	12	18	12	2	AS	SP
Palaeopneustes	*tholoformis*	4421	30	12	18	12	2	AS	SP
Paramaretia	*multituberculata*	1724	-23	-40	17	23	2	S	SP
Paramaretia	*peloria*	1333	-37	-42	5	37	2	S	SP
Paraster	*compactus*	7407	-10	-27	17	10	6	SC	SP
Paraster	*doderleini*	926	20	6	14	6	6	SC	SP
Paraster	*erythraeus*	556	20	10	10	10	6	SC	SP
Paraster	*floridiensis*	1852	28	8	20	8	6	SC	SP
Paraster	*gibberulus*	7037	28	-25	53	0	6	SC	SP
Paraster	*rotundatus*	648	3	-2	5	0	6	SC	SP
Pericosmus	*abatoides*	7619	-1	-34	33	1	11	PE	SP
Pericosmus	*akabanus*	2391	30	13	17	13	11	PE	SP
Pericosmus	*bidens*	1238	-11	20	31	11	11	PE	SP
Pericosmus	*cordatus*	1714	43	30	13	30	11	PE	SP
Pericosmus	*keiensis*	1905	-4	-12	8	4	11	PE	SP
Pericosmus	*macronesius*	5714	17	-21	38	6	11	PE	SP
Pericosmus	*mauritianus*	1238	-11	20	31	11	11	PE	SP
Pericosmus	*melanostomus*	4762	33	-10	43	0	11	PE	SP
Pericosmus	*oblongus*	1905	-4	-12	8	4	11	PE	SP
Pericosmus	*porphyrocardius*	6476	33	-20	53	0	11	PE	SP
Pericosmus	*tenuis*	1238	-11	20	31	11	11	PE	SP
Peripatagus	*cinctus*	895	43	35	8	35	1	AS	SP
Peronella	*analis*	2609	7	-11	18	0	13	LA	CL
Peronella	*hinemoae*	3478	-26	-48	22	26	13	LA	CL
Peronella	*japonica*	1196	38	29	9	29	13	LA	CL
Peronella	*keiensis*	1413	-3	-11	8	3	13	LA	CL
Peronella	*lesueri*	13478	30	-40	70	0	13	LA	CL
Peronella	*macroproctes*	8478	24	-13	37	0	13	LA	CL
Peronella	*minuta*	3152	24	3	21	3	13	LA	CL
Peronella	*oblonga*	1957	18	4	14	4	13	LA	CL
Peronella	*orbicularis*	13478	30	-40	70	0	13	LA	CL
Peronella	*pellucida*	6304	41	-10	51	0	13	LA	CL
Peronella	*peronii*	4239	-10	-45	35	10	13	LA	CL
Peronella	*rubra*	6087	41	-12	53	0	13	LA	CL
Peronella	*tuberculata*	2283	-13	-27	14	13	13	LA	CL
Pilematechinus	*vesica*	1183	-40	-50	10	40	1	U	HA
Plagiobrissus	*africanus*	2913	10	0	10	0	6	B	SP
Plagiobrissus	*costae*	7767	45	-18	63	0	6	B	SP
Plagiobrissus	*grandis*	8738	30	-12	42	0	6	B	SP
Plagiobrissus	*jullieni*	1748	4	-1	5	0	6	B	SP
Plagiobrissus	*pacificus*	4466	23	-3	26	0	6	B	SP
Plagiobrissus	*sp*	1845	-5	-12	7	5	6	B	SP
Platybrissus	*ellipticus*	882	-2	-8	6	2	4	AS	SP
Platybrissus	*grandiporus*	2353	15	5	10	5	4	AS	SP
Platybrissus	*ovalis*	2549	22	4	18	4	4	AS	SP
Platybrissus	*roemeri*	1373	3	9	6	0	4	AS	SP
Plesiozonus	*diomedeae*	3500	22	3	19	3	2	AS	SP

Appendix D. (continued)

GENUS	SPECIES	RANGE	NML	SML	ALR	AMLO	SPR	FMLY	ORD
Plesiozonus	*hirsutus*	1400	-5	-8	3	5	2	AS	SP
Plethotaenia	*angularus*	3265	29	10	19	10	2	B	SP
Plethotaenia	*spatangoides*	4082	39	13	26	13	2	B	SP
Plexechinus	*hirsutus*	10000	73	8	65	8	2	U	HA
Plexechinus	*nordenskjoldi*	4878	-58	-82	24	58	2	U	HA
Porterpygus	*kieri*	2400	-32	-51	19	32	1	AP	CA
Pourtalesia	*alcocki*	8000	27	-39	66	23	8	PO	HA
Pourtalesia	*aurorae*	9269	-60	-84	24	60	8	PO	HA
Pourtalesia	*debilis*	1794	-44	-50	6	-44	8	PO	HA
Pourtalesia	*hispida*	11063	-57	-78	21	57	8	PO	HA
Pourtalesia	*jeffreysi*	3619	86	60	26	60	8	PO	HA
Pourtalesia	*laguncula*	6667	46	-10	56	0	8	PO	HA
Pourtalesia	*miranda*	12190	70	-20	90	0	8	PO	HA
Pourtalesia	*tanneri*	9333	27	-38	65	0	8	PO	HA
Proraster	*affinis*	3889	21	-10	31	0	7	SC	SP
Proraster	*brachypetalus*	4444	29	7	22	7	7	SC	SP
Proraster	*jukesi*	4074	-9	-28	19	9	7	SC	SP
Proraster	*kempi*	3333	25	-1	26	0	7	SC	SP
Proraster	*limicolus*	2037	27	17	10	17	7	SC	SP
Proraster	*maximus*	1713	27	17	10	17	7	SC	SP
Proraster	*rotundus*	1296	43	31	12	31	7	SC	SP
Protenaster	*australis*	4694	-25	-27	2	25	2	SC	SP
Protenaster	*rostratus*	5102	6	-24	30	0	2	SC	SP
Pseudolovenia	*hirsuta*	2080	28	16	12	16	1	L	SP
Pycnolampas	*oviformis*	2400	29	15	14	15	1	AS	SP
Rhyncholampas	*pacificus*	4783	29	-3	32	0	1	CS	CA
Rhynobrissus	*hemiasteroides*	11650	28	-40	68	0	6	B	SP
Rhynobrissus	*macropetalus*	1845	-11.5	-22	10.5	11.5	6	B	SP
Rhynobrissus	*micrasteroides*	1942	33	20	13	20	6	B	SP
Rhynobrissus	*placopetalus*	2136	28	15	13	15	6	B	SP
Rhynobrissus	*pyramidalis*	6117	20	-10	30	0	6	B	SP
Rhynobrissus	*tumulus*	1748	-10	-17	7	10	6	B	SP
Rotula	*augusti*	4660	11	-18	29	0	2	R	CL
Rotula	*orbiculus*	5825	17	-20	37	0	2	R	CL
Sarsiaster	*greigii*	4762	45	12	33	12	1	H	SP
Saviniaster	*enodatus*	1412	26	20	6	20	1	SC	SP
Scaphechinus	*griseus*	2000	58	44	14	44	2	D	CL
Scaphechinus	*mirabelis*	7167	-28	-61	33	28	2	D	CL
Schizaster	*angularis*	3000	25	13	12	13	10	SC	SP
Schizaster	*barbatus*	1647	-11	-24	13	11	10	SC	SP
Schizaster	*canaliferus*	3100	47	31	16	31	10	SC	SP
Schizaster	*edwardsi*	2100	5	-10	15	0	10	SC	SP
Schizaster	*investigatoris*	5700	25	-20	45	13	10	SC	SP
Schizaster	*lacunosus*	12200	43	-32	75	0	10	SC	SP
Schizaster	*myorensis*	2471	-30	-40	10	10	10	SC	SP
Schizaster	*orbignyanus*	4000	38	8	30	8	10	SC	SP
Schizaster	*portjacksonensis*	2471	-30	-40	10	10	10	SC	SP
Schizaster	*savignyi*	7059	30	-28	58	5	10	SC	SP

Appendix D. (continued)

GENUS	SPECIES	RANGE	NML	SML	ALR	AMLO	SPR	FMLY	ORD
Scrippsechinus	*fisheri*	3265	-27	-55	28	27	1	AS	SP
Spatagobrissus	*mirabilis*	1920	-27	-37	10	27	1	B	SP
Spatagocystis	*challengeri*	3588	-50	-54	4	50	1	PO	HA
Spatangus	*altus*	1818	24	7	17	7	13	S	SP
Spatangus	*beryl*	2182	-33	-51	18	33	13	S	SP
Spatangus	*californicus*	2364	35	18	17	18	13	S	SP
Spatangus	*capensis*	1818	-30	-42	12	30	13	S	SP
Spatangus	*diomedreae*	2091	22	6	16	6	13	S	SP
Spatangus	*inermis*	455	43	38	5	38	13	S	SP
Spatangus	*lutkeni*	1545	44	30	14	30	13	S	SP
Spatangus	*mulitspinus*	2218	-33	-51	18	33	13	S	SP
Spatangus	*pallidus*	1455	43	30	13	30	13	S	SP
Spatangus	*paucituberculatus*	12364	46	-14	60	0	13	S	SP
Spatangus	*purpureus*	7727	70	0	70	2	13	S	SP
Spatangus	*raschi*	2909	69	44	25	44	13	S	SP
Spatangus	*thor*	2182	34	-51	85	34	13	S	SP
Stereopneustes	*relictus*	8387	44	-14	58	0	1	PO	HA
Sternopatagus	*sinensis*	1720	18	4	14	4	1	ST	HA
Studeria	*recens*	2391	-10	-14	4	10	1	PL	CA
Tripylaster	*philippi*	2833	-35	-61	26	35	1	SC	SP
Tripylus	*abatoides*	3321	-68	-75	7	68	4	SC	SP
Tripylus	*cordatus*	3813	-55	-72	17	55	4	SC	SP
Tripylus	*excavatus*	4428	-37	-50	13	37	4	SC	SP
Tripylus	*reductus*	984	-47	-52	5	47	4	SC	SP
Tropholampas	*loveni*	1667	-32	-39	7	32	1	N	NE
Urechinus	*giganteus*	2151	31	18	13	18	5	U	HA
Urechinus	*loveni*	15909	60	9	51	9	5	U	HA
Urechinus	*naresianus*	16774	70	-82	152	0	5	U	HA
Urechinus	*reticulatus*	2151	31	18	13	18	5	U	HA
Urechinus	*wyvillii*	6969	-37	-72	35	37	5	U	HA

Appendix E. Abbreviations for Modern Data

Orders (ORD)

1. Ca Cassiduloida
2. Cl Clypeasteroida
3. Ha Holasteroida
4. He Holectypoida
5. Ne Neolampadoida
6. Sp Spatangoida

Families (FMLY)

1. A Astriclypeidae
2. Ae Aeropsidae
3. Ap Apatopygidae
4. Ar Arachnoididae
5. As Asterostomatidae
6. B Brissidae
7. Ca Calymnidae
8. Cl Clypeasteridae
9. Cs Cassidulidae
10. D Dendrastidae
11. E Echinoneidae
12. Ea Echinarachiidae
13. El Echinolampadidae
14. F Fibularidae
15. H Hemiasterodae
16. L Loveniidae
17. La Laganidae
18. M Mellitidae
19. N Neolampadidae
20. Pa Paleostomatidae
21. Pe Pericosmidae
22. Pl Pliolampadidae
23. Po Pourtalesiidae
24. R Rotulidae
25. S Spatangidae
26. Sc Schizasteridae
27. St Sternopatagus
28. T Toxasteridae
29. U Urechinidae

VITA

Stacy Yvette Butler was born in east Tennessee on February 10, 1965. She attended Newport Grammar School where she developed an interest in both basketball and science. At Cocke County High School in Newport she earned the Science Award and Foreign Language Award from the faculty. She was selected "Most Likely to Succeed" by her classmates. Stacy graduated third in a class of 263.

After high school Stacy enrolled in the School of Radiologic Technology at the University of Tennessee Memorial Research Center and Hospital in Knoxville. She would work as a registered Radiologic Technologist for the next ten years. During this time she entered the University of Tennessee at Knoxville and graduated with a Bachelors in Science (1994) in geology and a Masters in Science (1997) also in geology. Stacy enrolled in the graduate program at the University of Georgia at Athens where she in currently seeking a Doctor of Philosophy degree.

Stacy has been married for seven years to Charles "Skip" Howard. They are the proud parents of a golden retriever, a cocker spaniel, nine cats, and an assortment of fish.