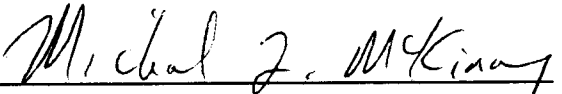
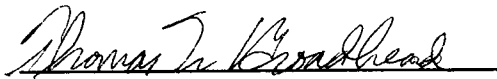
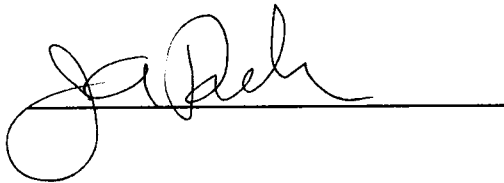


To the Graduate Council:

I am submitting herewith a thesis written by W. Gray Dean entitled "Evolutionary Flux in Fossil Echinoids: New Metrics for Old Dogmas." 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 Geology.


Dr. Michael L. McKinney, Major Professor





Accepted for the Council:


Associate Vice Chancellor
and Dean of the Graduate School

Evolutionary Flux in Fossil Echinoids: New Metrics for Old Dogmas

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

**W. Gray Dean
August 1997**

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ABSTRACT

The process and patterns of extinction is a fundamental aspect of evolution and concerns researchers in a multitude of disciplines, from ecology and biology to geology and paleontology. Recent interest has been heightened by the apparent dramatic increase in extinction rates, related, perhaps, to increased anthropogenic activities, which can threaten and destroy habitats of other organisms. While modern ecological study provides detailed insights of interaction between biota, only the rock record contains evidence of evolution on this planet.

Paleontological studies reveal that 95 - 99 % of all species to have ever existed are now extinct. However, extinction is not the sole descriptor of evolution; there is a positive correlation between new originations and extinction. Unfortunately, the fossil record is incomplete and subsequently many biases blur interpretations of evolutionary data. Taphonomic differentials, missing strata, and uncertainty in age-dating all contribute to variations in data sizes and magnify sampling error. Corrections for sample size differences, such as rarefaction, may complicate results further, by inducing mathematical artifacts and assuming random distribution; probability and statistics also assume random response to environmental gradients. This genera to order study of a Cenozoic echinoid database, utilized several approaches to analyze extinction and determine selectivity of some groups over others. Statistical methods yield results biased by sample size, and thus, ultimately by taphonomic constraints. A normalized variance approach was aslo used to reduce sample size artifacts, but it was determined that extinction alone is not

sufficient to understand biotic dynamics. The parameters of New Originations (N) and Stable Genera (S) are considered with Extinctions (E) and Genera Present (G), resulting in a new metric, termed Flux:

$$\text{Flux} = \frac{G - E + N + S}{S + G [(E+1)/(N+1)]}$$

This unit of measure is based upon mass balance, and is the first to consider these four parameters as co-functioning terms. Sample sizes are normalized to reduce sampling error and taphonomic biases are also diminished deriving all four terms from the same dataset. Results of Flux analysis seem to follow wave-form shapes and are consistent with a growing body of evidence indicating periodicity in the fossil record. Additionally, this methodology confirms that high extinction rates are not necessarily bad, since speciation is shown to be so closely linked to extinction. Results of this study show that selectivity is present, mainly as a taphonomic differential. Additionally, the individual trends of each order seem to indicate that response to forcing functions is not random. Variations between flux of similar groups may shed light on phenomena such as competition and predation, with the potential of wave modeling applicable to future study.

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INTRODUCTION

All species and genera will become extinct - it is the ultimate fate for all biotic groups. In fact, 95 % or more of all species that ever existed are extinct (Raup, 1994). This is not to imply that extinction alone is necessarily bad; indeed, it is an integral component of evolution (Raup, 1996; McGhee, 1996; Stanley, 1990). The fossil record indicates a long history of fluctuations in the rise and fall and the presence and/or abundance of various taxa, with some periods experiencing low turnover rates capped by subsequent peaks in taxa decline. However, these fluctuations are not consistent within the same taxon or between different taxa, and, the nature, intensity, and duration of extinction events appears to vary over time (Sepkoski, 1991). Low extinction rates are generally considered as "background" extinction, with high extinction rates being considered as "mass" extinction (Jablonski, 1995).

Recent calculations indicate that, in less than a millennium, extinction rates have increased by several orders of magnitude over normal background extinction (Pimm *et al.*, 1995). Ecologists concerned with this apparent increasing decline in species richness are seeking ways to protect threatened taxa. Therefore, understanding the dynamics of extinction is paramount to the implementation of strategies designed to maintain present biodiversity levels. Unfortunately for those studying extant taxa, the "human-window" of time is limited and only provides a glimpse of biotic behavior. However, over larger timescales, origination and extinction can be observed from fossil preservation in the rock record. While the use of paleontology for evolutionary studies is not new, only relatively

recently have interpretations of extinction derived from fossil evidence been applied to the present biodiversity crisis (Raup, 1991, 1994; Jablonski, 1995; McKinney *in press*).

Background

The rock record is far from complete (Paul, 1989). Paleontologists and evolutionary biologists are faced with a spartan data set, with absent or undescribed specimens, or conversely, with an over-representation of some taxa with respect to others (Raup, 1991a). Many biases exist, from actual abundance and rarity (McKinney, *et al.*, 1996, Sepkoski, 1994), to taphonomic considerations (Kidwell and Brenchley, 1996) and missing strata (Sepkoski, 1994), as well as taxonomic and morphologic biases contributing to "pseudoextinction" (Sepkoski, 1995; Gilinsky and Good, 1991; Paul, 1989). All of these effects can blur the results derived from reducing the fossil record to an input of numbers for analysis, causing even the use of paleontologic databases in evolutionary studies to incite some debate (Ager, 1988; Sepkoski, 1995).

Attempts to eliminate or reduce the artifacts of the fossil record have been met with varying success, usually contingent upon the assumptions made, which often center about some aspect of randomness (Sepkoski, 1994). The problem may lie with the paucity of adequate, much less consistent, extinction and speciation metrics (Jablonski, 1995; Sepkoski and Koch, 1995; Foote, 1994; McGhee, 1989, 1996). However, the apparent dearth of effective descriptive quantification has not impeded the rigorous statistical testing of evolutionary trends, which usually only examines speciation or extinction, rather than both, even though numerous studies have shown these to be highly correlated (Jackson *et al.*, 1996; Foote, 1994; Gilinsky, 1994; Sepkoski, 1994). Thus, it

has been duly noted that caution should be exercised when examining only one parameter of evolution, such as extinction rates or magnitudes (McGhee, 1989), as well as when making cross-taxa, or spatio-temporal comparisons (Jablonski, 1995).

Sampling biases. When employing statistical approaches to resolve questions of speciation and extinction, variation in taxa abundance can influence the results and contribute to sampling error. Quantifying and decreasing these effects is imperative in deciphering the rock record, and obtaining a valid model of the dynamics of life over geologic timescales. Sampling error has been recognized for some time, and is of concern to evolutionary paleontologists who must interpret an incomplete database (Flessa and Kidwell, 1995; Raup, 1991; Koch, 1991). Various statistical techniques exist which attempt to minimize errors introduced as an artifact of sampling (Koch, 1991). Rarefaction analysis, a useful tool when relative abundance is known, essentially reduces all sample sizes to the smallest known sample (Simberloff, 1974), within any data set. More fossils are available with increased sedimentary packages (Raup, 1976), and a higher variation of sample types is also likely to be found (Sepkoski, 1994). However, a major assumption made when shrinking all samples to the smallest size is that speciation and extinction are random; that the sample sizes differ only due to sampling errors and that all data sets can be equally compressed. Though unintentional, the data may be altered when performing such operations (McKinney, 1995); we simply do not know how to account for taxa we have not yet encountered.

Mathematical Biases. Use of linear math to describe system dynamics allows a predicted suite of potential outcomes (Paul, 1989). Traditional computation of extinction

metrics generally employs linear math for statistical analysis. Statistics and probability center upon random assumptions (Sepkoski, 1994), and more importantly, when applied in a paleontological context, may ignore physical laws, and imply that systems are not responding to forcing functions. Additionally, mathematical biases become more complex when other biases, such as those from sampling (see above), or those from metrics (see below) are present. It has been recognized that non-linear dynamics may be a more descriptive option, however, non-linear dynamics have also been shown to produce patterns that appear to be periodic (Paul, 1989).

Quantification Biases. A complete metric for quantifying evolutionary dynamics is lacking (Foote, 1994). Furthermore, most paleoecologic research quantifies the health of taxa in strict terms of “extinction” or “extinction rates”, monitoring the number of extinct per number present in a given timespan (McGhee, 1996, 1989; Foote, 1994; Gilinsky, 1991). Models based solely on extinction fail to consider the effect of speciation and taxa stability upon a biotic system. The apparent positive correlation between new originations and extinction has been intensively documented (see above), however most systems of measurement do not take this into account (Parker and Arnold, 1997; McGhee, 1996, 1989; Foote, 1994). Instead, observations of extinction data alone pervade the literature, though some studies of diversity (Sepkoski and Koch, 1995), taxa survivorship (Parker and Arnold, 1997), and system volatility (Gilinsky, 1994) do relate other components intrinsic to understanding the dynamics of evolution.

Chronostratigraphic Biases. Compounding the problem of quantification is the tendency to express extinction data in terms of time. Time normalized extinction metrics

introduce error that was intended to be alleviated (Foote, 1994). By dividing the derived metrics by interval length, one automatically assumes that the rates are constant throughout the interval in question (Gilinsky, 1991). The assumption of constant rate during a time interval should not be valid, plus, there is much uncertainty regarding the actual length of some intervals (Sepkoski and Koch, 1995; Foote, 1994; Prothero, 1994). These problems, too, add to the mathematical biases as discussed above.

Taxonomic Biases. Lack of taxonomic control has led some to question the validity of database analysis for evolutionary studies (Ager, 1988). Though this is of concern, it has been demonstrated that grouping schemes, even if arbitrary, exhibit trends which may be extended across taxa (Sepkoski, 1994, 1992). A more serious problem is the appearance of "pseudoextinctions" (Sepkoski, 1995; Gilinsky and Good, 1991; Paul, 1989) where the last appearance of a taxon is listed as extinct. This may only reflect phyletic speciation, where a taxon simply evolves into a distinct new morphology. The scant rock record would indicate the loss of the former taxa as extinction even though the lineage actually continues to survive. The effects of pseudoextinction are not fully recognized (Sepkoski, 1995), however, it would seem this bias would be enhanced when extinction is considered as the sole parameter for describing evolution. Taxa rarity is also cited as an area of concern, with apparent underrepresentation of rarer taxa (McKinney *et al.*, 1996; Sepkoski, 1994). Other taxonomic biases include nonrandom collection of fossils. A major premise of paleontology is that fossil specimens are randomly collected, though recent research indicates this may not be true (Sepkoski, 1994).

While much effort has been centered upon identifying potential biases in the rock record, randomness (nonpredictability) is usually assumed as a mathematical necessity and to minimize artifacts (Sepkoski, 1994). Though not addressed specifically, the mode of inquiry; i.e. types of stratigraphic or taxonomic resolution desired, metrics used, etc., can affect the certainty of data retrieved, in some cases introducing error that renders the results almost useless (Sepkoski and Koch, 1995; Koch, 1991). Therefore, it is imperative that adequate metrics first be applied to resolve the dilemma of biases (Foote, 1994; Gilinsky and Good, 1991; Paul, 1989). Further, the viability of random assumptions used in modeling must also be considered (Sepkoski, 1994). For instance, rarefaction, as utilized, also assumes a constant sedimentation rate when comparing sample sizes between and within stratigraphic layers (Raup, 1975). Many other random models also exist (Raup, 1996; Signor, 1991), but it is not the intent of this paper to critique the use of these techniques, but rather, to test the validity of the assumption made for random extinction in these models and derive new methods to estimate echinoid stability and diversity patterns.

Previous Work

Much current paleoecologic research is centered upon determining extinction selectivity patterns of particular taxa. Phylogenetically shared traits could make some groups more likely to suffer extinction than others (Sepkoski 1990; Raup, 1994; McKinney, 1995). Since phylogenetic branching during evolution is nested within clades, then it follows that morphologic, life mode, and other factors which influence extinction will also be nested (Gaston, 1994). It has been observed that this selectivity

occurs at many scales of resolution throughout the taxonomic hierarchy, because extinction-susceptible traits are nonrandomly distributed among groups at all scales. Selectivity at coarser taxonomic levels has been well-documented (Stanley, 1990). However, selectivity at the finer scales of resolution is poorly known. This has been cited as a main area for future paleontological research (Raup, 1994; McKinney, 1995). Many of the fine-scale selectivity studies analyze the effect of species richness upon genus extinctions (Jablonski, 1995). For example, Jablonski (1986) showed that high species richness promoted genus survival except during times of mass extinctions, while yet other research has alluded to species- or genus- rarity as an extinction susceptible trait (McKinney, 1997).

Most research, however, attempts to quantify diversity trends in terms of extinction alone (McGhee, 1996, 1989), or by subtracting the number of extinct taxa from the number of new originations in a particular timespan, and examining diversification (Foote, 1994; Gilinsky, 1991; Sepkoski, 1991; Koch, 1991). Both types of models measure important parameters of taxa dynamics, but assume randomness for predicted outcomes. Population growth models have also been incorporated (Sepkoski, 1991), but these can only measure extinction as a divergence from expected growth, and do not allow extinction as a component for evolution. Taxonomic survivorship curves have been developed as well, (Parker and Arnold, 1997), but these only estimate the probability of taxon success through time, doing little to describe the processes which influence survivability or extinction.

Both survivorship curves and population growth models use population dynamics to describe taxonomic dynamics, which may not be a fair assumption. Geologic timescales are vastly larger than population timescales, and indeed, the forcing functions between these spatial and temporal scales are probably different as well. Exponential growth or logistic decay (Sepkoski, 1991) may not be the appropriate solutions. Other methods, some simplistic, only examine extinction and new originations within a single time period (McGhee, 1996), which fails to consider the impact of stable taxa upon the system (Gilinsky and Good, 1994) and only examines dynamics in discrete time intervals.

Additionally, the use of traditional probability and statistics in determining extinction may not be valid (Sepkoski, 1994) and the expressed extinction rates may be very misleading (Raup, 1991; Koch, 1991; McGhee, 1996). Sample size variations affect such ratios, because larger sets translate into a larger denominator in such ratios, which inflates the perceived probability of extinction. For example, a value of .5 is realized from an extinct/present ratio of 1/2 or 2/4, 3/6 ... which disregards the variations in the number of survivors in each instance. Other ratios, like 1/2, 3/4, 5/6,... have increasing extinction probabilities, yet an equal number of survivors. The mathematical biases inherent when comparing data sets of varying size have been acknowledged for quite some time, and are compounded by the observation that most taxa do become extinct, some much faster than the timescales studied. Rarefaction and reverse rarefaction methods along with other procedures, have been used to make the size of the data packages equal, so that quantitative comparisons across taxa may be realized.

This has important implications for deriving estimates of past extinction, speciation and stability and may require that future models incorporate any intra-class differentials of evolution. Methods that assume randomness between groups do not yield any insight toward understanding the differences between the biotic groups which may make them extinction-susceptible. The random walk, or random coin toss (Signor, 1991) may not be an appropriate model for understanding the complex nature of evolution (Sepkoski, 1994). Even in a coin toss scenario, there is error, which is defined as falling within statistical confidence, because it is slight. Variables operating upon the coin, such as air current and density; initial coin velocity; intensity and duration of the launching force, as well as the internal balance of the coin, all determine the outcome (Koch, 1991). These factors affect the flipping coin, because, the coin toss does not operate within a vacuum, and neither do taxa. Systems respond to external forces and exhibit "system inertia", with a reaction for every action imposed upon them.

In a random walk, we are given a set of choices or pathways of movement. The choices presented in a random walk are determined, in part, by those on the walk, not by the observer. And others concur that a true random walk is "unrealistic" (Sepkoski, 1994; Stanley, 1990). Considering that a coin responds during a toss, or a group responds during its "walk", it is logical to express this idea to biota, which indeed, through extinction and speciation, do respond to the forcing functions which move them through time (McGhee, 1989). It is likely "system inertia" is a differential phenomenon, across all spatio-temporal scales and across taxa. Knowing that data sets do vary in size, and that manipulation of the data may blur the messages, it seems evident that another approach

may be necessary. In order to gain an understanding the dynamics of a taxon, one should consider other parameters such as counts of stable and new species, as well as those which became extinct.

The need for a more representative system of metrics has long been heralded (Sepkoski and Koch, 1995; Foote, 1994; McGhee, 1989). Extinction data have been widely accepted, but often misused (Jablonski, 1995) causing many warnings of the potential pitfalls relating to these metrics (McGhee, 1989). The positive correlation between new originations and extinction underscores the importance of considering these parameters together, rather than solitarily. Recent attempts to resolve this question have resulted in examinations of volatility (Gilinsky, 1994), as well as morphologic disparity (Jablonski, 1995), though these types of study still require complex compilations and manipulation of data.

The time transgressive, as well as incomplete, nature of the rock record provides many quandaries of the usefulness of data gleaned (Raup, 1991; Gilinsky, 1991; Koch, 1991; McGhee, 1989). One simply does not know when, exactly, an organism originated or declined, providing that it was even preserved, fossilized and found. However, patterns do exist in the fossil record (Signor, 1991; McGhee, 1989). While this notion has been realized for some time, it has been employed with random models that do not always work. If selectivity is indeed a mitigating factor, then either current models will need adjustment (Sepkoski, 1991) or new models must be developed.

In an oft-cited publication Raup (1975) modeled the strong correlation between genus and species diversity in echinoids. His reverse rarefaction curve (Fig. 1) has been

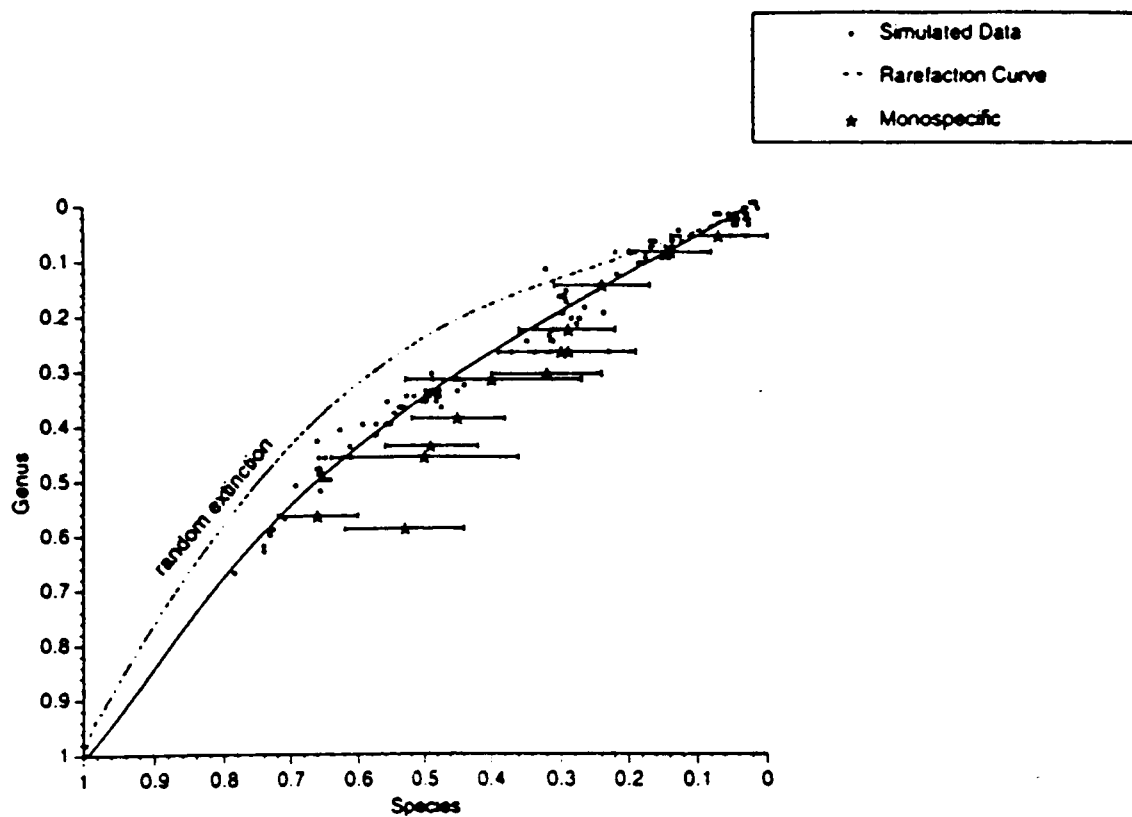


Figure 1. Reverse rarefaction extinction selectivity curve. Simulated “kills” produce nonrandom extinction. Source: McKinney, M.L. 1995. Extinction selectivity among lower taxa: gradational patterns and rarefaction error in extinction estimates. *Paleobiology* 21(3) 300-313.

used with many other taxa, with similar results (Stanley and Yang, 1994). But these rarefaction curves assume random extinction of species within higher taxa. Current paleo-ecologic studies, have revealed that genus membership can influence species extinction (Johnson *et al.*, 1994; Jablonski, 1995), and subsequent genus-species rarefaction curves do not agree with Raup's random selectivity curve (McKinney, 1995) (Fig 1). In fact, Raup (1991), noted that random extinction via the rarefaction method may not be met. To validate the use of reverse rarefaction analysis of echinoids, as well as with other techniques which assume randomness, the data should be tested for random distribution of extinction selectivity patterns.

Research Objectives

This study will analyze a data set representing the Class Echinoidea, and determine if extinction is random between genera, or is clustered within particular orders. Using statistical analysis, I will determine if some groups diverge significantly from the average extinction rate. If extinction values are clustered, then the use of techniques such as reverse rarefaction must at least be modified to include differential rates of extinction and speciation between intra-clade organisms (McKinney, 1995). Additionally, this research will examine the validity of traditional probability and statistics when applied to the fossil record. Most models seem to follow a statistical approach, and new methods for presenting and interpreting data will be considered.

Since so many of the sampling errors seem to be associated with arithmetic differences between group size, a relative weighting system of flux may be more appropriate rather than a measurement of taxa behavior based upon quantitative input.

Expanding or compressing a sample size, such as rarefaction, does alter data, perhaps blurring the signal. A system of relative measurement does not necessarily have to alter data, and may provide a more holistic assessment of evolutionary trends. To only examine extinction, without consideration for the other parameters involved will yield, at best, partial results. Extinction and speciation are inseparable because they function together. As Raup (1996, 1994, 1991b), noted, Darwin considered extinction a vital component of evolution. Therefore, this research will also study the potential for new metrics for the assessment and measurement of evolution in the fossil record.

While any group of organisms may be considered, this research examines the Cenozoic evolutionary patterns of the Class Echinoidea. The use of such marine organisms in paleoecologic study is common for numerous reasons. First, the majority of sedimentary rock, from which fossils come, is of marine origin (Raup and Stanley, 1978). The continuing presence of some echinoid taxa into the present provides a unique opportunity to examine past trends to compare with recent knowledge and observations of life modes and ecological relationships. Such analysis can yield insights well beyond implications for a specific taxa. Models following biogeographic occurrences can be developed which examine such topics as global and regional climate patterns (Flessa and Jablonski, 1996) or sea level fluctuations.

Echinoid Taxonomy, Ecology and Evolution

This study follows the classification of the Class Echinoidea in *The Treatise on Invertebrate Paleontology* (Durham, 1966). This scheme is continued in Kier and Lawson's (1978) compilation of echinoid citations from 1924 to 1970. Recent attempts

to organize ordinal echinoid phylogeny utilizing cladistics have been developed (Jensen, 1981; Smith, 1981), but these classifications have not gained widespread acceptance. An informal grouping system divides echinoids into two groups - the regulars and irregulars (Clarkson, 1993). While not a true phylogenetic system, this does serve as a means to analyze groups that differ in body form and function, and subsequently, mode of life.

There have been over 900 extant species described thus far (Smith, 1984), with all being both benthic and marine. Echinoids have been found in every habitable range of up to 7000 meters in depth. They are common in all oceans, although specific habitats vary with taxon. Regular echinoids are epifaunal, and are common on hard substrates or in conjunction with reef communities. They are algal feeders, and commonly “graze” plants, corals, sponges or even other echinoids, with some deep water species feeding upon detritus (Hendler *et al.*, 1995). Irregular echinoids, by contrast, prefer the infaunal lifestyle, which may in part, account for their remarkable preservational history, compared to that of the regulars (Kier, 1977). As burrowers, most irregulars are sediment feeders, and thus, occupy areas of deposition. This is in contrast to the high energy environments inhabited by the regulars. The mode of life differences between these two groups may account for preservational biases in the fossil record. However, morphological differences dictating life mode are indeed a heritable trait (McKinney, 1995), and these may influence the susceptibility of taxa to extinction and speciation in addition to controlling taphonomic qualities.

Echinoids first appeared during the Ordovician, and diversified until the end of the Carboniferous, when species and higher taxa were both reduced (Smith, 1984). By

the Permian, only six species remained, and after the Permian mass extinction, only the genus *Miocidaris* survived (Erwin, 1993). Diversification resumed in the Upper Triassic, and during the Jurassic, the irregulars first appeared (Kier, 1982). During the Paleocene, the last major evolutionary event for the echinoids was the first appearance of the irregular clypeasteroid echinoid or "Sand Dollar" (Mooi, 1993). Phylogeny of the Class Echinoidea since its inception has been characterized into five parts (Lehmann and Hillmer, 1983). These developments include: 1) Rigid test; 2) Preferred direction of locomotion; 3) Improved water-vascular system; 4) Adaptations of tube feet for specialized functions; 5) Specialized feeding habits. It is the intra-generic differentials of these five developments that may play a major role in any potential extinction selectivity.

Paleontology

Echinoid evolution is clearly evident in the rock record. This is mainly due to two reasons: 1) The sheer abundance of echinoid species, from 200 in the Paleocene to over 1000 in the Eocene (McKinney *et al.*, 1992); and 2) an unmatched propensity for echinoid preservation, resulting from the secretion of calcitic tests and other body parts (Smith, 1984), which tend to remain unaltered unlike aragonitic secretions of other marine organisms. Additionally, the infaunal life modes and subsequent morphology of some echinoids, namely the irregulars, makes them especially favorable for preservation, as does the near-shore facies preference exhibited by some of the regulars (Kier, 1974; Smith, 1984).

Second, in order to compare methodologies, the biotic group must have been sufficiently studied such that preliminary evolutionary trends have been ascertained.

Additionally, enough knowledge should exist to provide adequate stratigraphic range as well as an accurate taxonomic division of the individuals encountered. This seems to be best expressed when members of the same taxa exist well into the Recent, and can be scrutinized and organized as living, interacting organisms. Such luxuries with a mesh between geologic past and the present do not always occur. Echinoids, however, can provide ample data between past evolutionary trends and current diversity patterns (Smith, 1984), using modern behavior as analogues for paleoecologic study.

METHODOLOGY

Tabulation and Theory

This study will examine echinoid evolutionary trends in the Cenozoic as inferred by a data set compiled by the author. This time period was chosen for several reasons. First, echinoid taxa greatly diversified during the last 70 million years (Smith, 1984). Second, preservation of rock and subsequently fossils is much greater in the recent past than of the more distant geologic timespans, which aids greatly in the clarity of data retrieved (Raup, 1979). Third, knowledge of the Cenozoic indicates several pronounced extinction and radiation events concerning echinoids as well as other organisms (McKinney *et al.*, 1992; Prothero, 1994). Finally, the taxonomic and morphologic understanding of echinoids from the Cenozoic is greater than that of previous time periods, since some genera and families, as well as most orders are extant.

The database used for this study represents echinoid species cited between 1924 and 1996. The validity of a limited data set for higher taxic studies has been demonstrated, so that trends discovered at one level of taxonomic classification can be applied to both the higher and lower levels (Sepkoski, 1992). This database was compiled from Kier's and Lawson's (1978) citation index 1924-1970. New citations gleaned from literature 1970-1996 were also obtained (Appendix A). However, not all echinoid citations were considered. Only citations with approximately equal time intervals were admitted to the database, following the system derived by Kier and Lawson's compilation, with epochs being divided into upper- and lower- or upper-,

middle-, lower- time series. This methodology serves several functions - 1) it provides a consistent grouping scheme; and 2) species longevity is on the order of 5 million years or so (Stanley, 1990), and since genera can be monospecific, genus appearance or disappearance can only be examined at this scale of resolution. Additionally, it is likely that species/genus descriptions near stage-level resolution have a higher probability of being correctly categorized in taxonomy as well. This distillation of an echinoid database into finer resolution has several advantages, providing consistency in age-date input while yielding a more manageable database.

The data set was transferred into a stratigraphic range chart (Appendix B), as a visual and numerical tool depicting the database behavior over time. Each geologic epoch, with the exception of the Paleocene and the Oligocene, was divided into lower-, middle-, and upper- intervals, in accordance with the geologic time scale as derived by Harland *et al.* (1990). The Paleocene and the Oligocene were divided into upper- and lower- epochs only. Conveniently, the approximate time intervals realized by this system is from 4 to 7 million years, which allows for reasonable comparison between each time step. This is necessary to reduce time components of sampling artifacts (Foote, 1994; Gilinsky, 1991), and is consistent with average echinoid species longevity.

Extinct genera were indicated by disappearances of citations from the stratigraphic range chart. These were tabulated in Table I. Numerical ratios per each order were calculated by noting the genera per order present in a time period, versus whether or not the genera subsequently disappeared from record in the next interval and became extinct. The number extinct (E) was divided by the number of genera (G) present during that time

Table I - Database Parameters of Echinoid Orders																
Order	aramet	L. Paleo	U. Paleo	L. Eocene	M. Eocene	U. Eocene	L. Oligo	U. Oligo	L. Mioce	M. Mioce	U. Mioce	L. Plio	M. Plio	U. Plio	Pleisto	
Cidaroida	Genera	10	8	8	9	11	10	11	10	11	11	11	12	12	13	
	Extinct	2	0	0	0	1	0	1	0	0	0	0	0	0	0	1
	New	0	0	0	1	2	0	1	0	1	0	0	0	1	0	1
	Stable	8	8	8	8	8	10	9	10	10	11	11	11	12	12	
Euechinoida	Genera	2	2	2	2	2	2	2	2	2	2	2	2	2	2	
	Extinct	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	New	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Stable	2	2	2	2	2	2	2	2	2	2	2	2	2	2	
Diadematoidea	Genera	1	0	1	0	1	1	1	2	2	2	2	2	2	2	
	Extinct	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
	New	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0
	Stable	0	0	0	0	0	1	1	1	2	2	2	2	2	2	
Pedinoida	Genera	0	0	1	1	1										
	Extinct	0	0	1	0	1										
	New	0	0	1	1	0										
	Stable	0	0	0	0	0										
Salenioida	Genera	4	1	1	1	1	1	1	1	1	1	1	1	1	1	
	Extinct	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	New	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Stable	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Hemicidaroida	Genera	1	1	1												
	Extinct	0	0	1												
	New	0	0	0												
	Stable	1	1	0												
Phymosomatoida	Genera	5	3	4	5	7	1	0	0	0	0	0	1			
	Extinct	2	0	0	2	6	1	0	0	0	0	0	1			
	New	0	0	1	1	4	0	0	0	0	0	0				
	Stable	3	3	3	3	0	0	0	0	0	0	0				
Arbacioida	Genera	2	1	1	1	1	1	2	2	2	2	2	2	2	2	
	Extinct	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
	New	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0
	Stable	1	1	1	1	1	1	1	2	2	2	2	2	2	2	1
Ternoplecturoidea	Genera	1	1	4	3	6	3	6	6	6	5	4	3	3	4	
	Extinct	0	0	2	1	3	1	3	1	2	1	1	0	0	1	
	New	0	0	3	1	4	0	4	3	1	1	0	0	0	1	
	Stable	1	1	1	2	2	2	0	3	4	4	3	3	3	3	
Echinoida	Genera	1	1	1	1	1	1	1	1	1	2	3	2	2	2	
	Extinct	0	0	0	0	0	0	0	0	0	0	1	0	0	0	
	New	0	0	0	0	0	0	0	0	0	1	1	0	0	0	
	Stable	1	1	1	1	1	1	1	1	1	1	1	2	2	2	
Holoctypoida	Genera	3	1	3	5	6	1	2	2	2	1	1	1	1	1	
	Extinct	2	0	0	2	5	0	0	0	1	0	0	0	0	0	
	New	0	0	2	2	3	0	1	0	0	0	0	0	0	0	
	Stable	1	1	1	2	1	1	1	2	1	1	1	1	1	1	
Clypeasteroida	Genera	2	2	3	9	15	7	16	18	16	13	15	13	14	12	
	Extinct	0	0	1	5	8	0	5	7	5	1	2	1	3	1	
	New	0	0	2	7	11	0	9	7	5	2	3	0	2	1	
	Stable	2	2	1	2	3	7	7	9	8	11	12	12	11	11	
Cassiduloida	Genera	8	7	10	20	12	8	12	11	10	8	6	6	6	6	
	Extinct	1	0	0	10	4	0	2	2	2	2	0	0	0	1	
	New	1	0	3	10	2	0	4	1	1	0	0	0	0	0	
	Stable	7	7	7	9	8	8	7	9	8	6	6	6	6	5	
Disasteroida	Genera	2														
	Extinct	2														
	New	0														
	Stable	0														
Spatangoida	Genera	16	15	19	32	34	22	35	34	26	22	22	20	19	20	
	Extinct	3	1	4	10	12	0	10	11	6	1	2	1	0	2	
	New	1	2	5	17	12	0	13	9	4	2	1	0	0	1	
	Stable	12	13	12	14	17	22	21	18	18	20	20	19	19	18	
Pourtalesioidea	Genera	2														
	Extinct	2														
	New	1														
	Stable	0														
Neolampoida	Genera					1					1					
	Extinct					1					1					
	New					1					1					
	Stable					0					0					

period. Existence or extinction was determined if the genera in question was absent from the remainder of the stratigraphic chart. Missing data or an absence of citations during a particular time interval was allowed if the genera reappeared on the range chart; these gaps were not considered as extinctions and were not calculated as such. Instead, genera which had missing representatives during particular time intervals had inferred existence since it is very remote that a genus could become extinct and subsequently re-evolve.

Two other parameters besides G and E are also presented in Table I, these being the number of new (N) genera appearances, and the number of stable (S) genera. The stability of a genus was defined by a presence in both the preceding and subsequent time steps, to the time period in question. The four parameters G, E, N and S are major components of ordinal behavior. Each has subcomponents which can be isolated algebraically (Appendix C), due in part to the rigorous definition of stability, as discussed above. The subcomponents resolved become:

G_p = Genera previous, the number of genera entering the time step

E_p = Extinct previous, the number of G_p which went extinct

N_e = New extinct, the number of new originations that went extinct

N_s = New survivors - new originations surviving into next interval

O = Output, the total number leaving time interval ($S + N_s$ or $G - E$)

A formula relating these parameters correctly, may approach an understanding of flux and stability within a system. And while it may be argued that sample size from fossil data almost always endures some uncertainty of completeness (Raup, 1991), it can be countered that all four parameters here suffer equal biases since they were compiled

from the same set of data, and thus can be compared. Therefore, this metric should eliminate the biases associated with taxonomy and taphonomy while minimizing any mathematical artifacts incurred by considering input parameters derived outside of this system. Further, by using a formula based upon relative weighting, ordinal trends will still be evident, even with small data sets, and at worst, will only produce conservative estimates of echinoid stability.

Analytical Methods

A ratio of genera-extinct to genera-present was calculated for each order per time-step of the Cenozoic. To determine the relative weight of each extinction ratio, a mean ratio for each interval considered was computed by averaging all the genera extinct per genera present during each interval. By considering average extinction values for all genera regardless of taxonomy omits any biases imposed by order membership. Error bars were calculated about the weighted mean using the second standard deviation, formula $2(pq/n)^{.5}$, where p = (extinction ratio), q = $(1 - p)$, and n = (the number of genera considered during that time interval). The ratio value of each order was plotted, comparing the divergence from the average value, plus or minus the second standard deviation. Orders deviating significantly will be considered as selected either for (+) or against (-) extinction. Those falling within the error defined about the mean will be counted as average extinction values (0).

Another method to check the statistical approach is to use the derived average extinction ratios, and multiply these by the number of genera per stage in a particular order to obtain a predicted number of genera extinction. A normalized variance is

derived by subtracting the observed (O) extinction from the genera present (G) and dividing by the number of genera (G) minus the predicted number (P) of extinctions:

$$(G-O)/(G-P) = \text{normalized variance of predicted extinction from that observed}$$

Use of this variance test produces deviation from a value of 1, with values falling below .70 being considered as more favored than average for extinction (+), with those values above 1.30 as being favored against extinction (-) and those between .70 - 1.30 falling within average expectations (0). As has been noted, possible abundance variations between 10 - 25 % should be expected between different data sets, attributable to sampling error alone (Koch, 1991). The value of .30 was chosen, in part, as a conservative estimate of uncertainty, even though normalized variance probably minimizes mathematical biases.

However, since extinction alone is not sufficient to define ordinal behavior, a new metric will be introduced and utilized employing the four parameters of G, E, N, and S. Rather than considering extinction as an independent variable, other parameters from the database were also tabulated and utilized. New genera originations (N), and stable genera (S), are shown algebraically in Appendix C to be closely linked to the parameters of extinction (E) and the genera total (G). A metric relating these parameters was developed.

This was defined as a relative measure of internal flux of an order during a time interval, and was conceived to fulfill several constraints. First, input and output of genera through a time interval must be equal to be stable. Second, extinction should be weighed against new originations such that stability can still be met if extinct and new genera

equal. Third, both of the first items, input/output and new/extinct parameters are to be considered together, and not exclusive of one another. And, fourth, that data size does not significantly alter results; that missing or partial data can still be calculated. The formula derived considers stability, defined by both the ratio of extinct (E) to new (N) genera, and the total output (G-E) to stable (S) genera, and is presented here as Flux:

$$\text{Flux} = \frac{G - E + N + S}{S + G [(E+1)/(N+1)]}$$

where,
G = Genera
E = Extinct Genera
N = New Genera
S = Stable Genera (See text for definition)
and, all 4 parameters are from the same time step.

Flux is also normalized to sample size, and should provide an unbiased comparison of relative behavior between orders. Relative flux is determined by deviation from unity (1), with high values indicating an increase in speciation and stability, with low values indicating high extinction with low replacement and instability amongst the genera. Values that decrease to zero show complete extinction. Values approaching unity are indicative of equal extinction/speciation (E/N) values, and/or dominant numbers of stable (S) genera, relative to total (G) genera. The ratio of extinct (E) to new (N) genera appearances is calculated as (E + 1)/(N + 1) to include timesteps which did not endure any cited extinction. The addition of 1 to the denominator and numerator prevents the equation from becoming undefined when there is no recorded extinction. The effect of this manipulation is regarded as minimal since 1 is added to both terms.

Flux as shown here is not presented versus time, because it cannot be determined from most data sets the actual ranges of genera, but rather, only that they appeared or disappeared from record by the end of a particular time step (Raup, 1991). Additionally, rate metrics assume a constant value across an interval, which may not be valid (Foote, 1994). Therefore, to eliminate time biases flux will be shown as a net result of an order's dynamics at stage end, rather than a continuous rate.

By obtaining all parameters from one time interval, this metric should eliminate the biases associated with taxonomy and taphonomy while minimizing any mathematical artifacts incurred by considering input data or fitting parameters derived outside of the closed system. If all the biases are assumed to be equal per taxon, per interval, then, effectively they could be resolved by dimensional analysis. By treating these biases as "units", as calculated in the flux metric, they would eventually cancel out, as flux is unitless. Mathematical biases will also be further minimized since the result is normalized for sample size.

The use of such a technique seems appropriate because a more holistic approach weighting several key components of evolution may be necessary to present data in another form for analysis. The flux metric allows data to be retrieved and analyzed in a non-linear fashion, eliminating many of the problems associated with the use of linear math for paleoecologic studies (Sepkoski, 1994; McGhee, 1989). The internal variation of the echinoid orders within this database will be plotted, interpreted, and subsequent implications discussed.

RESULTS

Analysis and Presentation of Data

Comparison between the extinction rates versus time for this data set (Fig. 2) with other published echinoid extinction rates (McKinney and Oyen, 1989) (Fig. 3) shows similar patterns. Therefore, since this data is in general agreement with independent research, it is probable that this database is both applicable and valid, and that trends evident in this data set can probably be extended to Cenozoic echinoid behavior as a whole.

Statistical Analysis. The statistical analysis for selectivity resulted in trends deviating from random (mean) values. Each epoch and sub-epoch of the Cenozoic was evaluated and graphed (Appendix D). Tables II and III compile this data and categorize the orders into two groups, the regulars and irregulars. Deviation from mean extinction values, was denoted by either a "+", as favored for extinction; a "-" as favored against extinction (survival); or "0" which means that order had average extinction. Those orders with no citations for a particular time interval have an empty cell. Average extinction per time is the weighted mean, plus or minus the second standard deviation. Those orders whose extinction value fell within the range of standard deviation are considered as having average extinction. In addition to ordinal level trends towards or against extinction over time, other patterns are derived from these tables. Specific time periods seem to have affected each group differently. The Middle- and Upper Eocene, and the Lower-, Middle- and Upper Miocene target irregulars for extinction over the regulars.

extinction rate v. time (100,000 years)

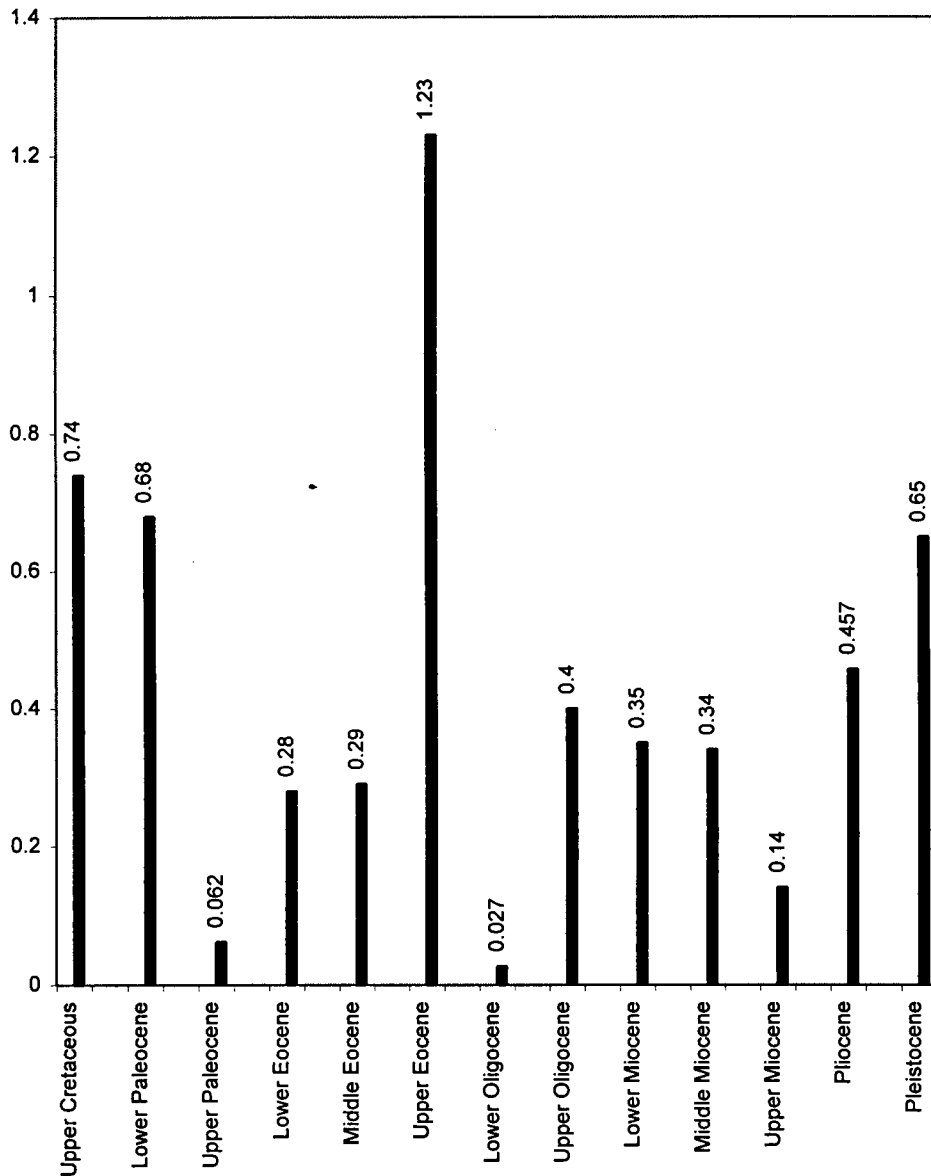


Figure 2. Average echinoid extinction rate for each time step of the Cenozoic computed from the data set used in this study. Formula for this derivation is the total number genera extinct (E), divided by the total number of genera present (G) for all orders, per each time period, divided by the length of the time interval (T). Extinction rates presented here are those per every 100,000 years.

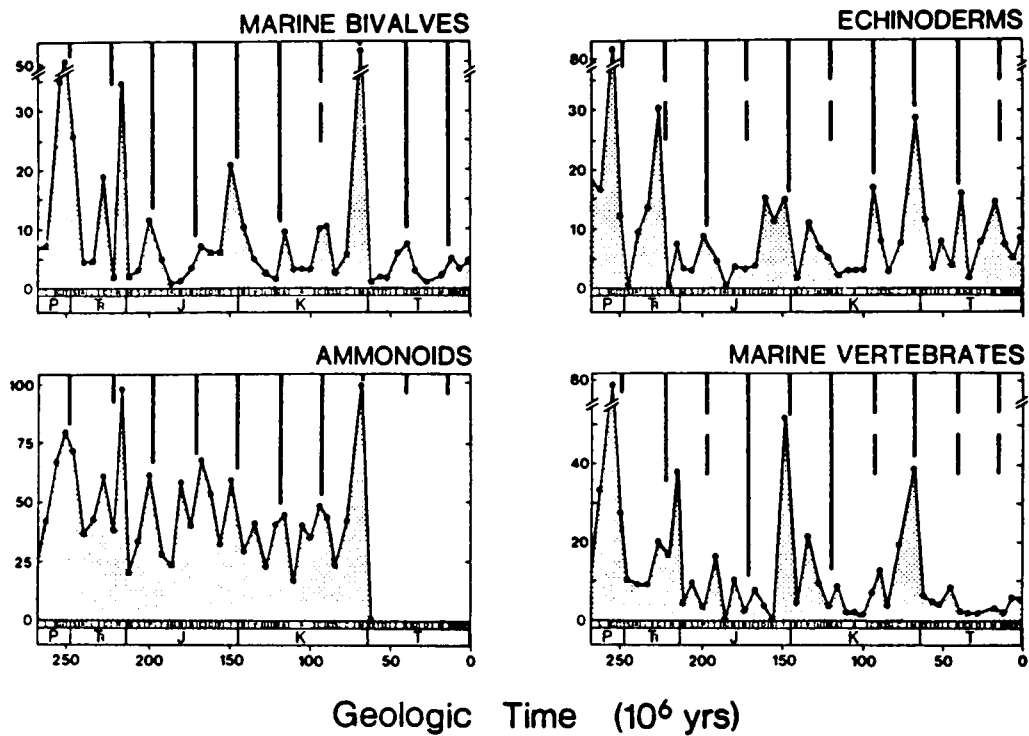


Figure 3. Other published extinction rates of marine genera, including echinoids. Source: Sepkoski, J.J., 1990. The taxonomic structure of periodic extinction. Pages 33-44 in Sharpton and Ward (eds.) *Global Catastrophes in Earth History*. GSA Special Paper 247, Boulder, Co.

Table II. Extinction trends of database for Regular echinoids.

Order	Cret		Pal		Eoc		Olig		Mio		Plio	Pleis
	U	L	U	L	M	U	L	U	L	M	U	
Cidaroida	-	0	0	-	-	-	0	-	-	-	0	0
Orthopsida	+	-										
Diadematoidea	-	+	0	+		-	0	-	-	-	0	-
Salenioida	-	+	0	0	-	-	0	-	-	-	0	0
Pedinoida	+	-	0	+	-	+						
Temnopleuroidea	-	-	0	+	0	0	+	+	0	+	+	+
Phymosomatoida	+	-	0			+	0	+				
Echinoida	-	-	0	-	-	-	0	-	-	-	0	+
Arbacioida	0	+	0	-	-	-	-	-		-	0	+
Hemicidaroida	+	-	0	+								
Euechinoida	-	-	0	-	-	-	0	-	-	-	0	0

Table III. Extinction trends of database for Irregular echinoids.

Order	Cret		Pal		Eoc		Olig		Mio		Plio	Pleis
	U	L	U	L	M	U	L	U	L	M	U	
Holactypoida	+	+	0	-	0	+	0	-	-	+	0	-
Cassiduloida	+	0	0	-	+	0	0	0	0	0	+	0
Clypeasteroida	-	-	0	+	+	+	0	0	+	0	0	+
Spatangoida	-	0	0	0	0	0	0	0	0	0	0	0
Disasteroida	+											
Pourtalesioida	0	+										
Neolampoida						+			+			

Notes: Data derived using extinction ratios of Genera extinct : Genera present per each order, per time step of the Cenozoic.

Extinction trends are compared to deviations from average extinction values:

"0" denoted average values; "+" is favored toward extinction; "-" is favored against extinction.

Time steps are divided into Upper (U), Middle (M), and Lower (L) intervals.

Other time periods, especially during times of rebound such as the Upper Paleocene and Lower Oligocene show no selectivity at all, with the majority of orders falling within average ranges.

In further analysis of the database, the extinction values (P) of each order were plotted against the number of genera membership (G). This was performed in two ways: 1) for each order over time, from Upper Cretaceous to Pleistocene; and, 2) for each time step, as an average value of all existing orders. A regression line was fitted to the both types of plots, which are included in Appendix V. The regression analysis yielded an apparent relationship between generic richness and extinction. Regression for the average extinction value of all orders, irrespective of time, shows a trend towards higher extinction with increased generic richness (Fig. 4). These trends continued when each order was examined separately. The clypeasteroids, spatangoids, holotypoids and cassiduloids, all irregulars, exhibit the same trend (Figs 5-8). This pattern is not as pronounced when examining the mean behavior of all taxa within a time interval, however, regression analysis did indicate the positive relationship between genera-rich favored extinction in some cases (Fig 9 and 10). Another graph plots the regression curve of the average extinction value of all orders in chronological fashion from Cretaceous to Pleistocene (Fig. 11). This plot indicates not only an 80 % decrease in extinction rates as we approach the present, but also illustrates the apparent relationship between generic richness and high extinction values. The general shape of this curve, is typical of a "pull to the Recent" effect, (Raup, 1978) which illustrates increasing resolution of knowledge with an increasingly less distant past.

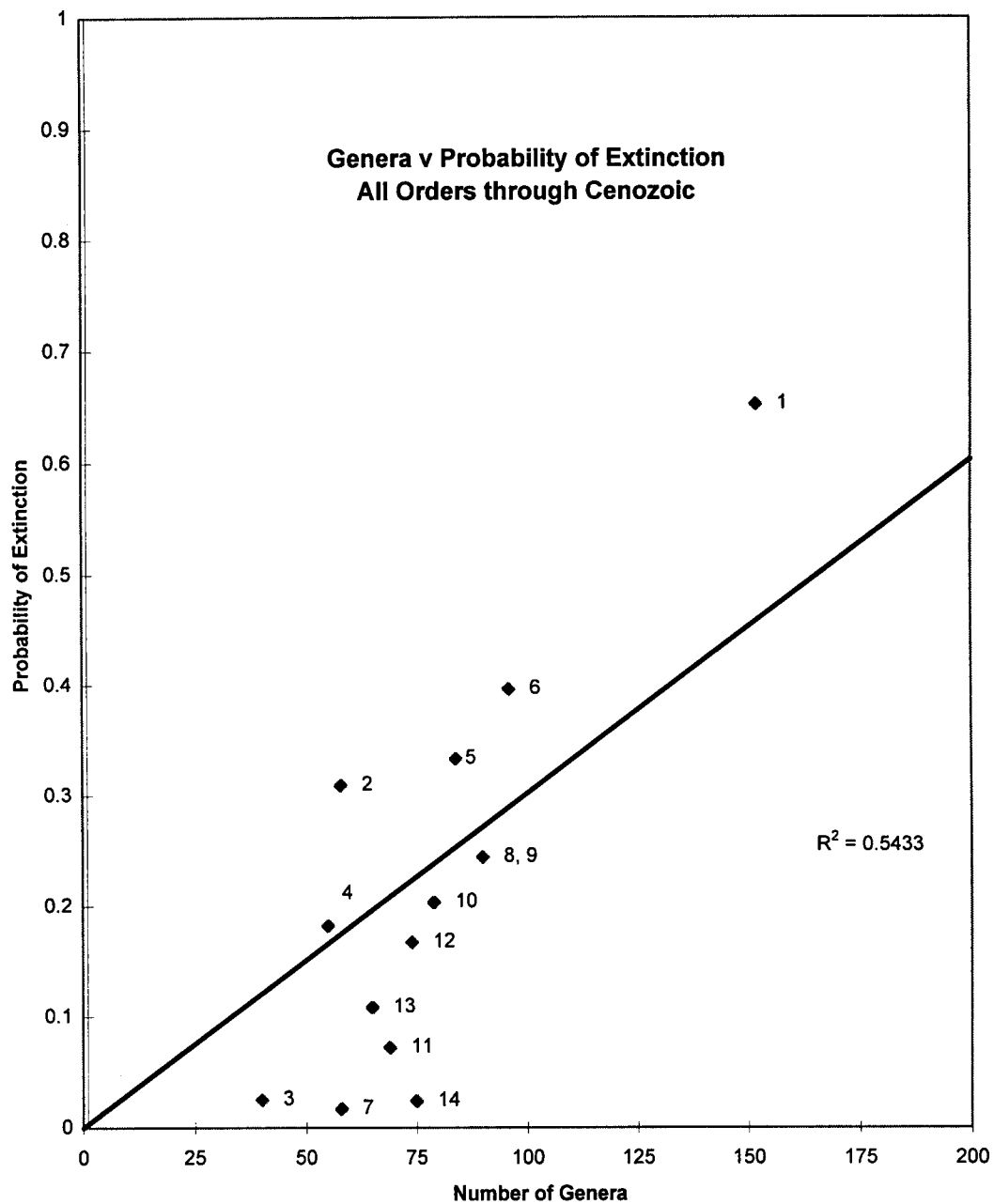


Figure 4. Linear regression analysis of ordinal extinction probability versus the number of genera present. The plot indicates a slight trend of increasing extinction probability with an increasing number genera. Each point represents the average extinction probability of a time step plotted against the number of genera within that interval. Timesteps are designated by the following system: 1) Upper Cretaceous; 2) Lower Paleocene; 3) Upper Paleocene; 4) Lower Eocene; 5) Middle Eocene; 6) Upper Eocene; 7) Lower Oligocene; 8) Upper Oligocene; 9) Lower Miocene; 10) Middle Miocene; 11) Upper Miocene; 12) Lower Pliocene; 13) Upper Pliocene; 14) Pleistocene.

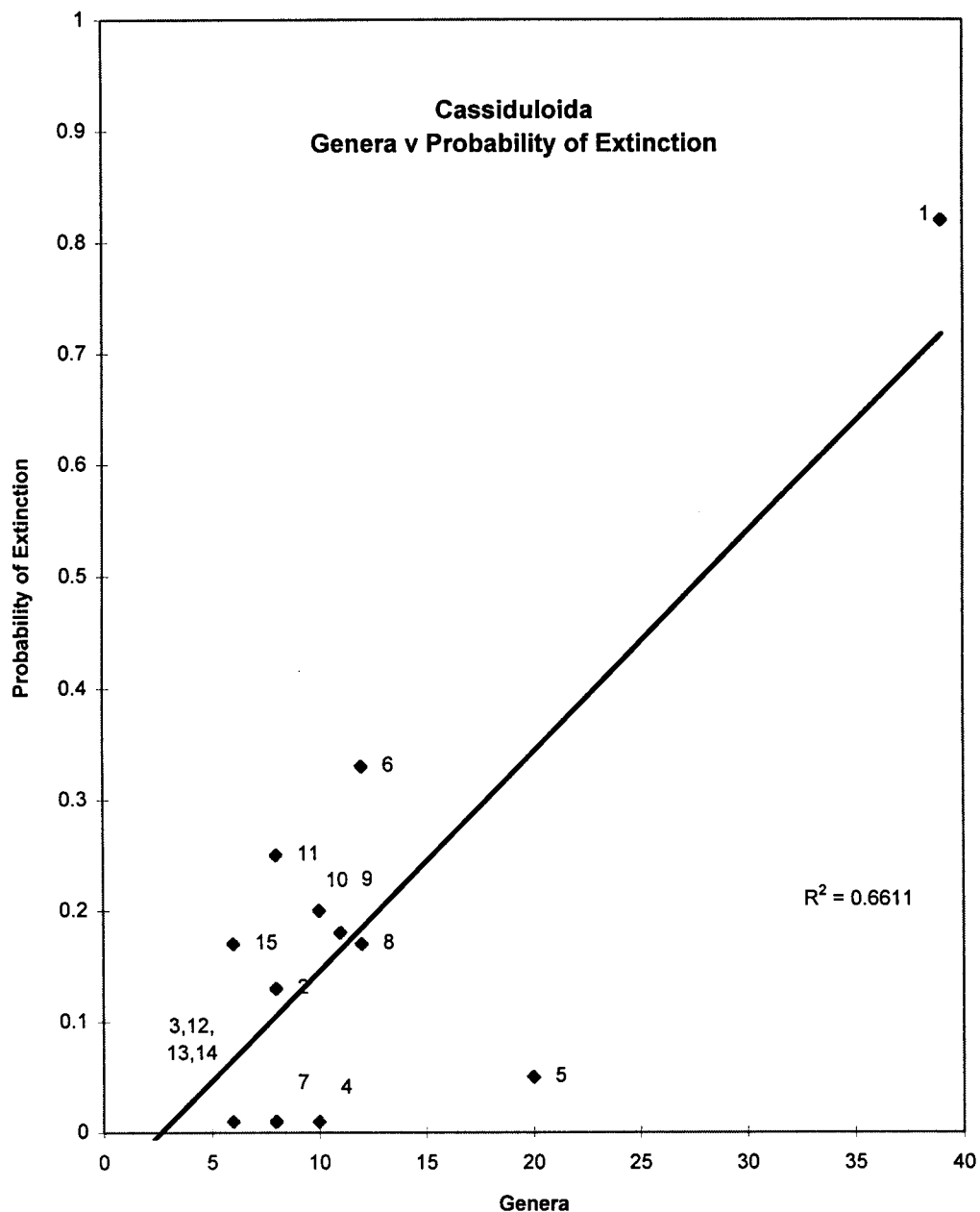


Figure 5. Linear regression of the extinction probability versus the number of genera present for the Order Cassiduloida. Each point represents the average extinction probability of each time step plotted against the number of genera present during each corresponding time step. Timesteps are designated by the following system: 1) Upper Cretaceous; 2) Lower Paleocene; 3) Upper Paleocene; 4) Lower Eocene; 5) Middle Eocene; 6) Upper Eocene; 7) Lower Oligocene; 8) Upper Oligocene; 9) Lower Miocene; 10) Middle Miocene; 11) Upper Miocene; 12) Lower Pliocene; 13) Upper Pliocene; 14) Pleistocene.

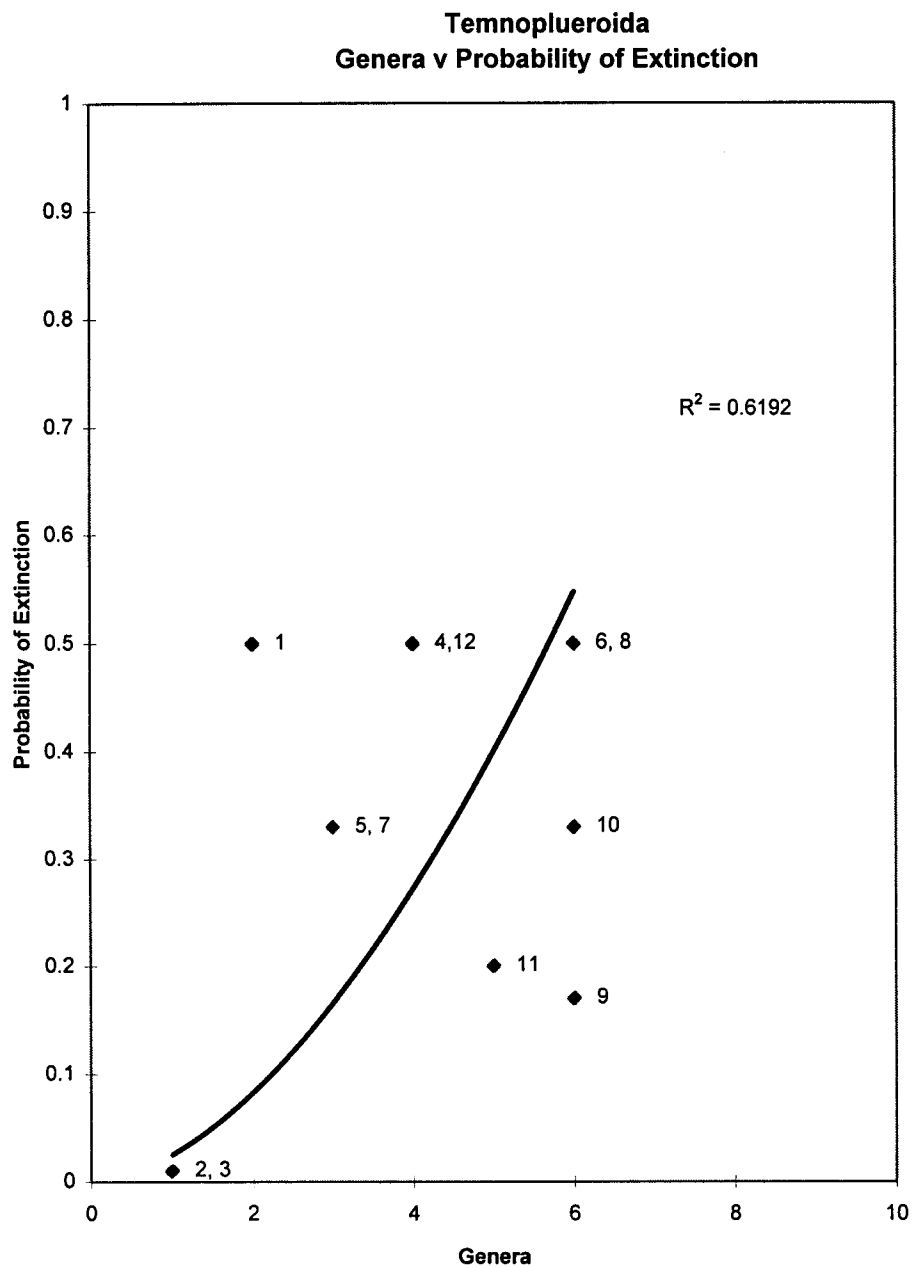


Figure 6. Exponential regression of the extinction probability versus the number of genera present for the Order Temnoplueroida. Each point represents the average extinction probability of each time step plotted against the number of genera present during each corresponding time step. Timesteps are designated by the following system: 1) Upper Cretaceous; 2) Lower Paleocene; 3) Upper Paleocene; 4) Lower Eocene; 5) Middle Eocene; 6) Upper Eocene; 7) Lower Oligocene; 8) Upper Oligocene; 9) Lower Miocene; 10) Middle Miocene; 11) Upper Miocene; 12) Lower Pliocene; 13) Upper Pliocene; 14) Pleistocene.

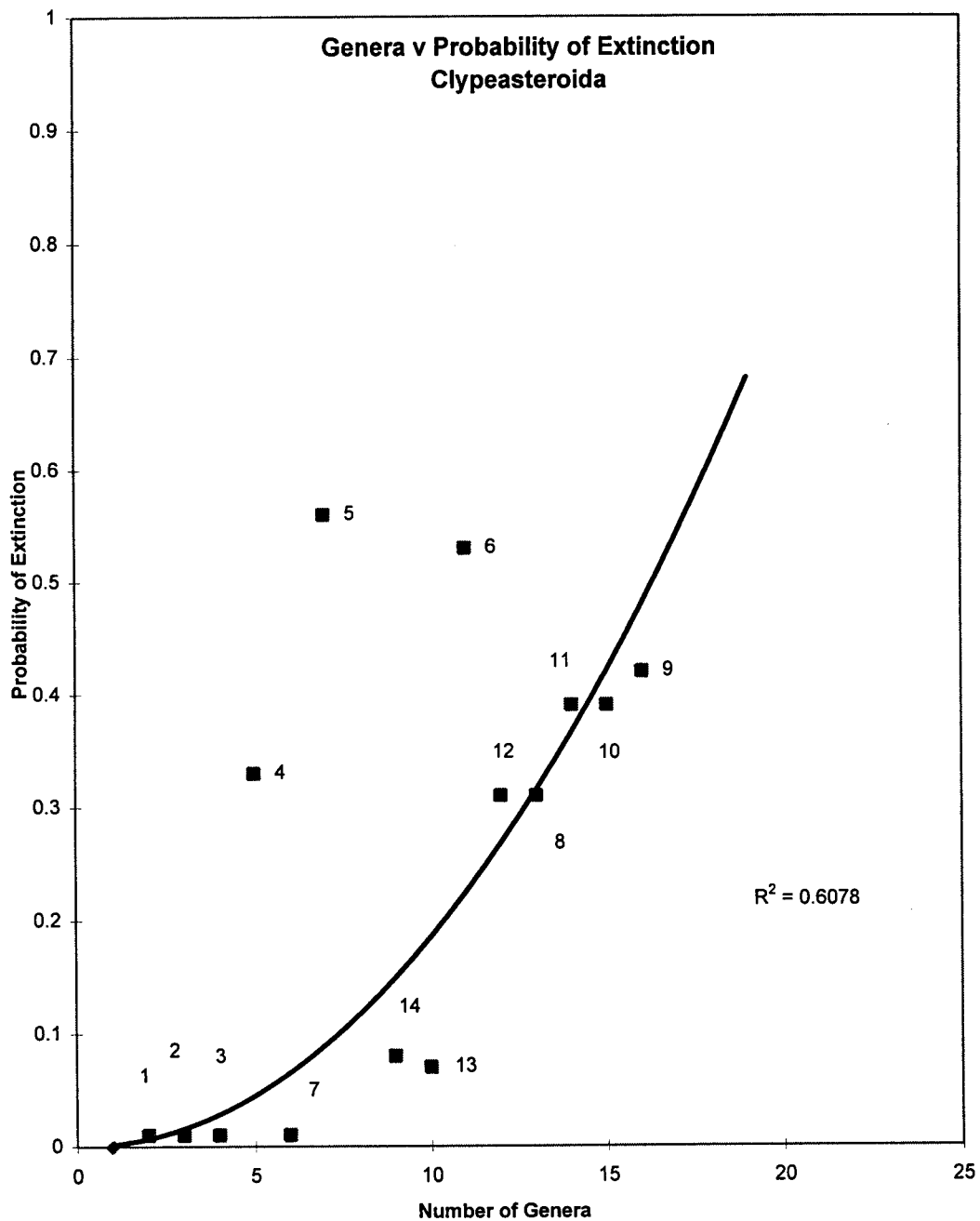


Figure 7. Exponential regression of the extinction probability versus the number of genera present for the Order Clypeasteroida. Each point represents the average extinction probability of each time step plotted against the number of genera present during each corresponding time step. Timesteps are designated by the following system: 1) Upper Cretaceous; 2) Lower Paleocene; 3) Upper Paleocene; 4) Lower Eocene; 5) Middle Eocene; 6) Upper Eocene; 7) Lower Oligocene; 8) Upper Oligocene; 9) Lower Miocene; 10) Middle Miocene; 11) Upper Miocene; 12) Lower Pliocene; 13) Upper Pliocene; 14) Pleistocene.

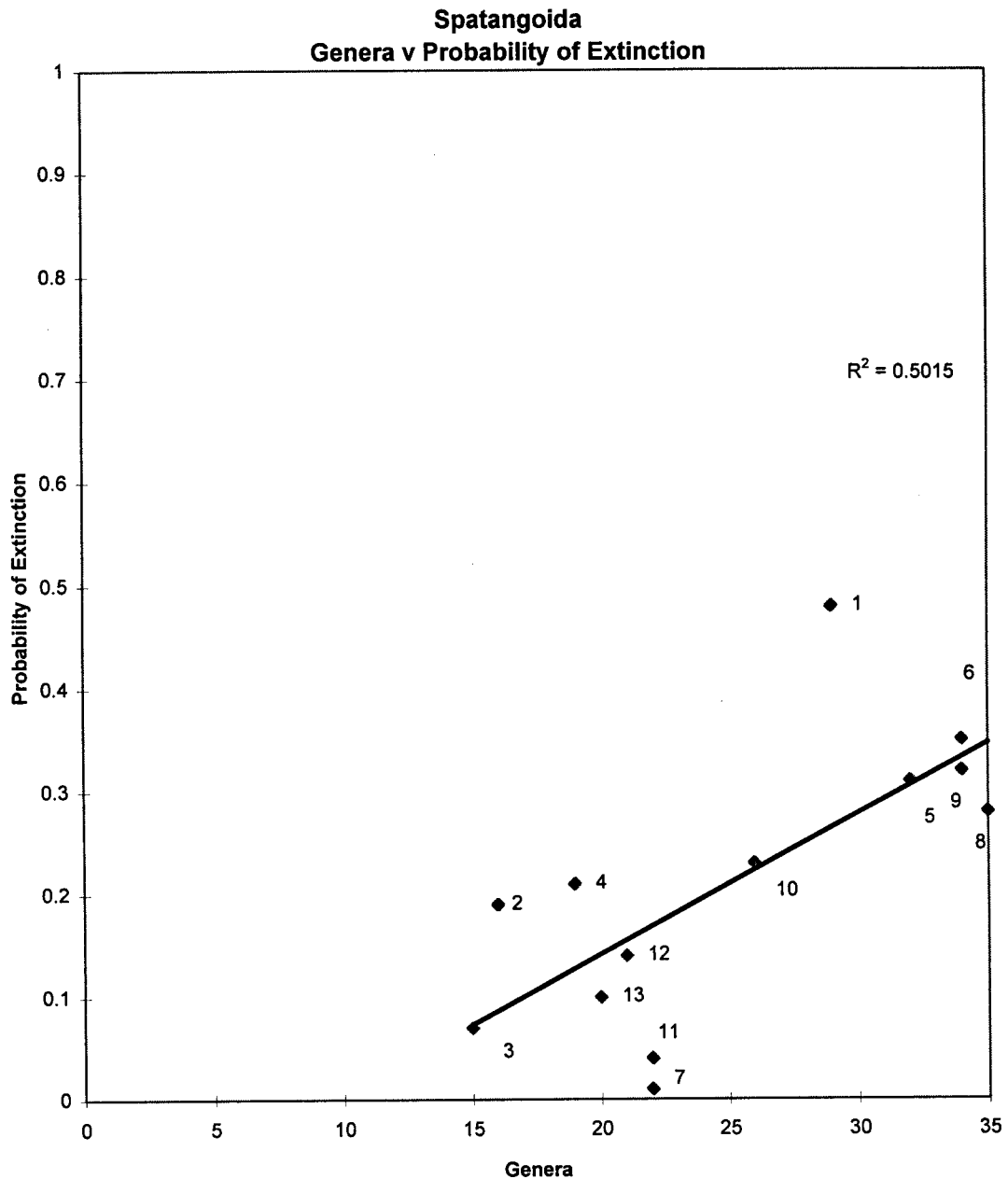


Figure 8. Linear regression of the extinction probability versus the number of genera present for the Order Spatangoida. Each point represents the average extinction probability of each time step plotted against the number of genera present during each corresponding time step. Timesteps are designated by the following system: 1) Upper Cretaceous; 2) Lower Paleocene; 3) Upper Paleocene; 4) Lower Eocene; 5) Middle Eocene; 6) Upper Eocene; 7) Lower Oligocene; 8) Upper Oligocene; 9) Lower Miocene; 10) Middle Miocene; 11) Upper Miocene; 12) Lower Pliocene; 13) Upper Pliocene; 14) Pleistocene

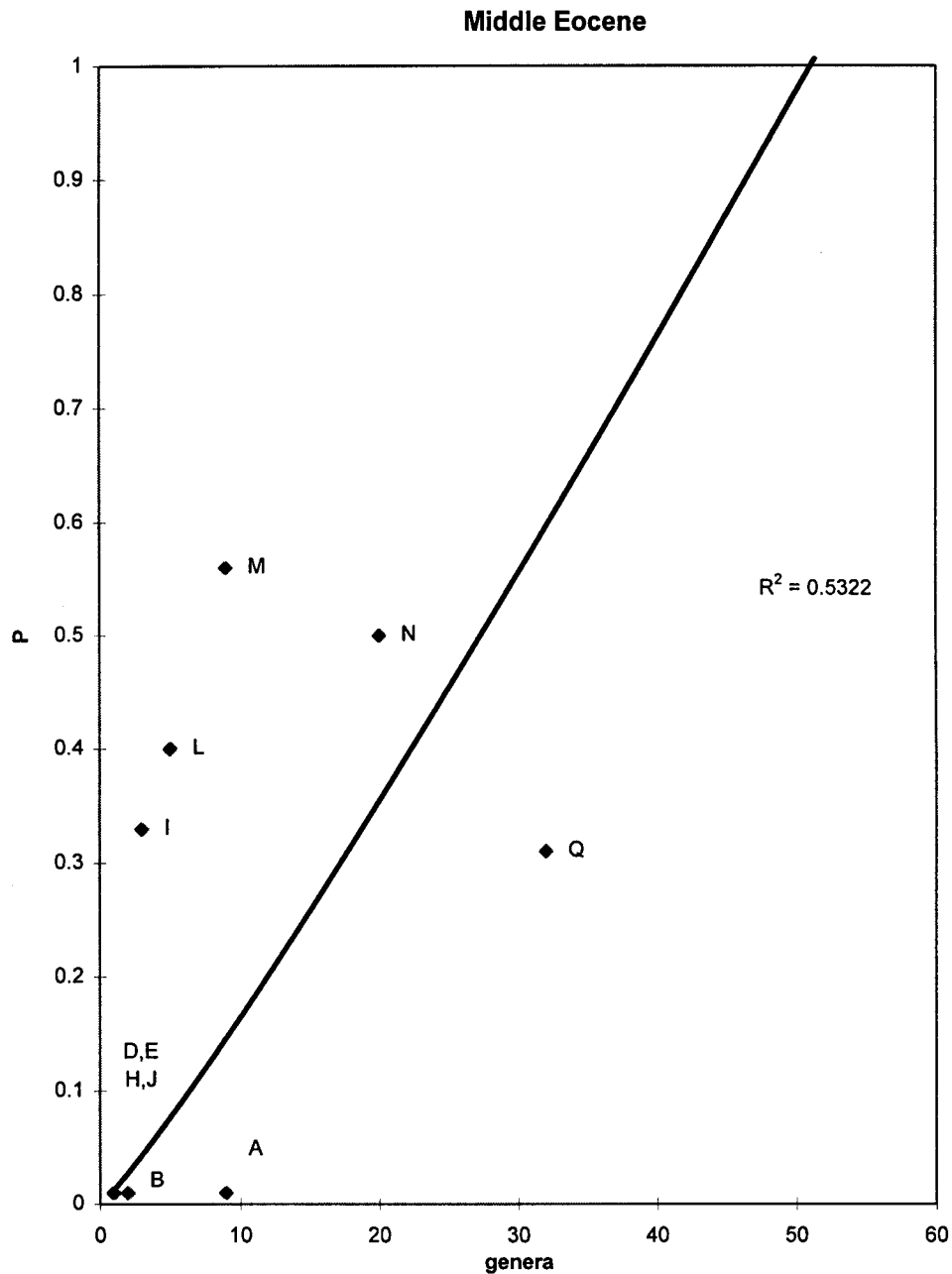


Figure 9. Linear regression of extinction probability with increasing genera for all echinoid orders during the Middle Eocene. Each data point represents one order and plots the number of genera on x-axis versus the extinction probability on the y-axis. Orders are designated by the following system: A) Cidaroida; B) Euechinoida; C) Diadematoidea; D) Pedinoidea; E) Saleninoidea; F) Hemicidaroida; G) Phymosomatoida; H) Arbacioidea; I) Temnopleuroidea; J) Echinoidea; K) Orthopsida; L) Holoctypoida; M) Clypeasteroida; N) Cassiduloida; O) Disasteroida; P) Pourtalesioidea; Q) Spatangoida. Note, not all orders may be present in the database during this timestep.

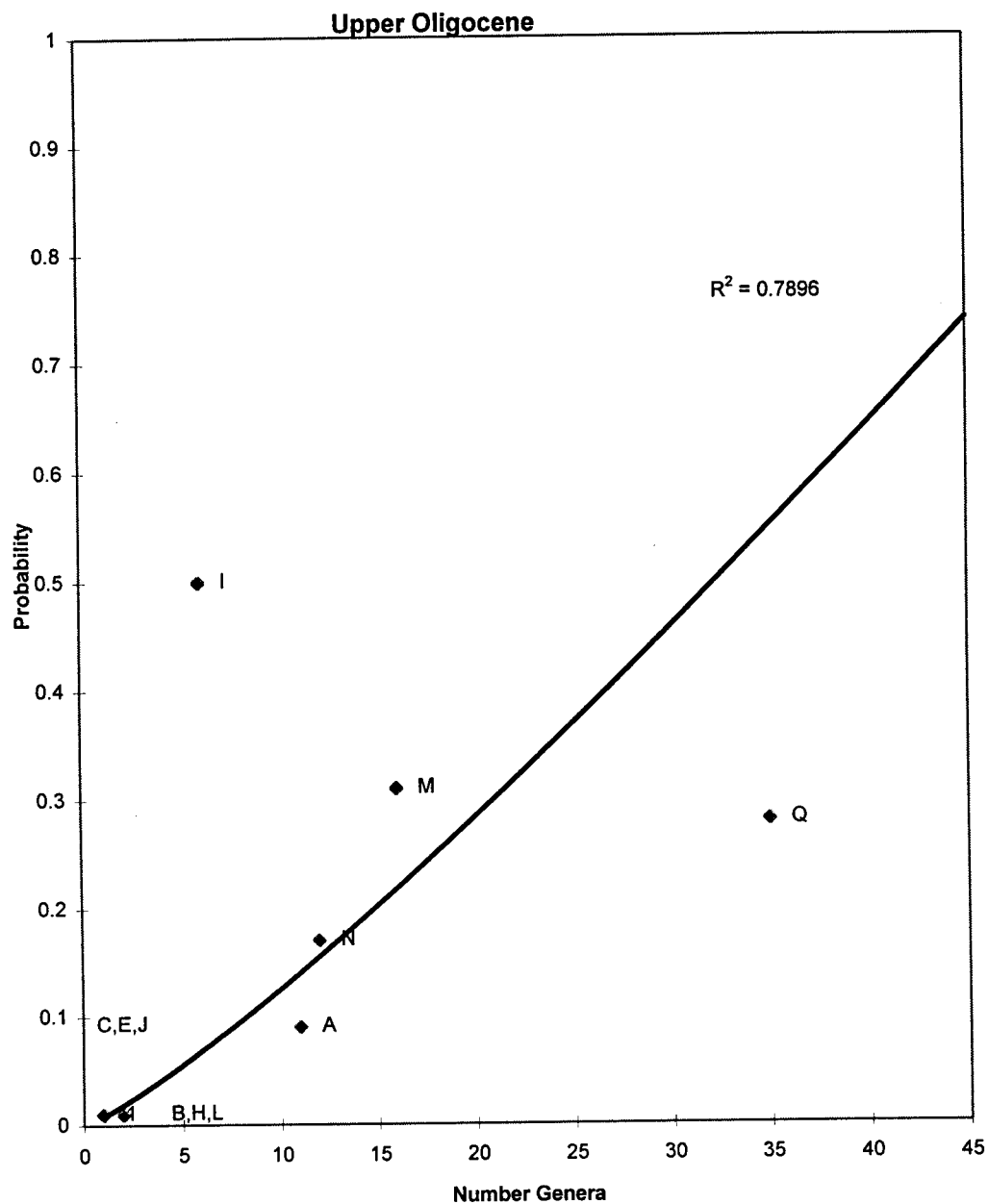


Figure 10. Linear regression of extinction probability with increasing genera for all echinoid orders during the Upper Oligocene. Each data point represents one order and plots the number of genera on x-axis versus the extinction probability on the y-axis. Orders are designated by the following system: A) Cidaroida; B) Euechinoida; C) Diadematoidea; D) Pedinoidea; E) Salenioida; F) Hemicidaroida; G) Phymosomatoida; H) Arbacioida; I) Temnopleuroidea; J) Echinoida; K) Orthopsida; L) Hololectypoida; M) Clypeasteroida; N) Cassiduloida; O) Disasteroida; P) Pourtalesioidea; Q) Spatangoida. Note, not all orders may be present in the database during this timestep.

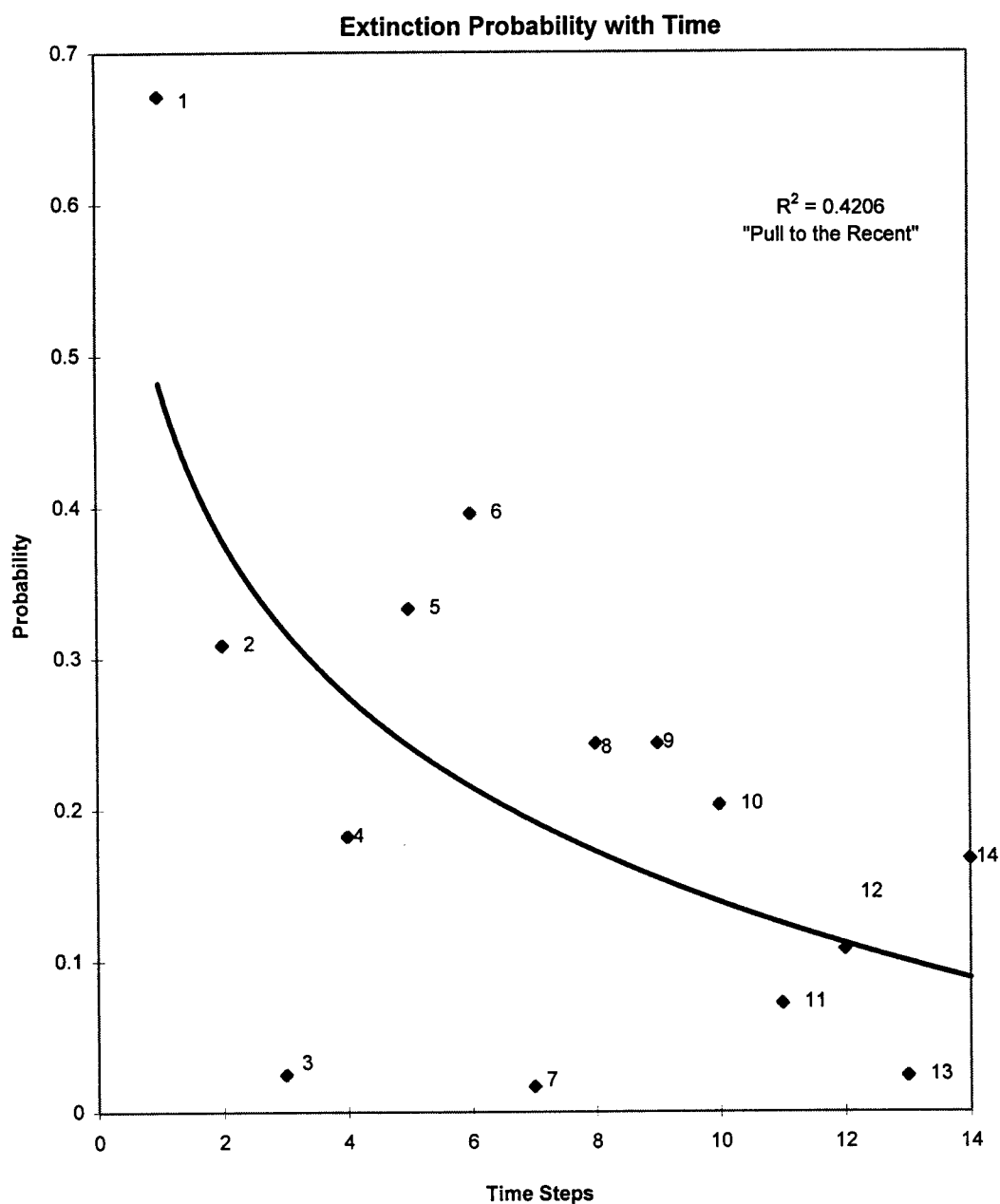


Figure 11. Chronologic plot of extinction probability against generic richness from Cretaceous to present. Each data point represents average ordinal echinoid extinction probability versus the number of genera recorded for each of 14 time steps, with 1 being the Upper Cretaceous and 14 being Recent. Note "Pull to the Recent" effect of less extinction probability as data approaches the present. Timesteps are designated by the following system: 1) Upper Cretaceous; 2) Lower Paleocene; 3) Upper Paleocene; 4) Lower Eocene; 5) Middle Eocene; 6) Upper Eocene; 7) Lower Oligocene; 8) Upper Oligocene; 9) Lower Miocene; 10) Middle Miocene; 11) Upper Miocene; 12) Lower Pliocene; 13) Upper Pliocene; 14) Pleistocene.

Normalized Analysis. In an attempt to lessen the sampling artifacts realized when comparing databases of various size, a normalized variance approach was utilized in conjunction with the method above. The average extinction ratio per each time interval, as derived above, was multiplied by the number of generic members for each order, giving a predicted number of extinct genera (Table IV). The observed extinctions were compared to the predicted by subtracting the values from the number of genera in question, and dividing the result yielding:

$$(G-O)/(G-P)= \text{normalized variance}$$

This analytical tool allows for equal comparison between groups, regardless of sample size, and gives a qualitative scale of variance, deviating from unity. Deviation from the mean was assumed at + or - .3 from 1, with values between .70 and 1.30 considered as falling with average extinction, with high values indicating low extinction (-), and low values indicating high extinction ratios (+). These data are presented in Tables V and VI, once again separating the two echinoid groups as regulars and irregulars. Comparisons to the data in Tables II and III show that the regular echinoid extinction trends remained basically unchanged. The irregulars do show some divergence between extinction trends using the different methodologies. The holcypoids, clypeasteroids, and cassiduloids have diminished extinction ratios, and tend to have more average values using the normalized approach. However, across all orders, there are particular time periods where heightened extinction seems evident, such as the Upper

Table IV. Predicted and observed extinctions, with variance of difference													
Order	L. Paleo	U. Paleo	L. Eocene	M. Eocene	U. Eocene	L. Oligo	U. Oligo	L. Mioce	M. Mioce	U. Mioce	Pliocene	Pleistocene	
Avg. Ext.	0.309	0.025	0.182	0.333	0.396	0.017	0.244	0.244	0.203	0.072	0.167	0.11	
Cidaroida	Predicted	3.1	2	1.5	3	4.4	0.17	2.7	2.4	2.2	0.8	2	1.4
	Observed	2	0	0	0	1	0	1	0	0	0	0	1
	Variance	1.16	1.02	1.23	1.5	1.5	1.02	1.2	1.32	1.25	1.08	1.2	1.03
Euechinoida	Predicted	0.62	0.05	0.36	0.66	0.79	0.034	0.49	0.49	0.41	0.14	0.33	0.22
	Observed	0	0	0	0	0	0	0	0	0	0	0	0
	Variance	1.45	1.02	1.22	1.5	1.65	1.02	1.32	1.32	1.26	1.08	1.2	1.12
Diadematoidea	Predicted	0.31	n/a	0.182	n/a	0.396	0.017	0.244	0.49	0.41	0.14	0.32	0.22
	Observed	1		1		0	0	0	0	0	0	0	0
	Variance	0		0		1.65	1.02	1.32	1.3	1.26	1.08	1.2	1.12
Pedinoida	Predicted												
	Observed												
	Variance												
Salenoida	Predicted	1.2	0.025	0.182	0.33	0.396	0.017	0.244	0.244	0.203	0.072	0.167	0.11
	Observed	3	0	0	0	0	0	0	0	0	0	0	0
	Variance	0.36	1.02	1.22	1.5	1.65	1.02	1.32	1.32	1.25	1.08	1.2	1.12
Hemicidaroida	Predicted	0.31	0.025	0.182									
	Observed	0	0	1									
	Variance	1.45	1.02	0									
Phymosomatoida	Predicted	1.5	0.075	0.73	1.67	2.77	0.017	0.244	n/a	n/a	n/a	0.167	
	Observed	2	0	0	2	6	0	1				1	
	Variance	0.57	1.02	1.22	0.9	0.23	1.02	0				0	
Arbacioida	Predicted	0.62	0.025	0.182	0.33	0.396							
	Observed	1	0	0	0	0							
	Variance	0.72	1.02	1.22	1.5	1.65							
Temnopleuroidea	Predicted	0.31	0.025	0.73	0.99	1.98	0.05	1.5	1.22	0.81	0.22	0.5	0.33
	Observed	0	0	2	1	3	1	2	1	1	1	1	1
	Variance	1.5	1.02	0.61	0.99	0.66	0.67	0.89	1.05	0.94	0.72	0.8	0.749
Echinoida	Predicted	0.31	0.025	0.182	0.33	0.396	0.017	0.244	0.244	0.203	0.072	0.5	0.22
	Observed	0	0	0	0	0	0	0	0	0	0	1	0
	Variance	1.5	1.02	1.22	1.5	1.6	1.02	1.3	1.3	1.25	1.08	0.8	1.12
Holectypoida	Predicted	0.309	0.025	0.55	1.67	2.4	0.017	0.488	0.488	0.41	0.072	0.167	0.11
	Observed	0	0	0	2	5	0	0	0	1	0	0	0
	Variance	1.4	1.02	1.2	0.9	0.27	1.02	1.3	1.3	0.62	1.01	1.2	1.12
Clypeasteroida	Predicted	0.62	0.05	0.55	3	5.9	0.12	3.9	4.4	3.25	0.94	2.5	1.21
	Observed	0	1	1	5	8	0	5	7	5	1	4	1
	Variance	1.45	0.51	0.81	0.66	0.76	1.01	1.9	0.81	0.86	0.99	0.88	0.98
Cassiduloida	Predicted	2.5	0.175	1.8	6.6	4.75	0.136	2.9	2.7	2	0.58	1	0.66
	Observed	1	0	0	10	4	0	2	2	2	2	0	1
	Variance	1.27	1.02	1.22	0.74	1.1	1.02	1.09	1.08	1	0.81	1.2	0.93
Disasteroida	Predicted	0.62											
	Observed	1											
	Variance	0.72											
Spatangoida	Predicted	4.9	0.4	3.5	10.6	13.5	0.37	8.5	8.3	5.2	1.5	3.5	2.2
	Observed	3	1	4	9	12	0	10	12	6	1	3	2
	Variance	1.2	0.95	0.96	1.08	1.08	1.02	0.94	0.84	0.95	1.02	1.03	1.01
Pourtalesoida	Predicted	0.62											
	Observed	2											
	Variance	0											
Neolampoida	Predicted					0.396		0.244					
	Observed					1							
	Variance					1.3							

Table V. Normalized variance of Regular echinoids.

Order	Cret		Pal		Eoc		Olig		Mio		Plio	Pleis
	U	L	U	L	M	U	L	U	L	M	U	
Cidaroida	-	0	0	-	-	-	0	0	-	-	0	0
Orthopsida	n/a											
Diadematoidea	-	+	n/a	+		-	0	-	-	-	0	0
Salenioidea	-	+	0	-	-	-	0	-	-	-	0	0
Pedinoida	+	n/a	n/a	+		+						
Temnopleuroidea	-	-	0	+	-	+	+	0	0	0	+	0
Phymosomatoida	-	+	0	-	0	+	0	+				
Echinoida	-	-	0	-	-	-	0	-	-	-	0	0
Arbacioida	0	+	0	-	-	-	0	0	-	-	0	0
Hemicidaroida	+	-	0	+								
Euechinoida	-	-	0	-	-	-	0	-	-	-	0	0

Table VI. Normalized variance of Irregular echinoids.

Order	Cret		Pal		Eoc		Olig		Mio		Plio	Pleis
	U	L	U	L	M	U	L	U	L	M	U	
Holactypoida	-	-	0	0	0	+	0	-	-	+	0	0
Cassiduloida	+	-	0	-	+	0	0	0	0	0	0	0
Clypeasteroida	-	-	+	0	+	+	0	0	0	0	0	0
Spatangoida	-	0	0	0	0	0	0	0	0	0	0	0
Disasteroida	+											
Pourtalesioidea	0	+										
Neolampoida						+			+			

Notes: Extinction trends of orders using normalized variance between Predicted and Observed extinctions (G-O)/(G-P). Predicted extinctions were derived by multiplying average extinction values for that stage by the number of genera (G) for that particular order. Deviations are ± 0.2 from unity. Extinction trends are compared to deviations from average extinction values: "0" denoted average values; "+" is favored toward extinction; "-" is favored against extinction. Time steps are divided into Upper (U), Middle (M), and Lower (L) intervals.

Eocene, and Lower Paleocene intervals. Of particular interest is the continued “average” extinction determined for the spatangoids, using both approaches. The fact that spatangoids dominate this database numerically as well as defining the extinction average implies that some selectivity is occurring, though the mathematical artifacts imposed by the larger data sets may conceal true behavior. Therefore, the development and implementation of new tools was deemed necessary to: 1) reduce any mathematical biases, and, 2) to consider other parameters thought to be intrinsic in evolutionary dynamics.

Flux Metric. The third facet of this study introduces a new approach and formula for resolving diversity and extinction patterns. A regression line through these data points shows the positive relationship between the number of extinct and new genera (Fig. 12), and confirms the necessity of considering both sets of data together rather than independently.

A formula meeting these requirements is defined here as:

$$\text{Flux} = \frac{G - E + N + S}{S + G [(E+1)/(N+1)]}$$

Understanding the dynamic of a biotic system may be more pertinent than extinction values alone, with the relationship between extinction and speciation being highly recognized (Stanley, 1990, McGhee, 1996)). Flux as defined here, is a measurement of internal variation within an order. Perfect stability is calibrated at 1, with

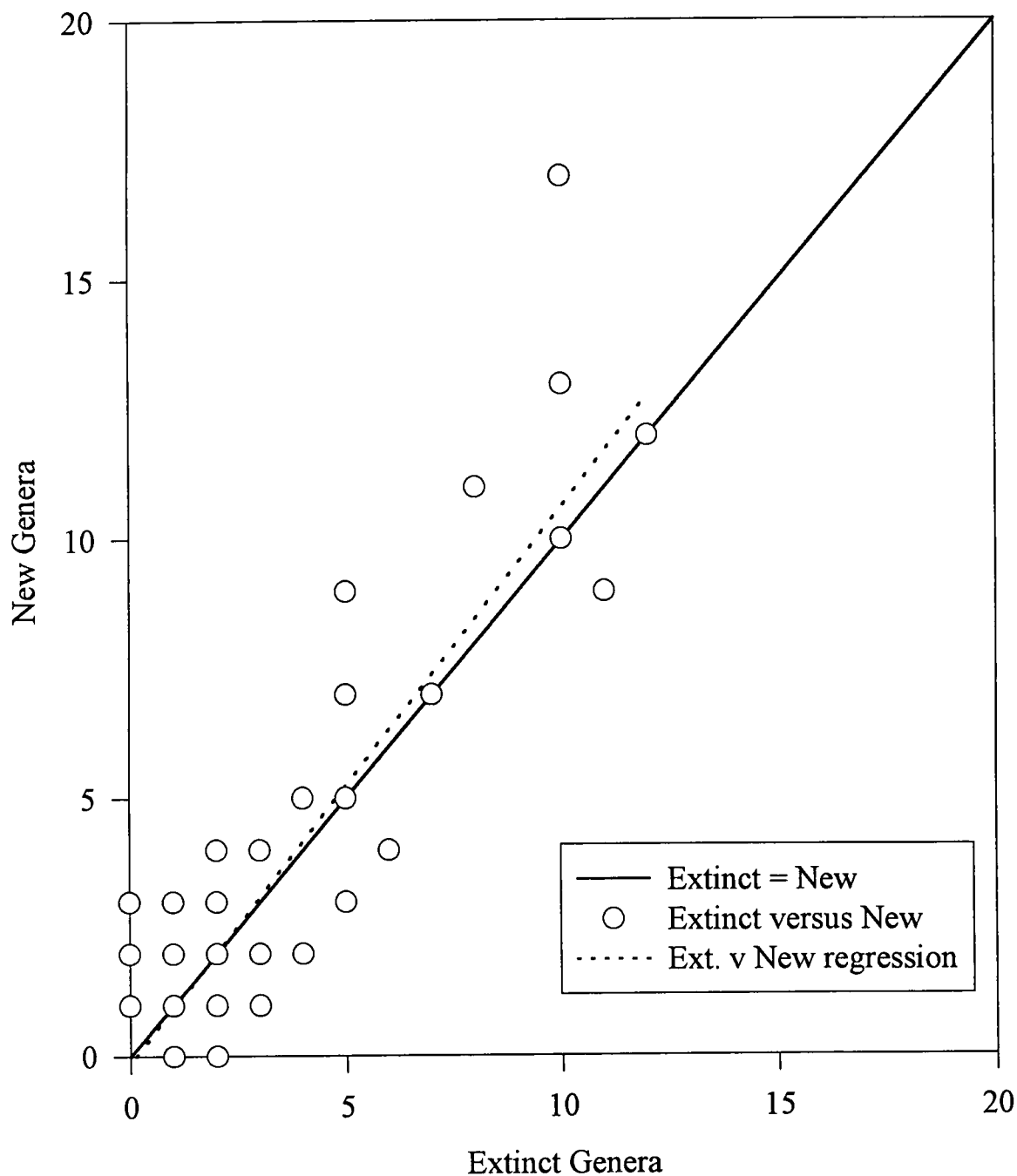


Figure 12. Plot of extinct genera versus new genera appearances for all orders for all time periods. The x-axis is number extinct and the y-axis is new appearances. Each point may contain multiple entries. Dashed line is linear regression of this data while the solid line is a 1:1 reference. Note the strong relationship between new appearances and extinction.

high flux > 1 , and low flux < 1 . When all genera become extinct, the values approach 0 for total extinction of an order.

Computational analysis of flux is presented in Table VII, of the regulars and irregulars, respectively, and the results do vary from the statistical measures employed previously in this work. Values above 1 indicate higher internal flux, with an increase in output, speciation or both. Values below 1 are a result of declining output, and/or extinction exceeding speciation. The results differ greatly from the first two analyses, and may depict a more realistic pattern of system dynamics. Spatangoids no longer define average behavior, and instead show variation of flux rather than "average" extinction as determined previously. Clypeasteroids, and cassiduloids also show more dynamic behavior than in the previous methods, showing both positive and negative flux modes. The regular echinoids actually expressed more stable values, whereas in Tables II and III and Tables V and VI, they are depicted as mostly below average extinction. Flux graphs of each order are presented in Figs 13a-g, along with an average flux graphs (Fig. 14a-b), constructed by computing the flux for all genera behavior for each timespan. This depiction of internal flux does show independent behavior between orders which may be due to selectivity.

While variations in magnitude and direction of flux between the orders is evident, there are still strong trends which transcend ordinal behavior. Flux graphs of higher taxonomic resolution (genera to family), are consistent with genera to order dynamics. Three examples of genera to family flux are shown (Fig. 15a-c) The Lower Paleocene is seen as a time of low flux for most orders, with the Lower to Mid Eocene, and the Upper

Table VII. Flux of all Orders per time interval, with average Flux calculated

	L. Paleo	U. Paleo	L. Eocene	M. Eocene	U. Eocene	L. Eocene	L. Oligo	U. Oligo	L. Mioce	M. Mioce	U. Mioce	L. Plio	M. Plio	U. Plio	Pleisto
Cidaroida	0.42	1	1	1	1.44	1.3	1	1	1	1	1.41	1	1	1.4	1
Euchinoida	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Diadematoidea	0	0	0.2			2	1	1	2	1	1	1	1	1	1
Pedinoida			0.2	4	0										
Salenoida	0.33	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Hemicidaroida	1	1	0												
Phymosomatoida	0.33	1	1.6	0.67	0.51	0									
Arbacioida	1	1	1	1	1	1	1	2	1	1	1	1	1	1	0.4
Tennopleuroidea	1	1	1.5	1	1.3	1.3	0.5	1.45	1.8	0.69	1	0.54	1	1	1
Echinoida	1	1	1	1	1	1	1	1	1	1	1	2	1	1	1
Holactypoida	0.2	1	3	1	0.5	1	2	1	1	0.4	1	1	1	1	1
Clypeasteroida	1	1	1.6	1.48	1.47	1	1.62	1	1	1	1.27	1.2	0.63	0.81	1
Cassiduloida	1	1	2.1	1	0.64	1	1.48	1	0.75	0.74	0.4	1	1	1	0.58
Disasteroida	0														
Spatangoida	0.59	1.26	1.15	1.58	1	1	1.2	0.85	0.77	1.24	0.77	0.64	1	0.77	
Pourtalesioidea	0.33														
Neolampoida						1									
Average Flux	0.35	1.22	1.4	1.28	1.02	0.48	1.4	1	0.82	1.08	0.82	0.48	0.84	0.74	

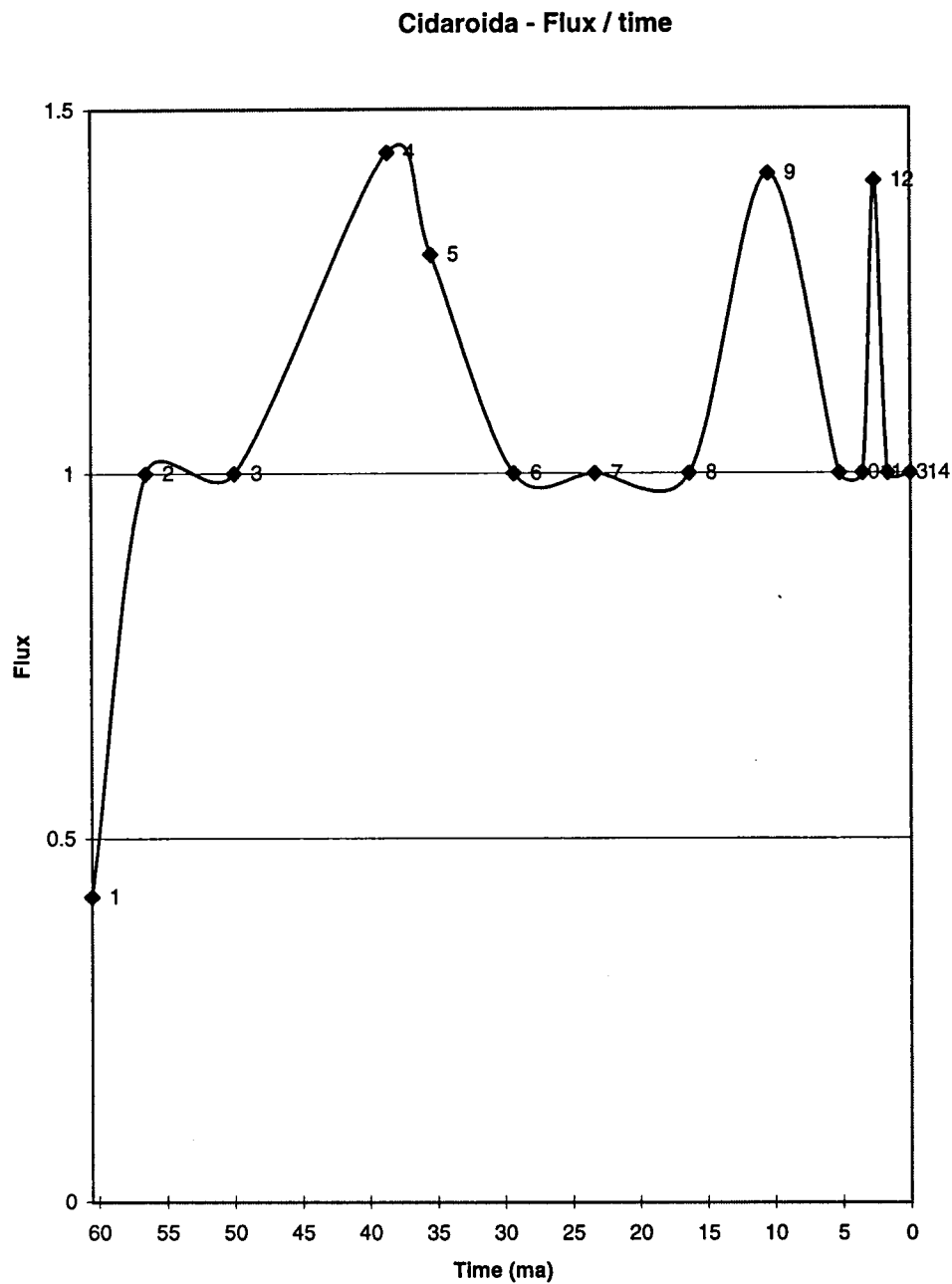


Figure 13. Flux graphs of selected echinoid orders. Figure 13a, flux versus time of the Order Cidaroida. Data points are designated by the following system: 1) Upper Cretaceous; 2) Lower Paleocene; 3) Upper Paleocene; 4) Lower Eocene; 5) Middle Eocene; 6) Upper Eocene; 7) Lower Oligocene; 8) Upper Oligocene; 9) Lower Miocene; 10) Middle Miocene; 11) Upper Miocene; 12) Lower Pliocene; 13) Upper Pliocene; 14) Pleistocene.

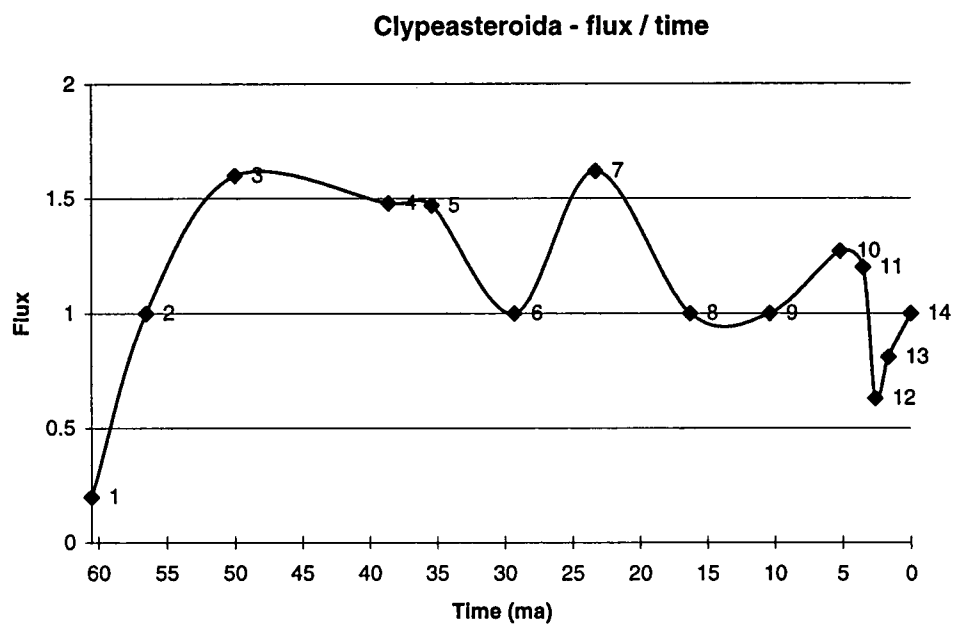


Figure 13 (continued). Figure 13b, flux versus time of the Order Clypeasteroida. Data points are designated by the following system: 1) Upper Cretaceous; 2) Lower Paleocene; 3) Upper Paleocene; 4) Lower Eocene; 5) Middle Eocene; 6) Upper Eocene; 7) Lower Oligocene; 8) Upper Oligocene; 9) Lower Miocene; 10) Middle Miocene; 11) Upper Miocene; 12) Lower Pliocene; 13) Upper Pliocene; 14) Pleistocene.

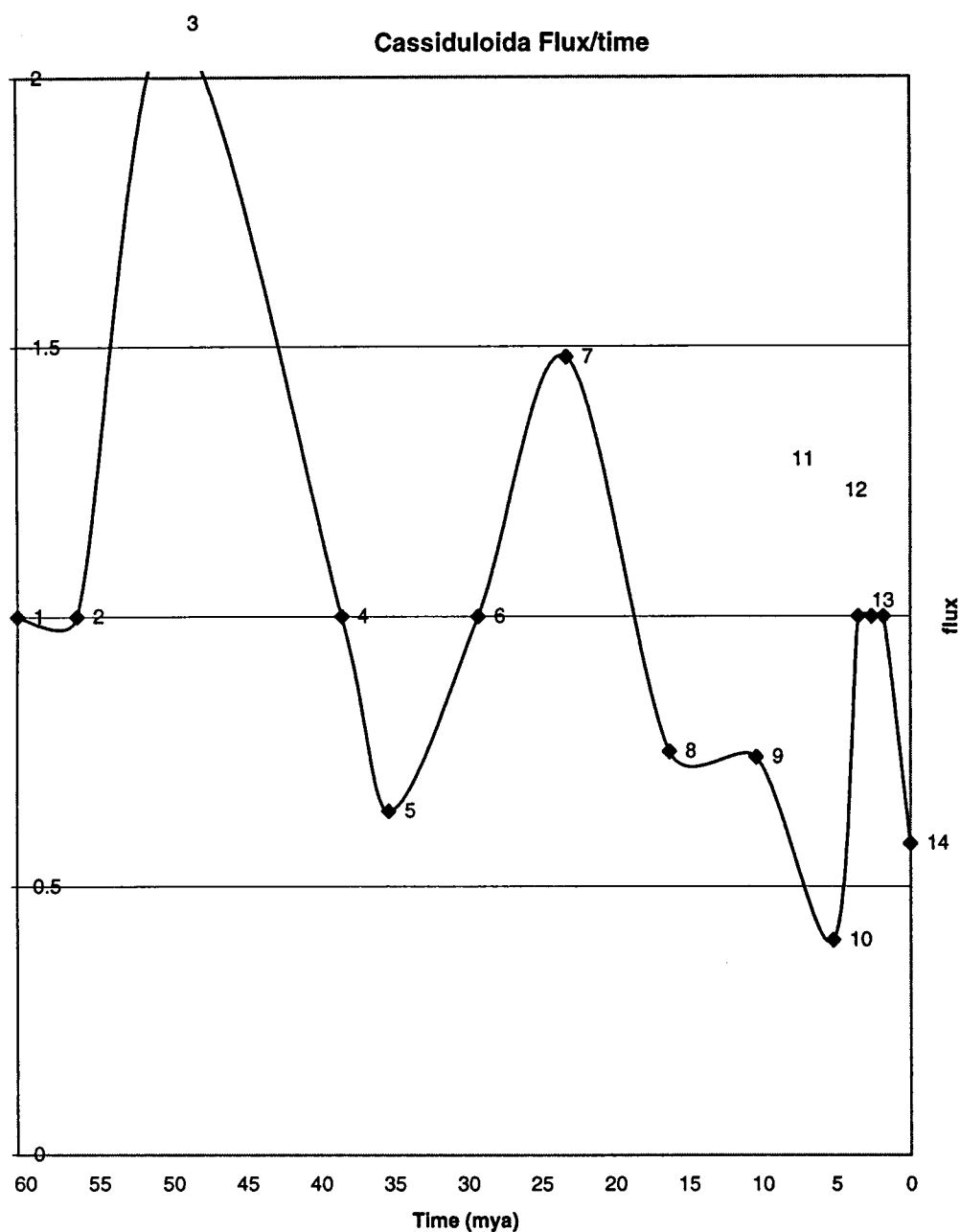


Figure 13 (continued). Figure 13c, flux versus time of the Order Cassiduloida. Data points are designated by the following system: 1) Upper Cretaceous; 2) Lower Paleocene; 3) Upper Paleocene; 4) Lower Eocene; 5) Middle Eocene; 6) Upper Eocene; 7) Lower Oligocene; 8) Upper Oligocene; 9) Lower Miocene; 10) Middle Miocene; 11) Upper Miocene; 12) Lower Pliocene; 13) Upper Pliocene; 14) Pleistocene.

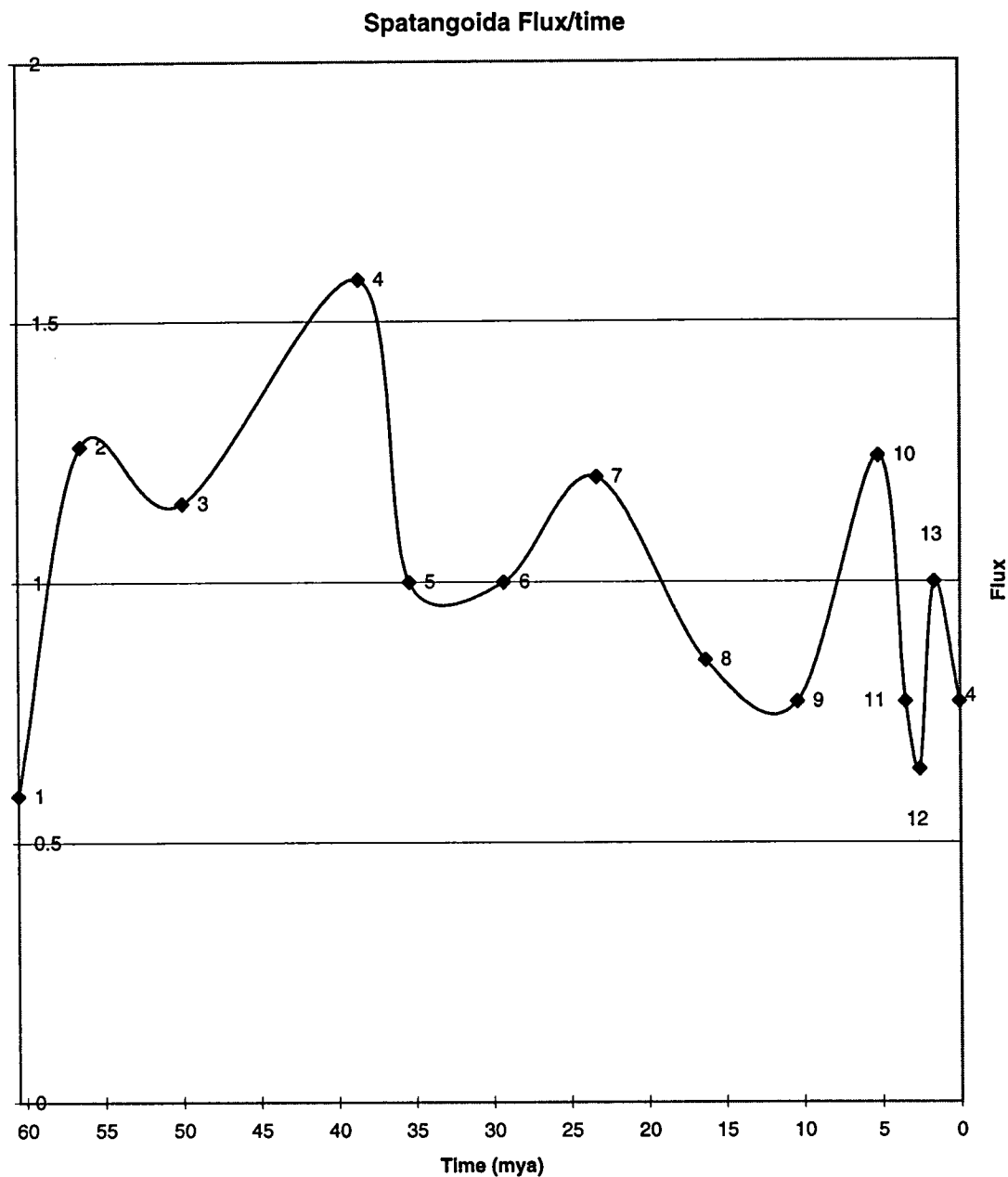


Figure 13 (continued). Figure 13d, flux versus time of the Order Spatangoida. Data points are designated by the following system: 1) Upper Cretaceous; 2) Lower Paleocene; 3) Upper Paleocene; 4) Lower Eocene; 5) Middle Eocene; 6) Upper Eocene; 7) Lower Oligocene; 8) Upper Oligocene; 9) Lower Miocene; 10) Middle Miocene; 11) Upper Miocene; 12) Lower Pliocene; 13) Upper Pliocene; 14) Pleistocene.

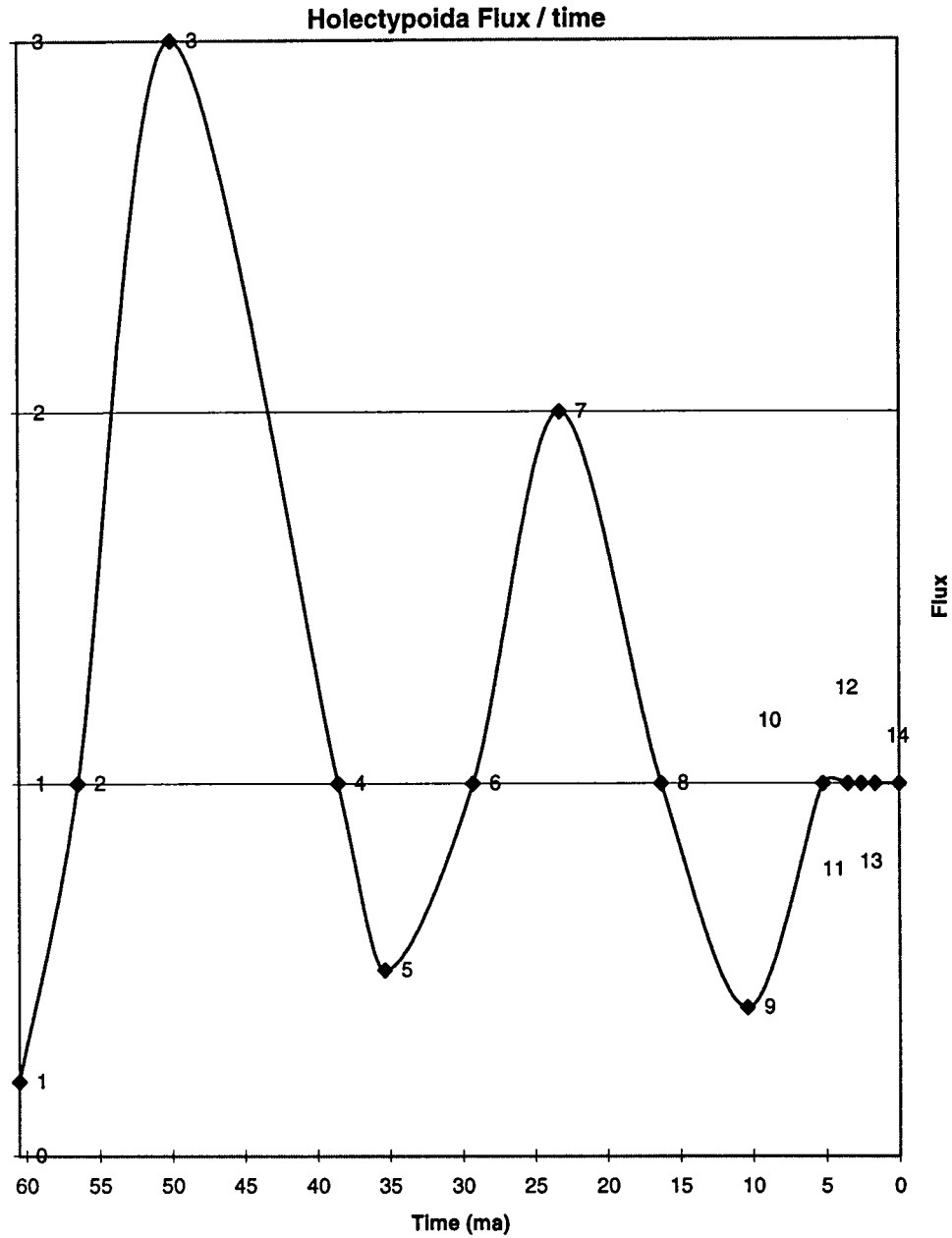


Figure 13 (continued). Figure 13e, flux versus time of the Order Holectypoida. Data points are designated by the following system: 1) Upper Cretaceous; 2) Lower Paleocene; 3) Upper Paleocene; 4) Lower Eocene; 5) Middle Eocene; 6) Upper Eocene; 7) Lower Oligocene; 8) Upper Oligocene; 9) Lower Miocene; 10) Middle Miocene; 11) Upper Miocene; 12) Lower Pliocene; 13) Upper Pliocene; 14) Pleistocene.

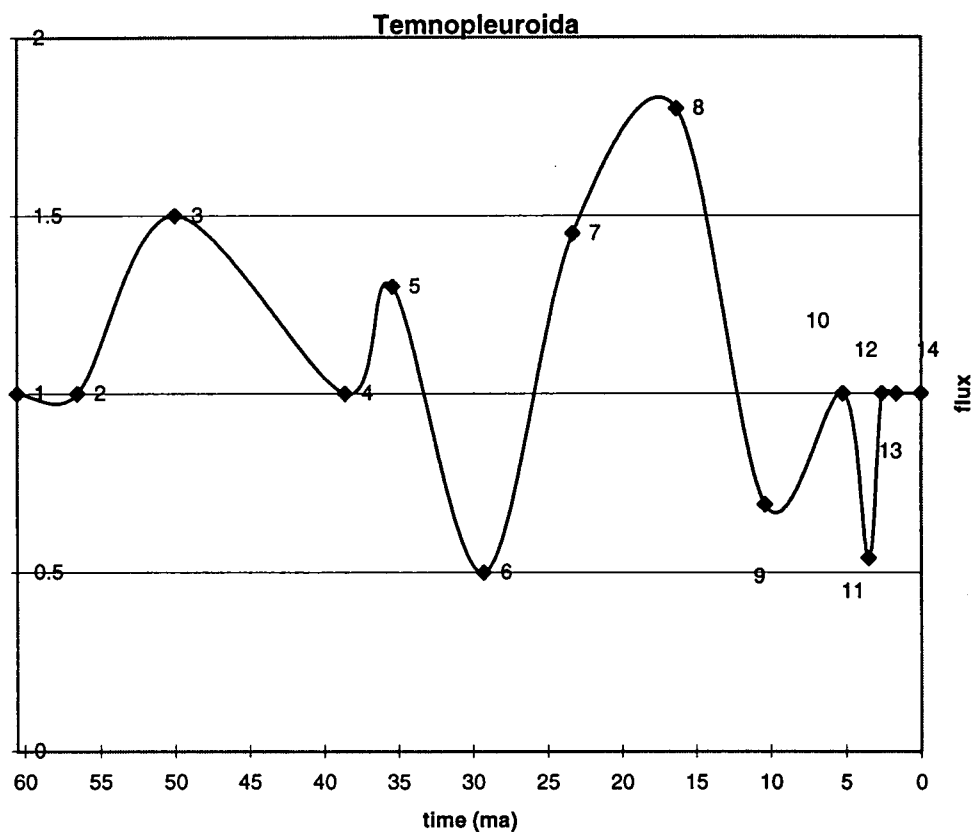


Figure 13 (continued). Figure 13f, flux versus time of the Order Temnopleuroida. Data points are designated by the following system: 1) Upper Cretaceous; 2) Lower Paleocene; 3) Upper Paleocene; 4) Lower Eocene; 5) Middle Eocene; 6) Upper Eocene; 7) Lower Oligocene; 8) Upper Oligocene; 9) Lower Miocene; 10) Middle Miocene; 11) Upper Miocene; 12) Lower Pliocene; 13) Upper Pliocene; 14) Pleistocene.

Phymosomatoida

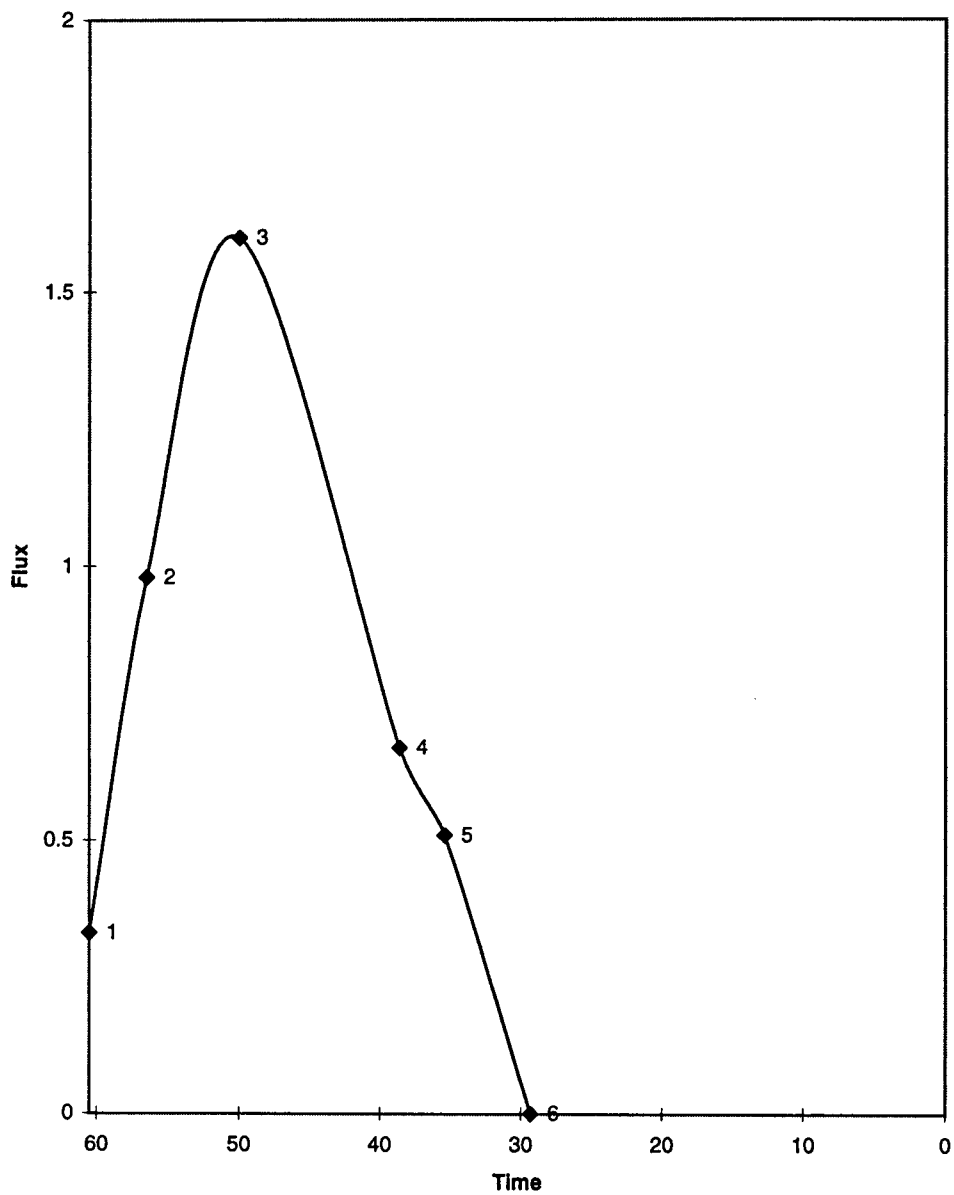
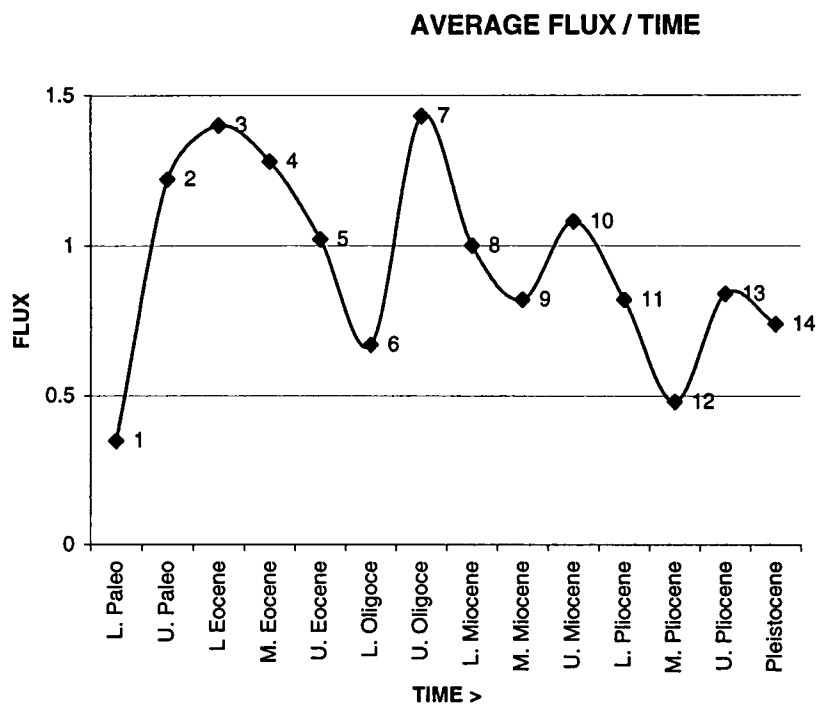


Figure 13 (continued). Figure 13g, flux versus time of the Order Phymosomatoida. Data points are designated by the following system: 1) Upper Cretaceous; 2) Lower Paleocene; 3) Upper Paleocene; 4) Lower Eocene; 5) Middle Eocene; 6) Upper Eocene; 7) Lower Oligocene; 8) Upper Oligocene; 9) Lower Miocene; 10) Middle Miocene; 11) Upper Miocene; 12) Lower Pliocene; 13) Upper Pliocene; 14) Pleistocene



Figures 14. Graphs of average flux for all orders. Figure 14a shows flux plotted against geologic time steps. Each data point is the average flux per time interval calculated by computing total G, E, N and S values (see text for explanation of variables) of all orders to determine flux. Data points are designated by the following system: 1) Upper Cretaceous; 2) Lower Paleocene; 3) Upper Paleocene; 4) Lower Eocene; 5) Middle Eocene; 6) Upper Eocene; 7) Lower Oligocene; 8) Upper Oligocene; 9) Lower Miocene; 10) Middle Miocene; 11) Upper Miocene; 12) Lower Pliocene; 13) Upper Pliocene; 14) Pleistocene.

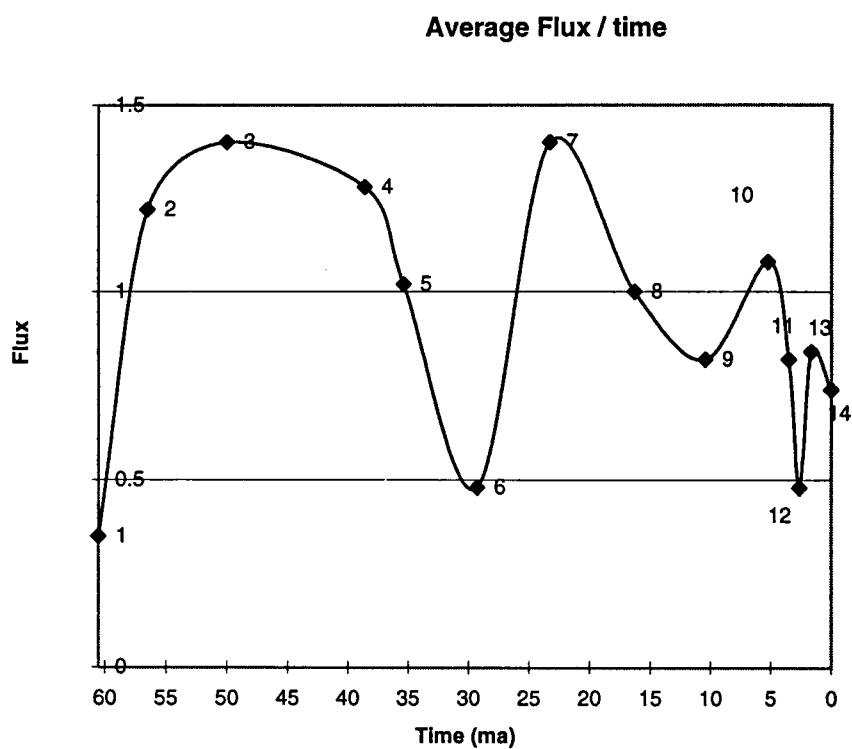
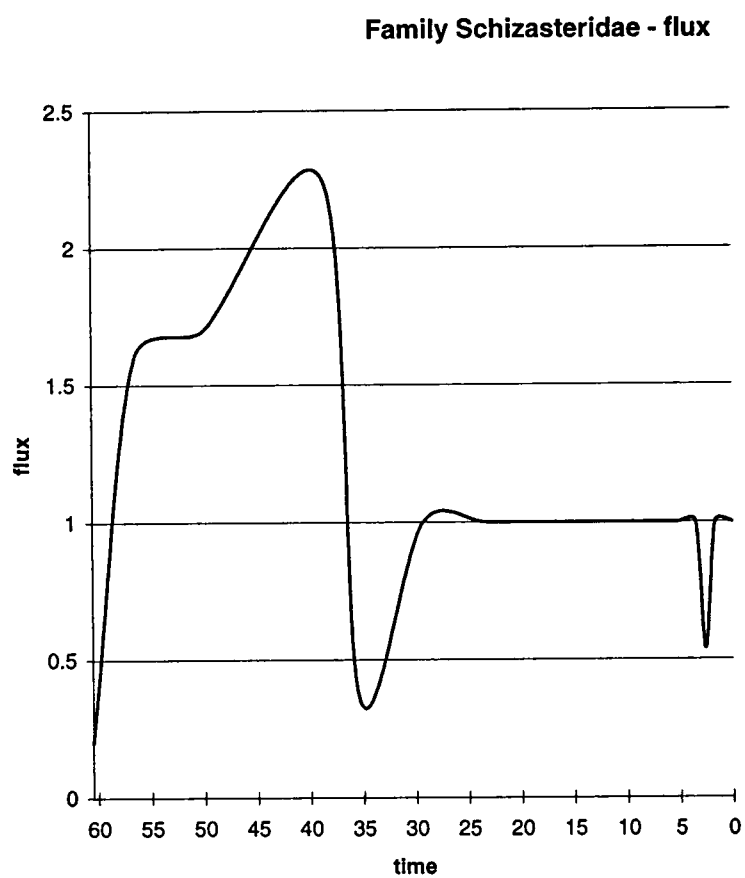


Figure 14 (continued). Figure 14b, flux graph of averaged flux of all orders plotted against absolute time. Each data point is the average flux per time interval calculated by computing total G, E, N and S values, as in Fig. 14a. Data points are designated by the following system: 1) Upper Cretaceous; 2) Lower Paleocene; 3) Upper Paleocene; 4) Lower Eocene; 5) Middle Eocene; 6) Upper Eocene; 7) Lower Oligocene; 8) Upper Oligocene; 9) Lower Miocene; 10) Middle Miocene; 11) Upper Miocene; 12) Lower Pliocene; 13) Upper Pliocene; 14) Pleistocene.



Figures 15. Examples of genera to family flux. Figure 15a, flux of the Family Schizasteridae over absolute time.

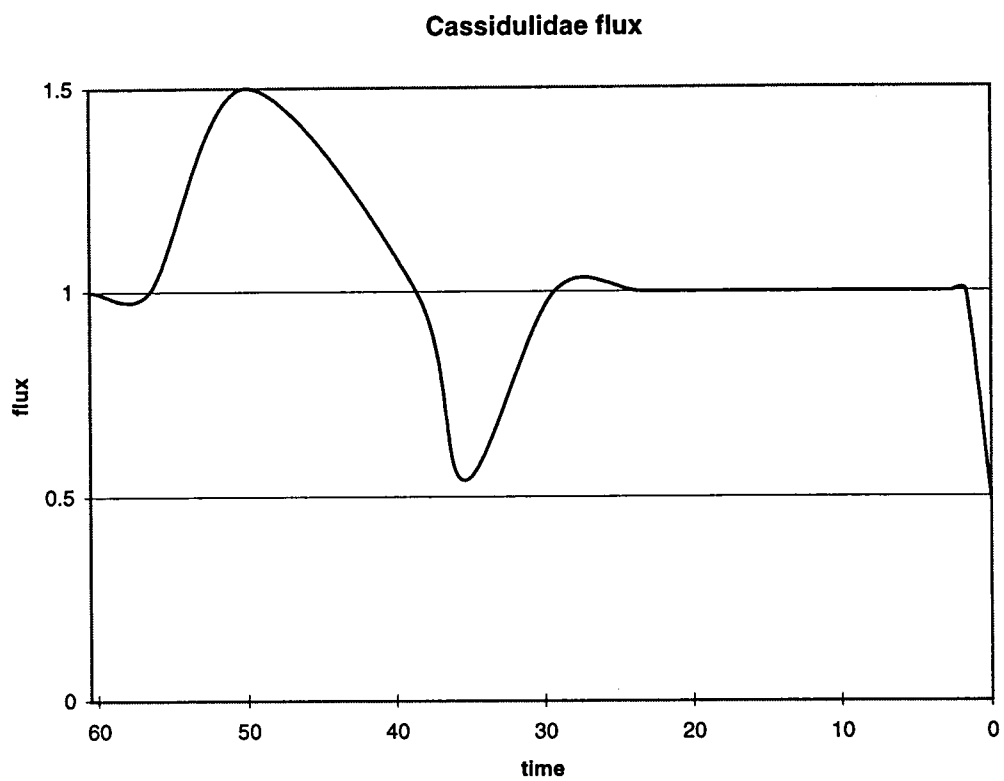


Figure 15 (continued). Figure 15b, flux of the Family Cassidulidae over absolute time.

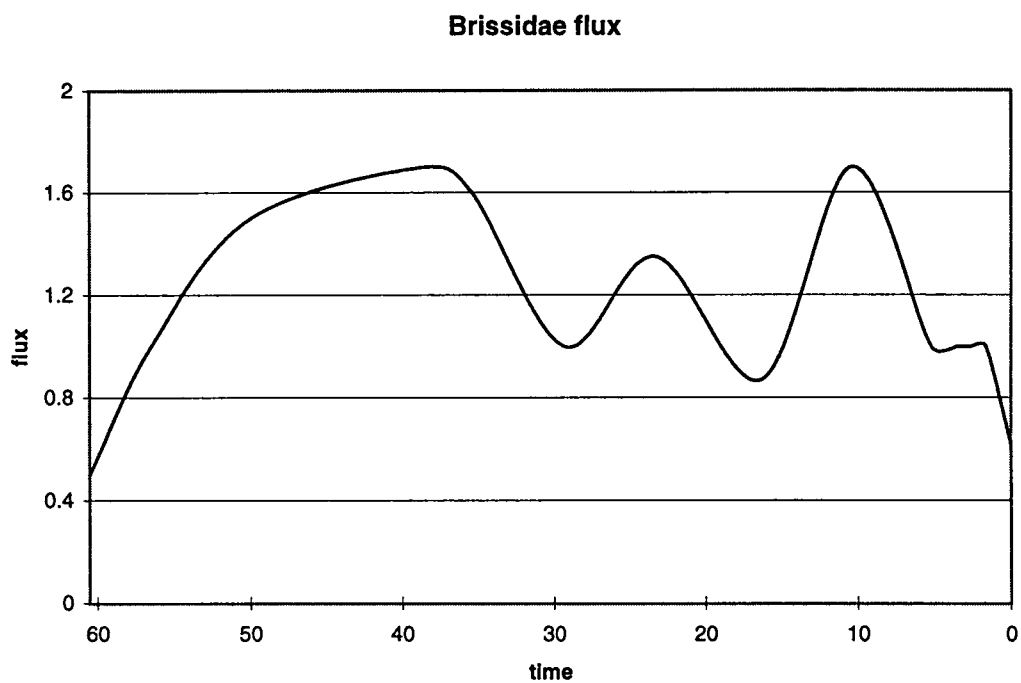


Figure 15 (continued). Figure 15c, flux of the Family Brissidae over absolute time.

Oligocene show crests indicative of high flux. Additionally, the trend towards recent shows an overall decrease in internal fluctuations, both across the orders and with the average flux graph. The changes in trends, when examining more than one parameter, also indicate the correlation between high extinction and high diversity. High extinction ratios (+) from the statistical approach are countered by high diversification trends with the normalized flux method. Similarly, low (-) or average (0) extinction values from the statistical analysis are met with low diversity trends using the flux approach. Thus a different picture develops as other parameters are considered, which only underscores the importance and interdependence of these relationships.

DISCUSSION

Interpretations of extinction data alone via statistical analysis show more extinction within the irregular group than the regulars, which would imply positive extinction selectivity towards the irregulars. A major exception is the spatangoids, which are consistently "average". Conventional wisdom and traditional theories would declare spatangoids as "extinction-resistant", with explanations such as infaunal life modes (Smith, 1984) contributing to resilience. However, examination of spatangoid flux shows that decline occurred significantly for this order. Clypeasteroids, which had higher extinction ratios, actually demonstrated higher flux, and thus increased diversity. These seemingly contradictory results can be resolved, considering the strong correlation between extinction and speciation, as shown earlier. High extinction rates may not necessarily indicate ordinal decline, they may instead relate to speciation events, or at least link the forcing functions that control extinction and speciation. Using extinction data alone, the spatangoids would appear healthy and average, with no selectivity evident. However, the apparent decline in flux may imply that reasons imposed for extinction resilience can also explain the decline in flux.

Being deep burrowers, spatangoids may be more resilient because of the sheltered, insulated habitat provided when occupying such a niche (Smith, 1984; McNamara, 1994). But, it can be argued, especially with flux data, that perhaps the more specialized nature of an infaunal mode, compared to the epifaunal nature of the regulars, makes the Spatangoids less adapted during increasingly dynamic environmental conditions. This is

in contrast to the more generalist types, like shallow water, reef-dwelling cidaroids (Hendler *et al.*, 1995) that seem to follow more stable flux patterns. The regulars which showed lower extinction ratios demonstrated positive flux correlations. This is not to discount the usefulness of the extinction data. In fact, considering the spatangoids again, was there no selectivity evident?

The interpretation that infaunal nature makes the spatangoids less adaptable to change does not explain the average extinction values observed when using traditional statistical approaches of extinction-ratio only data. This can be addressed because this database, and indeed the fossil record, is dominated by spatangoid occurrences. This may not be as indicative of abundance as it is for taphonomic biases, which may influence the propensity for preservation (Smith, 1984, Raup, 1991). The same argument made for deep burrowers having more environmental resilience than shallow or epifaunal genera can be applied to preservational qualities as well - deep burrowers are already in place for fossilization, due merely to life mode. This indeed is selectivity, with taphonomic biases skewing data. However, it should be noted that life mode traits may be a heritable (McKinney, 1995), therefore some selectivity could still occur. Life mode traits can be linked to environmental conditions (McNamara, 1994; McKinney *et al.*, 1992), which also indicates selectivity.

Conversely, the cidaroids had low extinction ratios, due in part to their small sample size. However, they appear quite stable with the flux method. As epifauna, in nearshore dynamic areas, they are considered generalists in comparison to the specialized deep water and burrowing spatangoids (McNamara, 1990). One interpretation may be

that they are stable during extinction events, because as generalists, they can better adapt to changing environments. And, as one of the oldest echinoid lineages, cidaroids may experience incumbency (Sepkoski, 1996; Rosenzweig and McCord, 1991), which is the condition where long-lived lineages trend towards less extinction.

The low extinction ratios derived for the regulars contrast with the generally high and/or stable flux calculations. Once again, taphonomy may be responsible. Lower abundance and smaller data sets do not greatly influence the average extinction ratios. Lack of preservation would account for depauperate datasets, which is a reasonable expectation considering the epifaunal, high energy environment life mode exhibited by some of the regulars along with their tendency to become disarticulated during diagenesis (Smith, 1984). Similar reasoning can also explain the high flux and stability of these genera - that as generalists they are better adapted for dynamic environments than their more specialized and somewhat sessile counterparts. The change to high energy conditions may be the result of some forcing function (s) responsible for extinction in the first place. Increasing the dynamics of the environmental forcing functions may increase sedimentation, and subsequent differentials between preservation and fossilization of specimens, which may only compound the artifacts of sampling bias. This may be evident in the positive correlations between taxa richness and extinction probability as noted in this research and with others (Lawton, 1995).

In fact, it may be that extinction events as previously interpreted, are actually periods of increased sediment influx. Raup (1976) noted that an increased volume of sedimentary rock would preserve more fossil types than a smaller rock package. Higher

extinction rates are shown here to be due in part to larger sample sizes. This could imply interpretations of some extinction events may actually be indicative of increased deposition, or increased deposition *because* of some environmental gradient. Additionally, orders may improve their taphonomic quality, responding to external factors. Spatangoids have been observed in an offshore retreat in Tertiary Australia (McNamara, 1994), which may be a response to environmental gradients.

Substrate control has been suggested on echinoid distribution (McKinney, 1986), and upon functional morphology (McNamara and Philip, 1980). Displacement into new substrate as a bathymetric response has also been pondered (Jablonski and Bottjer, 1988; McNamara, 1990). McNamara (1990, 1994) proceeds with evidence of gastropod predation on some echinoids as a mitigating factor influencing displacement. He documents defensive strategies in morphology or habitat preference as responses. In the Australian fauna, niche replacement from cassiduloids to clypeasteroids has been postulated for the lower Miocene. This is thought to be a result of gastropod predation (cassid) which seemed to target the cassiduloids (McNamara, 1994) over the clypeasteroids, which differ in morphology yet share similar ecospace. Flux graphs of cassiduloid and clypeasters (Fig. 16) show an inverse behavior during this time, which seems to indicate selectivity. A similar pattern between cassiduloids and clypeasters is observed in the Upper Eocene, which is also the time cassid gastropods are first observed in the global fossil record (McNamara, 1994).

Though many generalizations may be inferred by using data from treatments like flux graphs, it is certainly should be mentioned that selectivity at higher taxonomic levels

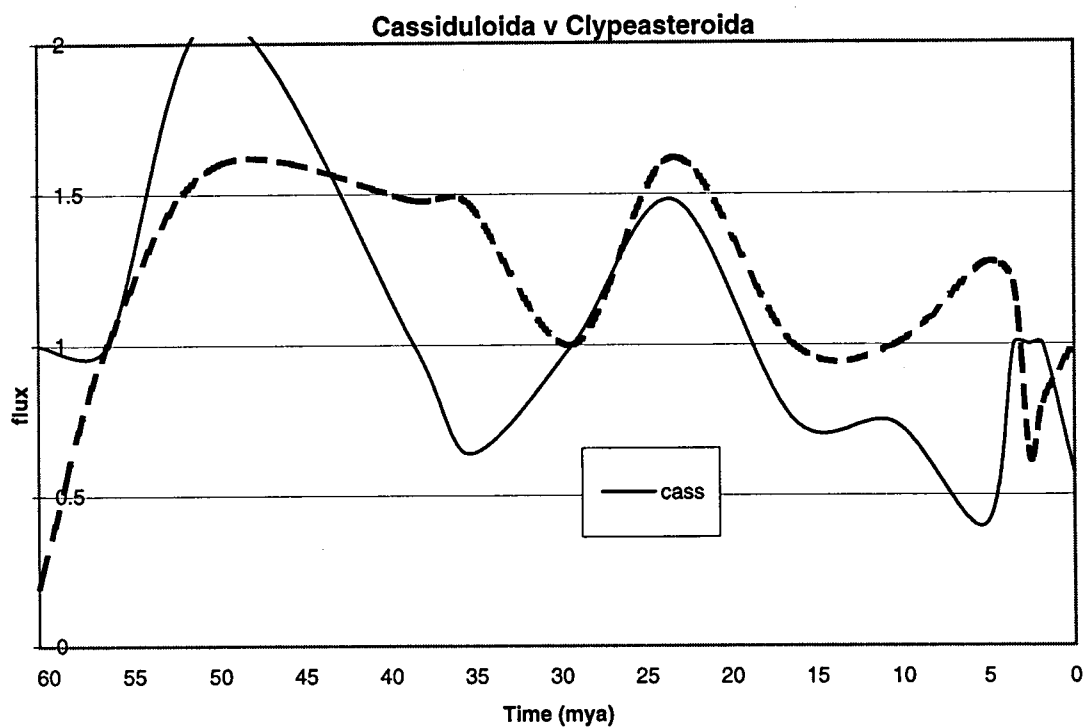


Figure 16. Differential flux of the Orders Cassiduloida and Clypeasteroida. Both orders are irregulars and occupy similar niches, however, cassiduloida decline at 45 to 35 mya may be linked to preferential predation by gastropods which may target the cassiduloids over the clypeasteroids.

is difficult to relate to biologic variables (Jablonski, 1996). This is due in part to the diverse nature of such a large group. However, overall patterns of this database do seem to confirm previously reported correlations between diversity and ocean temperature (McKinney *et al.*, 1992). Diversity plots (Fig. 17) of echinoid diversity and temperature during the Cenozoic follow the same pattern as flux graphs, as does a global sea temperature graph of southern high latitude oceans (Fig. 18). The relationship between flux and temperature should also be cautiously interpreted since many variables such as sea level and sedimentation rates often vary with temperature change (McKinney *et al.*, 1992), and these are intrinsic environmental gradients as well as factors enhancing taphonomic biases.

The similarity of flux graph results with other published data seems to confirm this method. Consistent trends with independent published data of echinoid diversity patterns (McKinney *et al.*, 1992) or of inter-order dynamics with possible niche competition (McNamara, 1994) in the Miocene are present with this method. Additionally, major dynamics of echinoid diversity during the Cenozoic as presented by various authors, such as Eocene and Oligocene peaks are also coincident with the data presented with flux. These strong correlations confirm the validity and usefulness of using an approach such as flux when measuring and interpreting the fossil record.

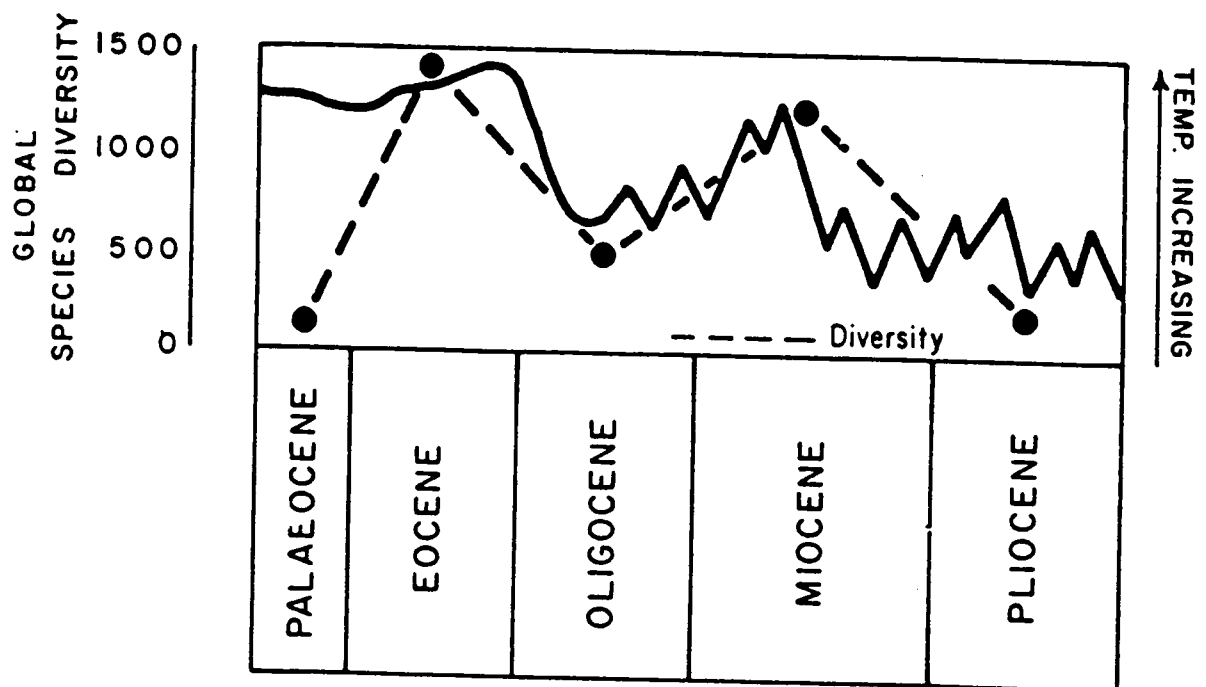


Figure 17. Published echinoid diversity plotted against global temperature. Source: McKinney, M.L. and Oyen, C.W., 1989. Causation and non-randomness in biological and geological time series: Temperature as a proximal control of extinction and diversity. *Palaios* 4:3-15.

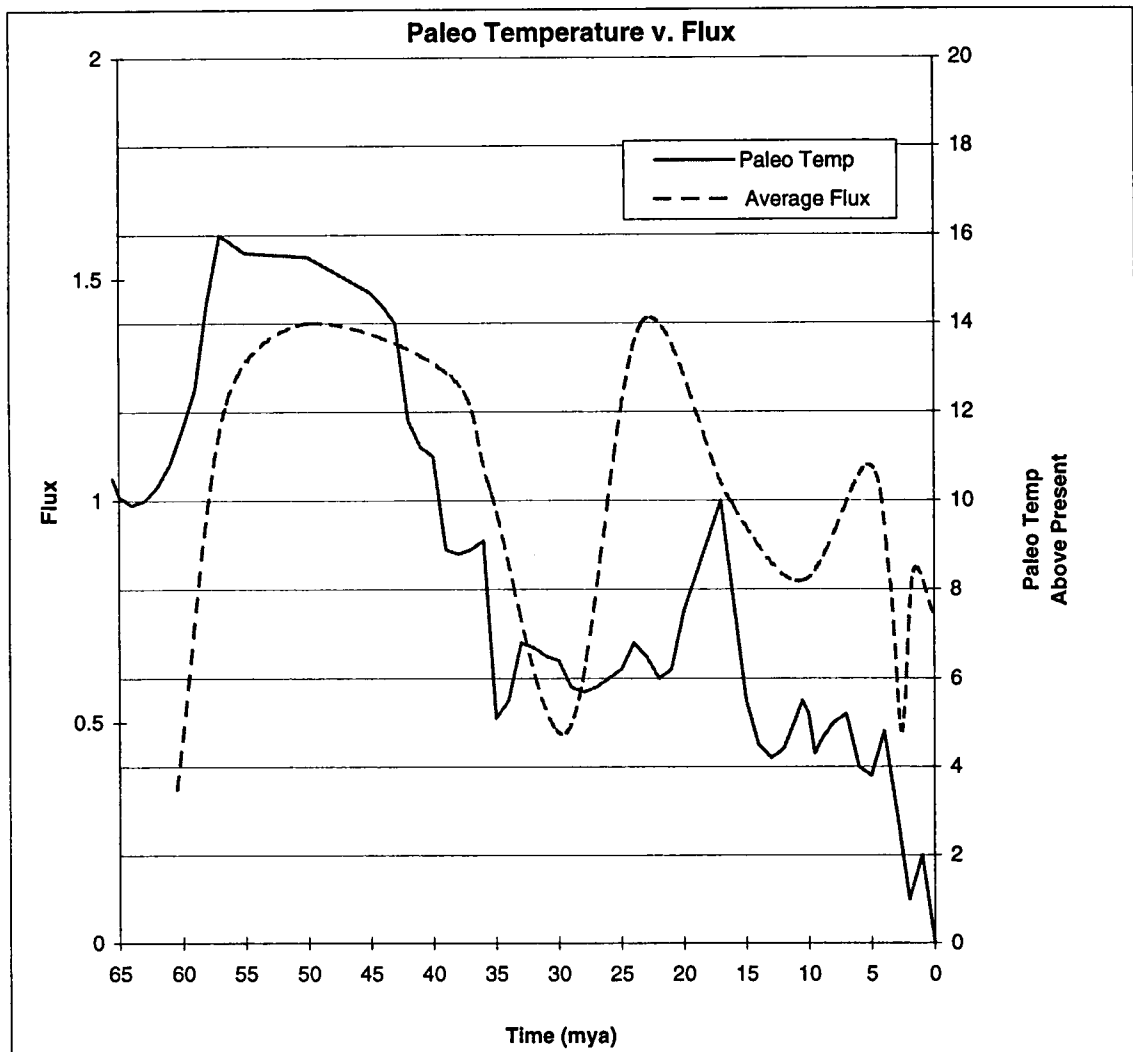


Figure 18. Echinoid genera to order flux plotted with Cenozoic paleotemperatures, showing a correlation between temperature and flux. Flux scale on left y-axis, temperature scale on right y-axis. Temperature data taken from (source): Crame, J.A., 1993. Latitudinal range fluctuations in the marine realm through geologic time. *Tree* 8 (5) 162-164.

SUMMARY

Extinction alone is not the sole descriptor of evolution. Numerous citations abound in professional research confirming the positive correlation between origination and extinction. The trend of extinct/new ratios from this database also shows the proportionality between these two parameters. Relative changes in behavior may be a more succinct and appropriate choice for understanding taxa dynamics. We cannot expect to have equal fossil sets presented to us; and the first option should not be to recreate the data to fit mathematical expectations. Rather, the relative flux of one group compared to that of other groups can provide insight to differential behavior through time and space. Though not quantitative, relative measures are probably a more realistic comparison since the fossil record is not quantitatively complete. Phase two of this project used a normalized variance approach to assess extinction behavior, and yielded results from small data sets which previously would have had to be ignored due to statistical insignificance. Too much concern is placed about high extinction rates, because, when one puts geologic time into perspective, the message is clear - most taxa do become extinct. Therefore, perhaps other parameters such as speciation and stability should be considered along with extinction data, requiring the use of new metrics.

The third phase of this project centered upon measuring other evolutionary dynamics, in addition to extinction which could be gleaned from the data set. The flux metric, as derived, provided a working tool with which data packages of various sizes could be compared and analyzed for a number of parameters simultaneously. Using the

concept of normalized variance and by considering other factors which contribute to evolutionary flow, a different picture emerges. High extinction rates are not necessarily bad, they may be indicative of an order's growth and speciation, or a response to an environmental gradient, or total decline and disappearance. By comparing the total health of an order in this fashion, perhaps a better understanding may be incurred of the forcing functions which acted upon biotic systems in the geologic past. Trends in relative flux are probably more indicative of environmental controls than extinction data alone, which has been assumed, and shown, to be linked closely to speciation (Raup, 1994; Appendix C).

The equation developed for this study:

$$\text{Flux} = \frac{G - E + N + S}{S + G [(E+1)/(N+1)]}$$

$$S + G [(E+1)/(N+1)]$$

G= number of genera present during a time interval

E= number genera extinct

N= number of new appearances

S= number of stable genera

is deemed appropriate on several levels. First, it is normalized for sample size. Second, it considers generic stability with input and output parameters. Third, it also considers extinction relative to speciation. Fourth, the model is applicable to small data packages, and missing entries. The discerning element to this formula is the definition of stability (S), which mandates generic presence both prior and anteceding the time period in question. Current predictive models usually only consider extinction, or extinction, speciation and genera number (McGhee, 1996) which basically examines each time unit

as a discrete interval and has no linkage or stability components between the time periods. This may be only a relict of how most databases are compiled (Raup, 1991), however this type of approach views time unidirectionally - forward. It may be more prudent to maintain a link to previous behavior if continuous trends are to be discerned.

The exponential and logistic growth models as well as survivorship curves, do consider past behavior and trends, but hinge upon the assumption that population growth and taxonomic growth are analogues. The magnitude and nature between population timescales and paleontologic timescales are vast, and it may be fair to assume that the forcing functions and the dynamics would vary accordingly. The usefulness of these growth models in paleontology should not be diminished, however. Considering the timescale differences, it could be that these models may indeed describe aspects of taxa growth, albeit over a narrower timespan. The wave-shape graph of flux would allow periods of dynamic growth, but also describe periods of stability and decline. The concepts of growth models and flux interpretations need not be mutually exclusive; Sepkoski (1991) described the parabolic shapes he resolved from his models which may be only one part of a wave.

The trends of potential periodicity seen in this work are consistent with a growing body of evidence indicating periodicity in the rock record (McGhee, 1989; Paul, 1989). Though extinction periodicities of the many studies do not always coincide, this work emphasizes that yet another method describes it. The main point may not be to focus on one harmonic or frequency, but to consider that the periodicities may be differential, or in some cases, as in competition, have an additive or dampening effect. It is not fair to

assume that a system will respond to forcing functions exactly as do the other systems. Periodicity has been described in many processes, from climatic, to bolide theory, to periodic convection in the mantle, all which have been cited as possible extinction mechanisms (McGhee, 1989). However, there is no clear reason to expect them to overlap and/or coincide. If true, this would imply there is one single mechanism controlling biotic as well as planetary evolution, plus a wealth of other phenomena. Therefore, perhaps analysis of the dynamics *between* the periodicities and wave forms of different systems (taxa and forcing functions) may provide new insights to evolution.

Future Work

The wave appearance of flux over time may possibly lend usefulness in modeling. As the fossil record is replete with patterns (Signor, 1991), it seems perfectly reasonable to expect wave patterns as well. Many natural phenomena already coincide with sine and cosine functions. Mean annual temperatures have been shown to follow such a distribution of flux. Mean annual precipitation has also been shown have periodicity, as does the Milyankovitch Cycle, and other phenomena relating to climate. Since climate and subsequent eustatic sea level changes are thought to be related to extinction events, it may be reasonable to consider evolution in terms of wave functions. A test of this hypothesis may include a regional echinoid database, another marine invertebrate taxa, or another type altogether. The frequency and amplitude of wave phenomena, if found, may confirm and further describe the periodicity thought to be associated with extinction events (McGhee, 1996; Raup, 1994, 1991a, 1991b,; Sepkoski, 1991). Interaction between wave equations of different taxa, especially between predator and prey, or niche

competitors, could provide modeling insights, showing dampening effects or increased oscillations. Predictive models could be constructed, and by constraining input parameters, such as starting numbers, wave-interactive models may show the dynamics between taxa and the environment.

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APPENDICES

APPENDIX A - New and Stratigraphically Important Citations 1970 - Present

- Trachypatagus tuberculatus* Middle Miocene
Ali, M.S., 1989. Middle Miocene Trachypatagus from Egypt: J Afr Earth Sci 8 (1) 57-63.
- Echinolampas qattamiaensis* (n. sp.) Middle Eocene
Ali, M.S., 1983. A new echinolampas species from the Middle Eocene of Egypt: Journal Palaeont. Soc. India (28) 56-58.
- Hattapsis sphericus* (n gen/sp) Upper Cretaceous
Ali, M.S., 1992. A new genus and species of regular echinoid from the Late Cretaceous of Gebel el Rowdan Hatta area Oman-uae: J Paleontol 66 (4) 693-696.
- Hemipneustes indicus* (n. sp.) Upper Cretaceous
Azzi, S.A. and Badve, R.M., 1990. Occurrence of Hemipneustes Agassiz echinoid from Tirucharalli Cretaceous Tamil Nadu India: J Geol Soc India 36 (3) 326-330.
- Gongrochanus chipionkari* Upper Cretaceous
G. stoliczkai Upper Cretaceous
G. kieri Upper Cretaceous
G. ottakovilensis Upper Cretaceous
G. circularis Upper Cretaceous
G. tamilnaduensis Upper Cretaceous
G. herschelians Upper Cretaceous
Badve, R.M. and Aziz, S.A., 1983. Revision of the Cassiduloid genus Gongrochanus echinodermata echinoidea from the south India Cretaceous deposits: Proc Indian Acad Sci Anim Sci 92 (3) 231-246.
- Porterpygus kieri* (n gen/sp) Lower Eocene
Baker, A.N., 1983. A new Apatopygid echinoid genus from New Zealand echinodermata cassiduloida: Natl Mus N Z Rec 2 (15) 163-173
- Almucidaris durhami* (n. gen/sp) Upper Cretaceous
Blake, D.B. and Zinsmeister, W.J., 1991. A new marsupiate cidaroid echinoid from the Maastrichtian of Antarctic: Palaeontology 34 (3) 629-636.
- Linthia oliveirai* Upper Cretaceous
Linthia romani Upper Cretaceous
Brito, I.M., 1981. Os equinoides fosseis do Brasil. 2 - espatangoides, exeto Hemiasteridae: Anais Acad. Bras. Cienc. 53 (3) 569-578.
- Brissus bridgeboroensis* (n. sp.) Lower Oligocene
Carter, B.D., 1987. Brissus bridgeboroensis, a new spatangoid echinoid from the Lower Oligocene of southwestern Georgia: J Paleontology 61 (5) 1043-1046.
- Prionocidararis cookei* Middle Miocene
P. spinidentatus Middle Miocene
P. cojimarensis Middle Miocene
P. clevei Middle Miocene
Cutress, B.M., 1976. A new Prionocidararis Echinodermata Echinoidea from the Middle Miocene of Florida USA: Proc Biol Soc Wash 89 (12) 191-198.
- Echinoneus cyclostomas* Upper Oligocene
Brissus unicolor Mid Eocene

- Haimea ovumserpentis* Mid Eocene
Haimea conexa Mid Eocene
Asterstoma excentricum Mid Eocene
 Donovan, S.K. and Veale, C., 1996. The irregular echinoids *Echinoneus* Leske and *Brissus* Gray in the Cenozoic of the Antillean region: Journal of Paleontology 70 (4) pp 632-640.
- Dendraster sullivanii* (n. sp.) Lower Pliocene
 Durham, J.W. and Morgan, S.R., 1978. New sand dollars for the genera *Merriamaster* and *Dendraster* from Purisima Formation, California: Proceedings Calif. Acad. Sci. 41 (11) 297-305.
- Scutellina supramarginalis* (n. sp.) Upper Cretaceous
 Engel, H., 1976. On a new echinoid from the Cretaceous of Maastricht: Bulletin Zool. Mus. Univ. Amsterdam 5 (7) 55-57.
- Phymosoma maastrichtensis* (n. sp.) Upper Cretaceous
 Engel, H., 1972. *Phymosoma maastrichtensis* spec. nov., a fossil echinoid from the Cretaceous of Maastricht: Zoologische - Mededelingen (47) 540-545.
- Raciosoma gigasei* (n. sp.) Upper Cretaceous
 Geys, J., 1983. *Raciosoma gigasei* nov. spec. an addition to the echinoderm fauna of the Maastrichtian of Belgium: Bulletin de la Societe Belge de Geologie 92(4) 255-259.
- Salenidia sactipetri* (n. sp.) Upper Cretaceous
 Geys, J.F., 1979. Salenoid echinoids from the Maastrichtian Upper Cretaceous of Belgium and the Netherlands: Palaeontol Z 53 (3-4) 296-322.
- Tylocidari clavigera* Upper Cretaceous
Gauthieria radiata radiata Upper Cretaceous
Salenia cherei (sp. n.) Upper Cretaceous
 Geys, J.F., 1982. Regular echinoids from the Turonian and the Coniacan Upper Cretaceous of the Mons Basin Belgium: Bull Inst R Sci Nat Belg Sci Terre 53 (3) 1-20.
- Porosoma kaspicum* (n. sp.) Upper Cretaceous
 Geys, J.F., 1984. *Porosoma kaspicum* n. sp. from the Campanian of Mangyshlak (Kazakhstan, USSR): Neues Jb Geol. Palaont. MH. (1) 27-32.
- Hemicidaris bandeli* (n. sp.) Upper Cretaceous
 Geys, J.F., 1989. Hemicidaroid echinoids from Upper Cretaceous deposits in the Wadi Qena area eastern desert Egypt: Bull Inst R Sci Nat Belg Sci Terre 59 (0) 127-136.
- Typocidaris cidaroida* Upper Cretaceous
 Geys, J.F., 1987. The genus *Typocidaris cidaroida* echinoidea in the Upper Cretaceous of the Maastricht area Belgium and the Netherlands: Bull Inst R Sci Nat Belg Sci Terre 57 (0) 201-216.
- Salenia sigillata pozaryskae* Upper Cretaceous
 Geys, J.F. and Machalski, M., 1992. A new salenoid echinoid, *Salenia sigillata pozaryskae*, subs. n., from the uppermost Maastrichtian of the middle Vistula Valley, central Poland: Acta Geologica Polonica 42(1-2), 135-139.
- Echinolampas tanyptetalis* (n. sp.) Upper Eocene
 Harper, J.A. and Shaak, G.G., 1974. A new echinolampas echinodermata echinoidea from the Ocala Limestone of Florida USA: J Paleontol 48 (6) 1166-1169.

- Micraster malekii* (n. sp.) Upper Cretaceous
Micraster rogalae Upper Cretaceous
 Hynda, VA and Maczynska, S., 1979. *Micraster malekii* sp. n. from the Santonian of the environs of Cracow, a new echinoid *Micraster rogalae* Nowak: *Prace Muz. Ziemi* 32:21-28.
- Tylocidaris* (*Psychocidaridae*) *inexpectata* (n. sp.) Upper Cretaceous
 Jagt, J.W. and Van der Ham, R.W., 1995. First record of the echinoid genus *Tylocidaris* from the Maastrichtian of the Netherlands: *Palaeontologische Zeitschrift* 69 (1-2) 233-239.
- Clypeaster maoadentroensis* (n. sp.) Early Pliocene
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Clypeaster ogasawarenensis Pleistocene
Clypeaster paishatunensis Pleistocene
Clypeaster pitouensis Pleistocene
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Appendix B. Stratigraphic range chart																			
Order	Family	Genus	U. Cretac	L. Paleoc	U. Paleoc	L. Eocene	M. Eocene	U. Eocene	L. Olig.	U. Olig.	L. Mio	M. Mio	U. Mio	L. Plio	M. Plio	U. Plio	Pliocene	Holocene	
Number of species per time interval																			
Cidaroida	Cidaridae	Hitocidaris	4	0	0	0	0	0	0	0	0	2	0	0	0	0	0	9	
		Cenocidaris																1	
		Austrocidaris																	2
		Eurocidaris																	2
		Notocidaris														1	0	0	2
		Gonocidaris											1	0	0	0	0	0	13
		Palocidaris																	1
		Rhaplocidaris																	2
		Schizocidaris																	1
		Stereocidaris	1	0	0	0	1	5	0	0	0	0	0	0	1	1	0	0	2
		Phalacrocidaris																	1
		Actinocidaris	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
		Chondrocidaris										1	3	0	0	0	0	0	1
		Phylacanthus	0	0	0	0	0	0	0	2	3	3	3	1	1	1	0	1	2
		Leiocidaris	4	0	0	1	1	0	0	0	2				0	0	0	0	1
		Perocidaris								1	0	0	0	0	0	0	0	0	1
		Typocidaris	3	2															
		Almucidaris	1																
		Rhabdocidaris	0	0	0	0	0	1											
		Pronocidaris						1	0	0	1	2	3	0	1	1	1	1	4
Euechinoida	Echinophoridae	Cidaris	3	0	0	0	0	3	0	1	0	0	0	0	0	0	0	2	
		Dorocidaris	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	
		Cyathocidaris	1																
		Eucidaris							1	0	0	1	0	0	0	0	0	3	
		Hesperocidaris																	
		Konicidaris																3	
		Lusocidaris																1	
		Syllocidaris																8	
		Psychocidaris																	
		Tylocidaris	2	5															1
Diadematoidea	Diademidae	Araetoma	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8
		Aethenotoma	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4
		Calvertosoma																	1
		Hapalosoma																	1
		Sperosoma																	4
		Echinotoma																	1
		Phoronotoma																	1
		Hemiphoronotoma																	1
		Paraphoronotoma																	1
Aspidodiadematoidea	Microtyphidae	Diadema						1	0	0	1	0	0	0	0	0	0	2	
		Astropyga																2	
		Centrostephanus										1	0	0	0	0	0	3	
		Chaetodiadema																	3
		Edemopyga																	1
		Goniodiadema																	1
		Kerechinus						1											1
		Paleodiadema	2	1															
Aspidodiadematoidea	Microtyphidae	Microtypha																1	
		Aspidodiademata																	5

Appendix B. Stratigraphic range chart (cont.)																		
Order	Family	Genus	U. Cretac	L. Pale	U. Pale	L. Eocene	M. Eocene	U. Eocene	Number of species per time interval					L. Plio	M. Plio	U. Plio	Pleist	Holocene
									L. Olig	U. Olig	L. Mio	M. Mio	U. Mio					
Pedinoida	Pedinidae	Pedina						1	1									
		Coenopodina																
		Leiopodina				1												3
		Micropedina	1															
		Pseudorhopis	1															
Salenioida	Acrosalenidae	Eurysalenia	1															
		Polyvalenia	2															
		Salenia	12	0	0	0	0	1	0	0	1	1	1	0	0	0	0	3
		Salsenida	3	3														
		Valsalenia	1	1														5
Hemicidaroida	Hemicidaridae	Salenocidaris																
		Pellastes	1															
		Goniophorus	2															
		Hemicidaris	2															
		Heterodiadema	3															
Pseudodiademidae		Diplopodia	4															
		Loriola	1															
		Polydiadema	1															
		Tetragramma	3															
		Pedinopsis	0	0	0	1												
Phymosomatoida	Phymosomatidae	Tochotara	1															
		Phymosoma	9	2	0	0	0	1	1									
		Cyphosoma	3	0	0	0	0	0	1									
		Dixieus							1									
		Gautheria	2	1														
		Narindschinus																
		Porosoma	3	0	0	0	0	1										
		Rachiosoma	5	2														
		Winkleria	1															
		Thytechinus				2	1	1	1						1			
	Stomechinidae	Glyptocidaris																
		Citropeltis	1															
		Echinotara	1															
		Gomphschinus	1															
		Noeltingaster	5															
		Phymotaxis								1	1							
		Stomopneustes	1															
		Leiosoma																
		Boletschinus																
		Uncertain	1															
Artacioida	Artaciidae																	
		Arbia													1	0	0	1
		Baueria		1														
		Codopsis	6															
		Ceolopseus	1	0	0	0	0	0	1	0	1	1	0	0	0	0	0	3
		Goniopyrus	7															

Appendix B. Stratigraphic range chart (cont.)														
Order	Family	Genus	Number of species per time interval											
			U. Cretac	L. Paleoc	U. Paleoc	L. Eocene	M. Eocene	U. Eocene	L. Olig.	U. Olig.	L. Mio	M. Mio	U. Mio	L. Plio
Tennopleuroidea	Glyptocypitidae	Amblopleurus												
		Medocochinus				1								
		Archiolepleurus					1							
		Dichopleurus						2						
		Echinoopsis				2								
		Herbertia	2	0	0	0	0	1	0	0	1			
Tennopleuroidea	Tennopleuridae	Amblypneustes												
		Brochopleurus								1	0	0	0	0
		Tatichinus								1	1	0	0	1
		Triplacidia							1	1				
		Zenopleurus	3											
		Tennopleurus												
		Pymnechinus												
		Copiolepleurus												
		Asterochinus												
		Cryptechinus								1				
		Genocidaris									1	0	0	0
		Martinechinus											0	1
		Megaplia												
		Lamproechinus												
		Microcypus												
		Opochinus												
		Paratrema												
		Prinechinus												
		Pseudochinus												
		Notochinus												
		Salmaciella												
		Stimacis												
		Tennotrema												
		Dicopitella												
		Trigonocidaris												
Tosopneustidae	Cyttechinus	Cyttechinus												
		Gymnechinus												
		Lutichinus								1	2	0	0	1
		Nudochinus												
		Sphaerochinus												
		Tripneustes												
		Mirechinus												
Uncertain	Gagaria	Gagaria												
Echinoida	Echinidae	Echinus												
		Dermechinus												
		Gracilechinus												
		Paracentronus												
		Polyechinus												
		Pannochinus												
		Stereochinus	0	0	0	0	0	1	1	0	1	0	1	
Echinomeltridae	Echinomeltridae	Echinomeltrus												
		Helicoidaris												
		Zenocentronus												
Strongylocentrotidae	Strongylocentrotidae	Strongylocentrotus												

Appendix B. Stratigraphic range chart (cont.)																			
Order	Family	Genus	U. Cretac	L. Paleoc	U. Paleoc	L. Eocene	M. Eocene	U. Eocene	L. Olig.	U. Olig.	L. Mio	M. Mio	U. Mio	L. Plio	M. Plio	U. Plio	Plioceno	Holocene	
Orthopoda	Orthopidae	Orthopsis	2																
Holestypoida	Conulidae	Conulus	13																
		Pyrina	6																
		Galeraster	3	0	0	0	1												
		Globator	1																
		Pseudopyrina	3	2															
		Pygopyrina	1																
		Echinoconus	1																
	Galeriidae																		
	Conoclypidae	Conoclypus				5	1	0	0	0	0	1							
	Holestypidae	Holestypus	7																
Coniolectypus		1																	
	Anorbopygidae	Anorbopygus	2																
	Discoididae	Discoides	4																
		Discoides	2																
		Canerogalerus	1																
		Dixonella	1																
		Lanieria	1																
	Echinoneidae	Echinoneus							4	0	0	0	0	0	0	0	0	1	
		Dupertaria						1											
		Paleochinoneus	1																
	Oligopygidae	Oligopygus						19											
		Bonaireaster																	
		Haimia				1	7	6											
		Pauropygus							1										
	Uncertain	Amblypygus						1											
		Echinogalerus	1																
Chyasteroida	Echinarachnidae	Echinarachnius											2	1	0	1	0	1	
		Astrodiapsis											1	29	0	0	2		
		Kevia											0	0	0	1			
		Pseudastrodiapsis													1				
		Tenuarachnius																	
		Vaguerocella																	
		Remondella																	
		Mellitia																	
		Encope																	
		Astrochypidae	Astrochypus																
		Aurochypus																	
		Amphiope																	
		Echinodiscus																	
	Scutellidae	Scutella																	
		Prasaculla																	

Appendix B. Stratigraphic range chart (cont.)																			
Order	Family	Genus	U. Cretac.	L. Paleoc.	U. Paleoc.	L. Eocene	M. Eocene	U. Eocene	L. Olig.	U. Olig.	L. Mio.	M. Mio.	U. Mio.	L. Plio.	M. Plio.	U. Plio.	Pliocene	Holocene	
Cypasteroidea	Protoscutellidae	Protoscutella						2											
		Periarctus						3											
	Dendrosteridae	Dendroster												2	1	1	1	4	
		Orchoporus										1					1		
		Aenoboscium																	
	Eoscutellidae	Eoscutella							2										
		Fibularia						2	2	0	0	1	2	0	0	0	0	0	2
		Echinocyanthus	1	0	0	2	4	2	0	4	0	0	0	0	0	0	0	1	7
		Fibulariella																	3
		Lenticulus						1											
Porpella							2												
Scutellina		1	0	0															
Tarphycypris								2											
Laganidae	Laganum							4	0	0	1	0	0	0	0	0	0	8	
	Jackonaster						1	2										5	
	Peronella							3	0	0	0	0	0	0	0	0	0	5	
	Raunophia									1									
	Simondia				1	0	0	0	0	1	1								
Neolaganidae	Neolaganum							2											
	Cubanaster							6											
	Durhamella						1												
	Weisbordella							1											
	Neonumphia									1									
Cypasteridae	Cypasteridae	Wyndelia						1											
		Cypaster						2	1	13	6	20	2	1	1	1	2	11	
		Anomalanthus									3								
		Bunactus									1								
		Coronanthus																1	
		Rapidocyclus									2	0	0	0	0	0	0	0	2
		Rajaster									2								
		Zonitella									1								
		Herreraia										1							
		Hesperaster																1	
Arachnoidea	Arachnoidea	Stolonocyclus																2	
		Arachnoides																1	
		Tellaster																1	
		Ammotrochus																2	
		Pentidium						1											
Abertellidae	Abertellidae	Abertella									2	2							
		Scutaster										1							
Rotalidae	Rotalidae	Rotalia																1	
		Rotaloides										1							
Rotalidae	Rotalidae	Rotalia																	
		Rotaloides																	

Appendix B. Stratigraphic range chart (cont.)																				
Order	Family	Genus	U. Cretac	L. Pale	U. Pale	L. Eocene	M. Eocene	U. Eocene	Number of species per time interval						U. Mio	L. Plio	M. Plio	U. Plio	Piceto	Holocene
									L. Olig	U. Olig	L. Mio	M. Mio								
Cassiduloida	Clypeolampadidae	Clypeolampas	1																	
	Plicolampadidae	Callilampas						1												
		Phiolampas						1	0	0	0	0	0	1						
		Bryozella	1																	
		Euriodia				1	1	1	0	0	0	0	0	1	0	0	0	0	1	
		Giolampas	1	0	0	0	0	0	0	0	0	0	1							
		Giolampopsis	1																	
		Ilarionia						2												
		Neocatopygus						1												
		Sanciolampas						1												
		Suderia												1						
		Zuffardia	1																	
		Termeria			1															
		Apotopygidae	Portopygus						1											
			Apotopygus																1	
		Uncertain	Astropygulus	1																
			Echinodus	1	0	0	1	2												
			Lovenilampas	1																
	Disasteroidea																			
Holasteridae		Holastus	6																	
		Basseaster	1																	
		Cardiaster	7																	
		Echinocorys	15	5																
		Galeola	1																	
		Spatangoides	4																	
		Galaster	1	1																
		Hagenovia	3																	
		Martiniagra	2																	
		Hemipneustes	5																	
		Imbridaster	1																	
		Lampadaster	1																	
		Pseudananchus	2																	
		Pseudoflaster	1																	
		Rispolia	1																	
		Stegaster	4																	
		Cardabia	1																	
		Seunaster	3																	
		Giraster	2																	
Poutalesioida																				
	Poutalesiidae	Poutalesia						1											3	
	Somalasteridae	Somalaster	1																	
	Uncertain	Conaster			3	2														
		Turanaster	1																	
		Corechinus			1															

Appendix B. Stratigraphic range chart (cont.)																				
Order	Family	Genus	U. Cretac	L. Palco	U. Palco	L. Eocene	M. Eocene	U. Eocene	Number of species per time interval				U. Mio	L. Plio	M. Plio	U. Plio	Plioste	Holocene		
									L. Olig.	U. Olig.	L. Mio	M. Mio								
Spatangoida	Micasteridae	Micaster	12	1	0	0	0	0	0	0	1									
		Paramicaster	2																	
		Brissopneustes	1	2	0	1														
Brissidae	Apoxypetalus	Apoxypetalus								1										
		Brissus					1	1	1	0	2	0	1	0	0	0	1	2		
		Allobrissus												1	0	0	0	2		
		Anabrissus											1	0	0	0	0	1		
		Anametalia																2		
		Hysteraster											1							
		Sandigoaster							1											
		Aquavaster							1											
		Arachinus					1													
		Brissopetagus					2		3	0	1	1								
	Brissopoda	Brissopoda					1		1	0	1	3	1	1	0	0	0	0	7	
		Brissoma									1	1								
		Kleina											1							
	Cyclaster	Cyclaster	3	0	0	0	0	1	0	1	1	3	0	0	0	0	0	0	2	
		Conobrinus																	1	
	Spatangidae	Spatangidae	Protobrinus	1	1															1
			Eupatagus					1	7	7	0	8	2	2	0	0	0	0	2	2
			Eupatagus						1											
			Megapetagus							1	0	1								
			Gaultheria										2							
			Zanotettaster										1							
			Gillechinus							1										
			Lajaster																	
Idiobryasus													1							
Macropneustes																				
Deakia																				
Maurhamaster																				
Micoma									2	0	0	0	1	0	0	0	0	0	2	
Micalia													1	0	0	0	0	0	1	
Plethoecenia														1	0	0	0	1		
Schizobrinus																				
Prometalia							4	0	0	0	0	1	0	0	0	0	1			
Plagiobrinus											1	0	0	0	0	0	1			
Rhynobrinus																				
Taimanava											1									
Rhabdobrinus								1												
Plesister																				
Spatangomorphia	Spatangomorphia	Plesister	1	0	0	0	1													
						1														
Unifasciidae	Unifasciidae	Unifascia																		
						1														
Spatangidae	Spatangidae	Spatangus	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	4		
		Alciopetagus																		
		Hemipetagus																		
		Nacopetagus	1															2		
		Propetagus												2					2	
Hemimorpha	Hemimorpha	Mareta																		
		Hemimorpha																1		

Appendix B. Stratigraphic range chart (cont.)			Number of species per time interval																	
Order	Family	Genus	U. Cretac	L. Paleoc	U. Paleoc	L. Eocene	M. Eocene	U. Eocene	L. Olig.	U. Olig.	L. Mio	M. Mio	U. Mio	L. Plio	M. Plio	U. Plio	Plioc	Holocene		
Spatangoida	Loveniidae	Lovenia	1	0	0	0	0	2	0	1	0	1	0	1	0	0	0	2		
		Brevia						1					2	1	0	0	0	3		
		Echinocardium																1		
		Homolampas																		
	Asterostomatidae	Asterostoma					5													
		Anillaster						1	0	5	1	1								
		Brisolampas								1		1	0	0	1					
		Paleopneustes								1		0								
		Pseudostereostoma								2					1					
		Archaeopneustes																1		
		Linopneustes												1						
		Opponeustes																1		
		Planorbis																	1	
		Pezomachus																	1	
		Scrippsachinus																	1	
	Uncertain	Barrumia								1										
		Coltraneocorya								1										
		Nudobristus							1											
Neolampoida	Neolampadidae	Nannolampus																1		
		Piscolampus						1				1								
		Noolampus																		
Uncertain	Uncertain	Oligopodia						1												

APPENDIX C - Algebraic Relationship of GENS Formula

Given these:

G= Number of genera present

E= Number extinct during interval

N= Number New Apperances

S= Number stable before and after interval

To determine these:

G_p= Genera previous; the number coming into stage

N_e= New that went extinct

E_p= Extinct previous; the G_p which became extinct

N_s= New survivors; New originations which survived stage

Mass Balance: Input = Output

G - E = Output (O)

O - S = N_s N_s = New originations that survived; G - E - S = N_s

* N_s/N = % new survival per new evolved

N - N_s = N_e N_e = New which went extinct; N - G + E + S = N_e

* N_e/N = % new which went extinct per new evolved

* N_e/E = % New extinctions per all extinction

E = G - S - N_s results in N_s = G - E - S

E = N_e + E_p results in E_p = E - N_e

E_p = Number Extinct coming in from previous stage

E_p + S = G_p

G_p = Number of genera coming into stage

G_p = G - N

* E_p/E = % of extinction of old genera per total extinction

E_p/E + N_e/E = 1

* E_p/G_p = % of old genera which went extinct

* S/G_p = % of old genera still stable

* (G-E)/(G-N) = % of net increase or decrease

* N_s/O = % output from new genera

N_s/O = (G-E-S)/(G-E)

N_e = N - N_s; N_e = N - G + E + S

* (N - G + E + S)/E = % Extinction from New; N_e/E

* Output - Stable/Output = % of new in output

(G - E - S)/(G-E)

* S/(G-E) = % of stable in ouput

* Denotes potential useful relationships derived when only collecting G, E, N, and S.

Appendix D - Graphical representation of echinoid extinction ratios for each timestep of the Cenozoic.

Cretaceous - n=152

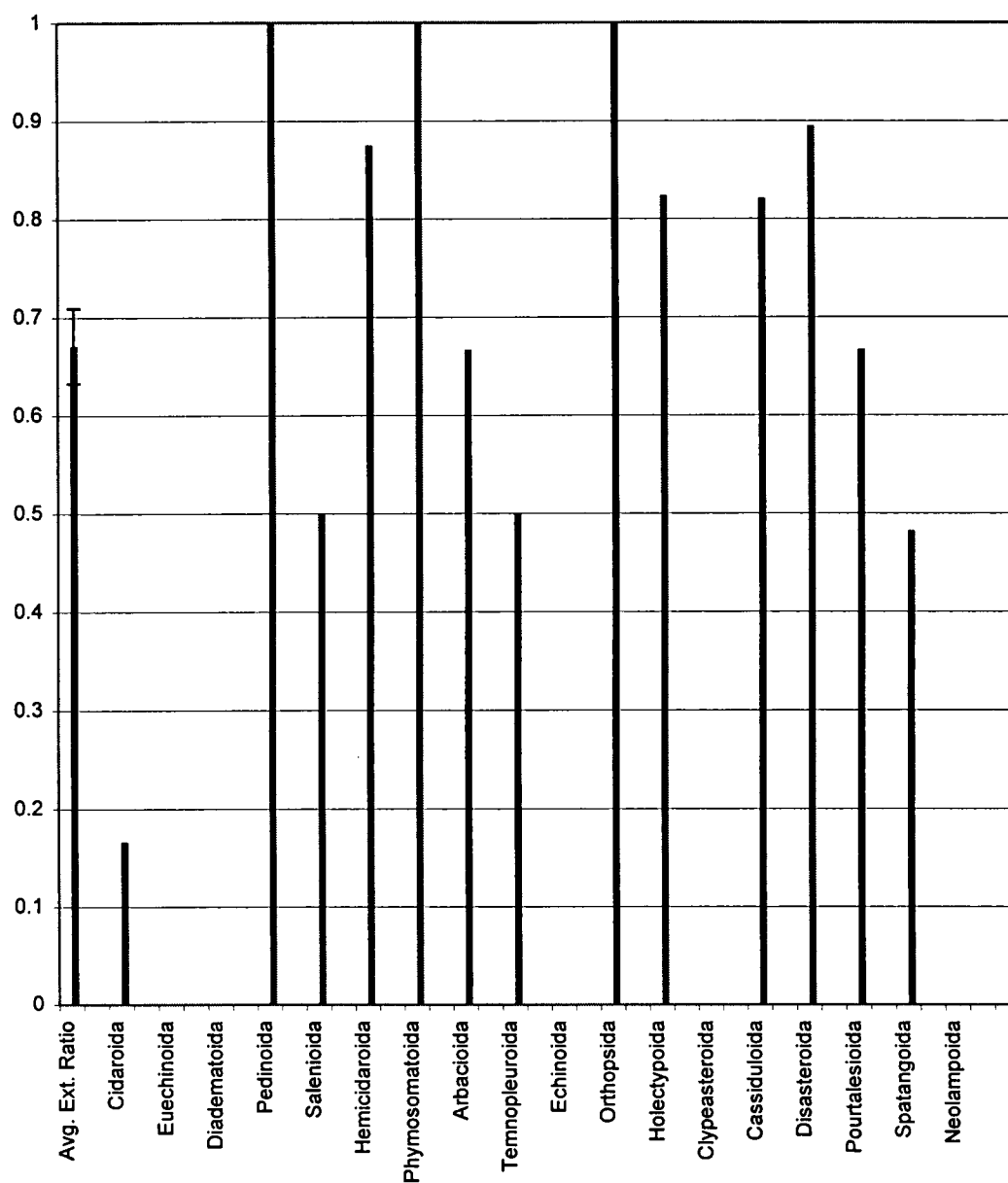


Figure D1. Bar graph representation of each ordinal extinction ratio compared to the weighted mean average extinction ratio for the Upper Cretaceous. The number of data entries is denoted by “n”. Orders without data for this time interval have values of zero.

Lower Paleocene n = 58

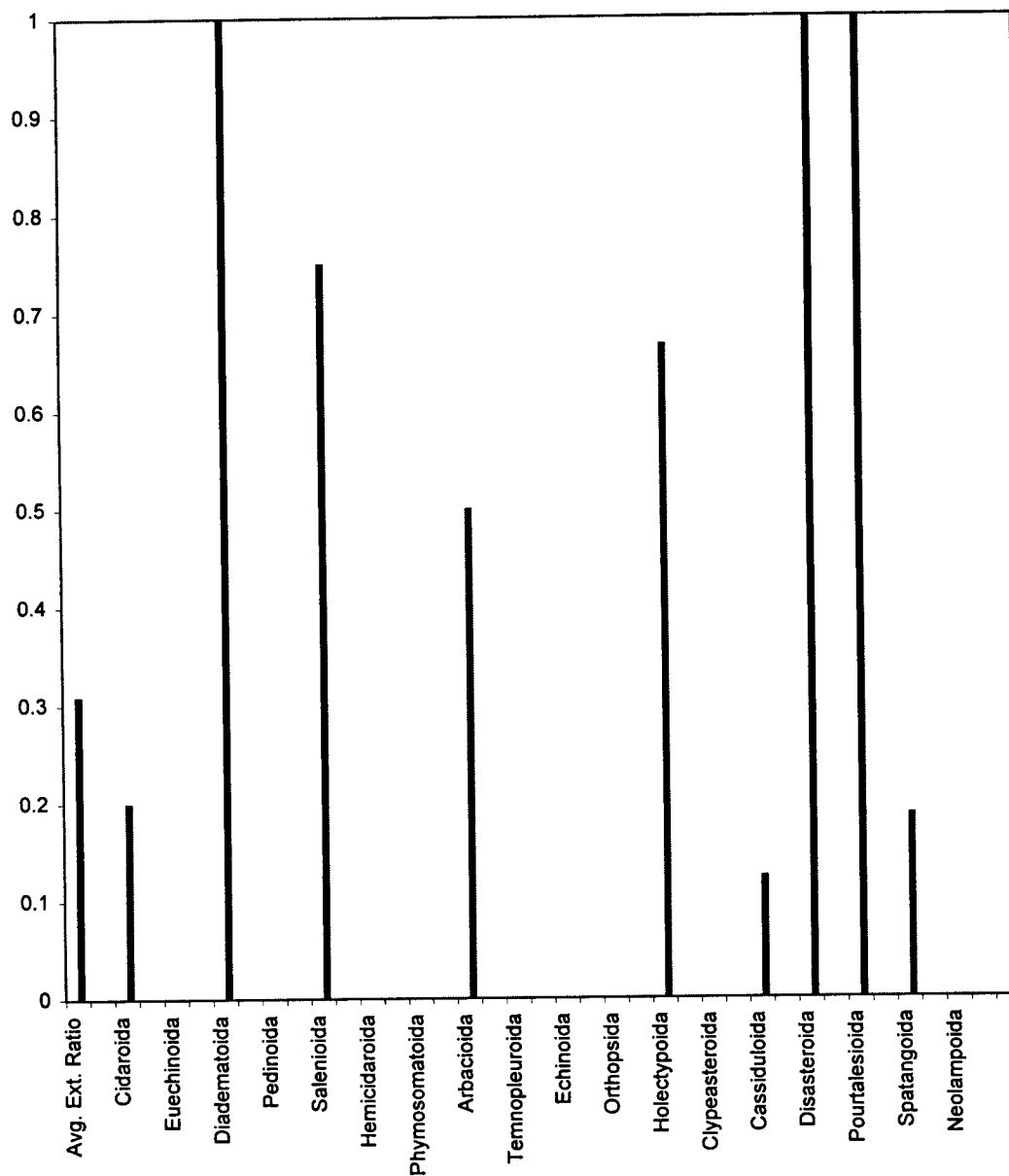


Figure D2. Bar graph representation of each ordinal extinction ratio compared to the weighted mean average extinction ratio for the Lower Paleocene. The number of data entries is denoted by “n”. Orders without data for this time interval have values of zero.

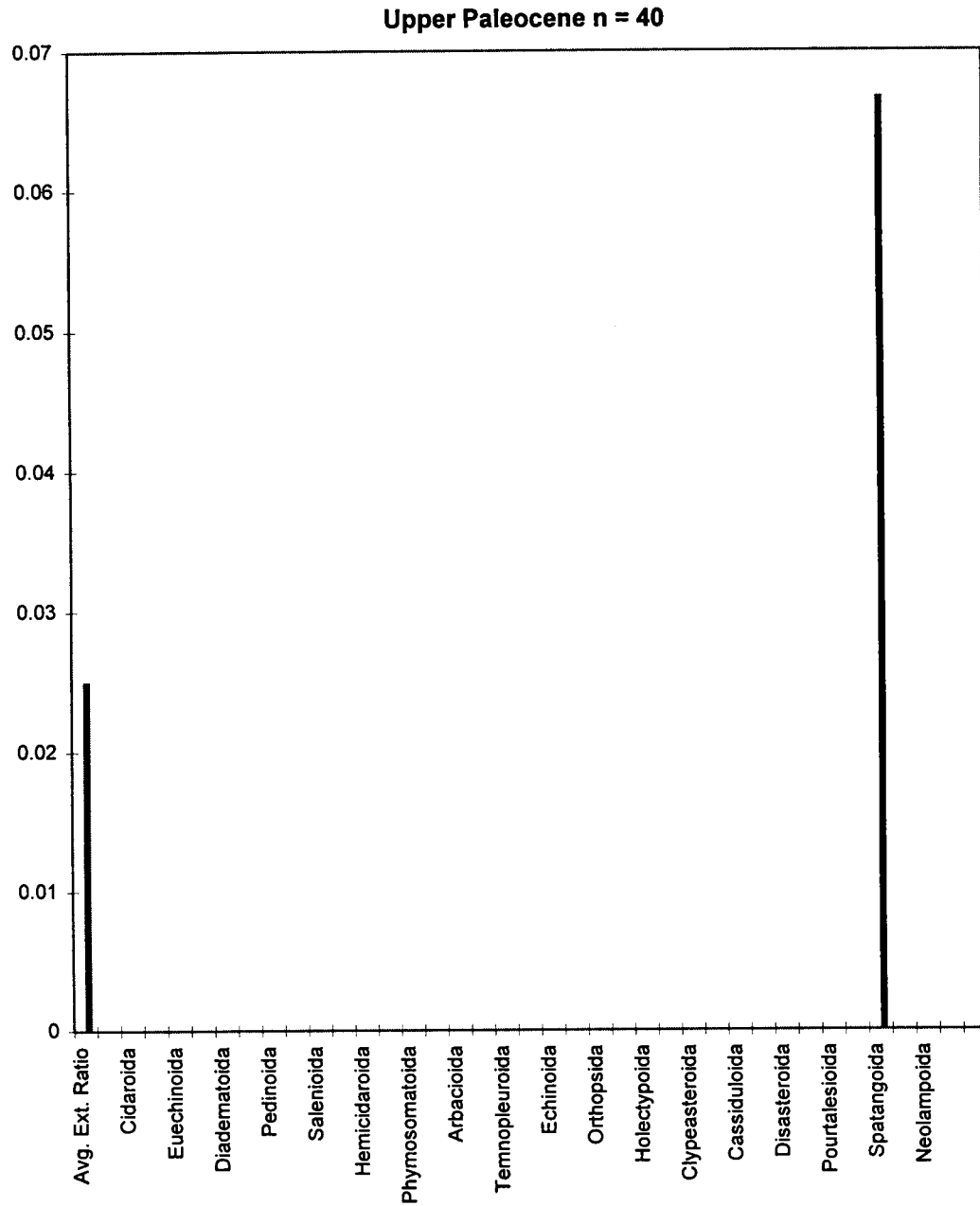


Figure D3. Bar graph representation of each ordinal extinction ratio compared to the weighted mean average extinction ratio for the Upper Paleocene. The number of data entries is denoted by “n”. Orders without data for this time interval have values of zero.

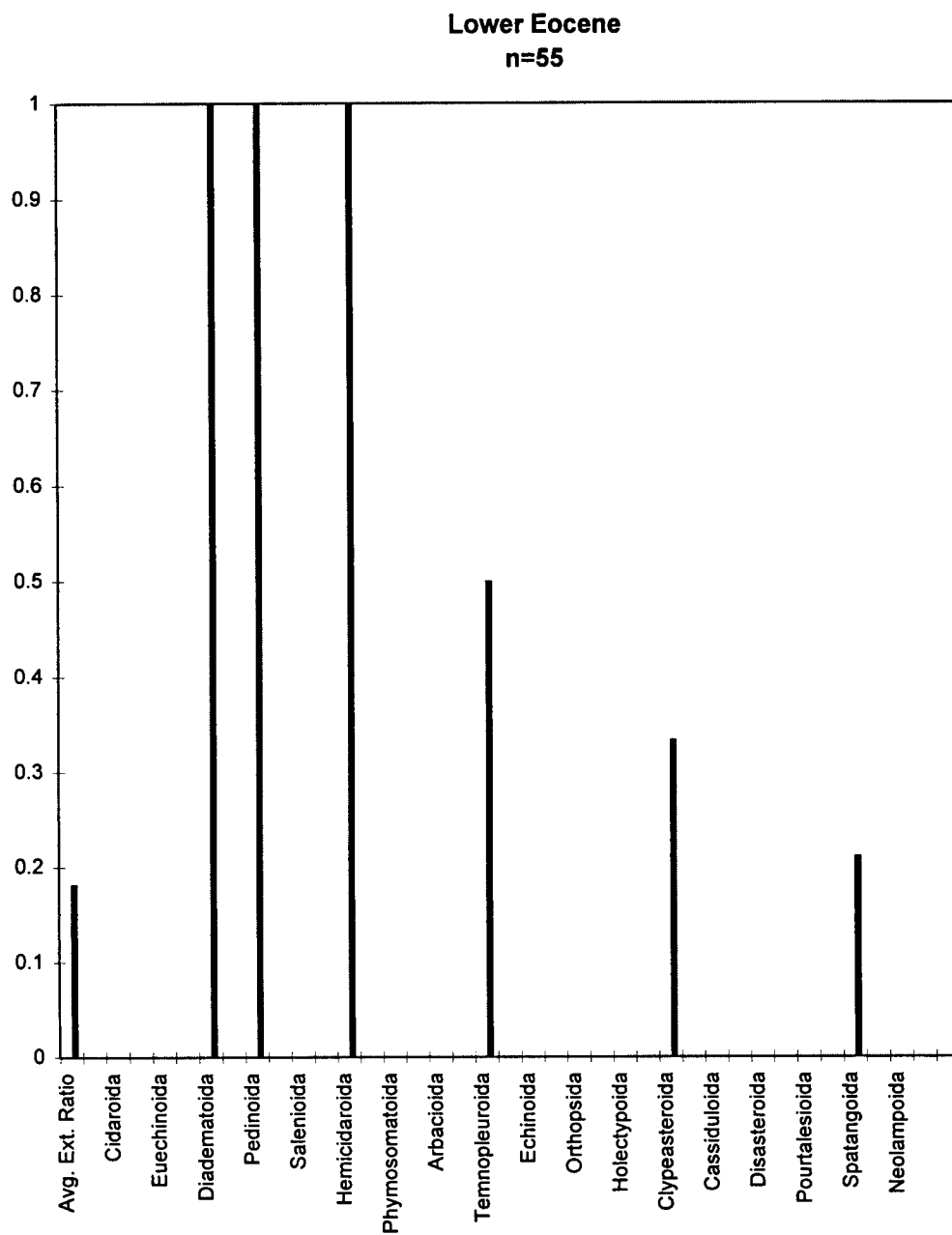


Figure D4. Bar graph representation of each ordinal extinction ratio compared to the weighted mean average extinction ratio for the Lower Eocene. The number of data entries is denoted by “n”. Orders without data for this time interval have values of zero.

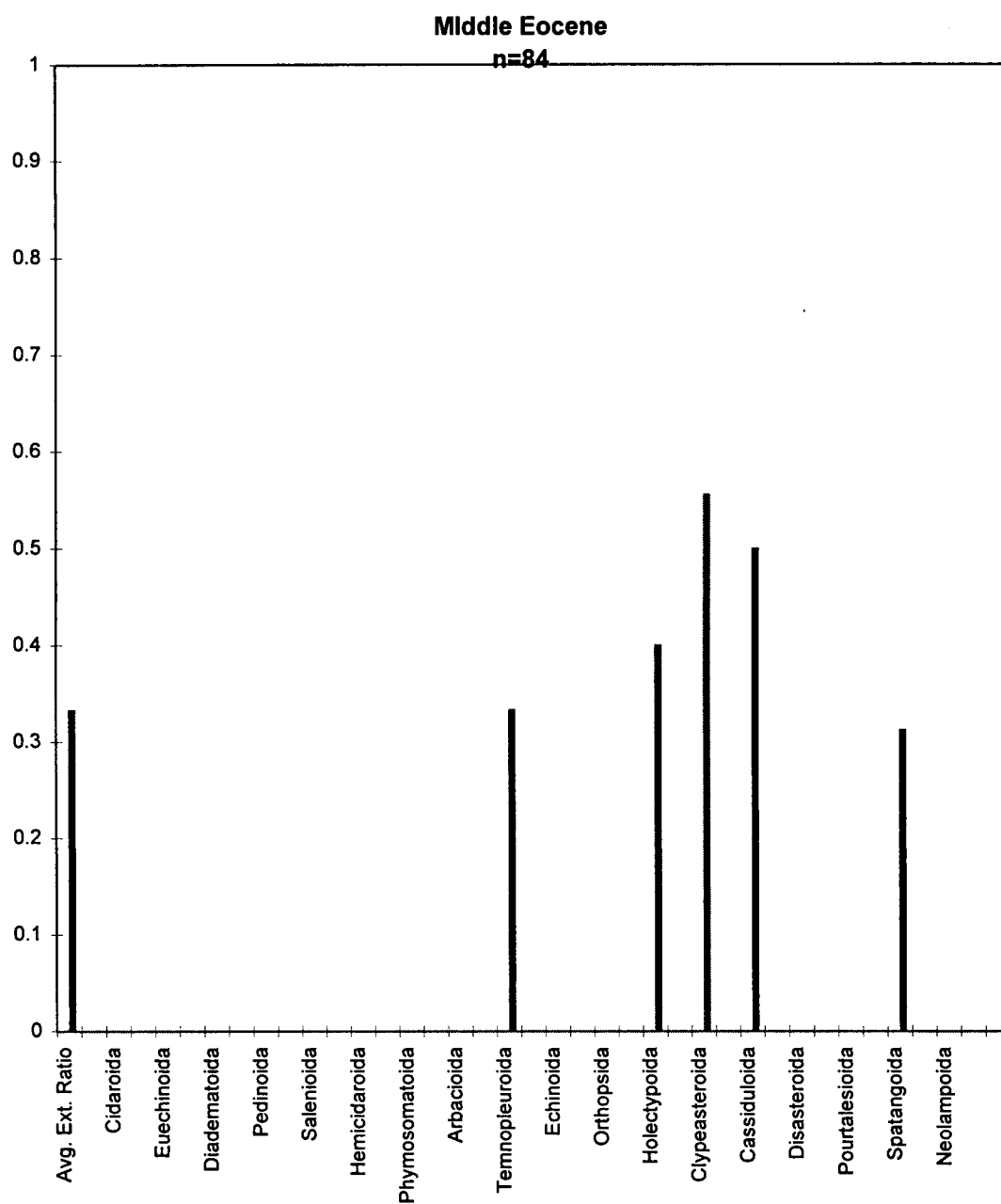


Figure D5. Bar graph representation of each ordinal extinction ratio compared to the weighted mean average extinction ratio for the Middle Eocene. The number of data entries is denoted by "n". Orders without data for this time interval have values of zero.

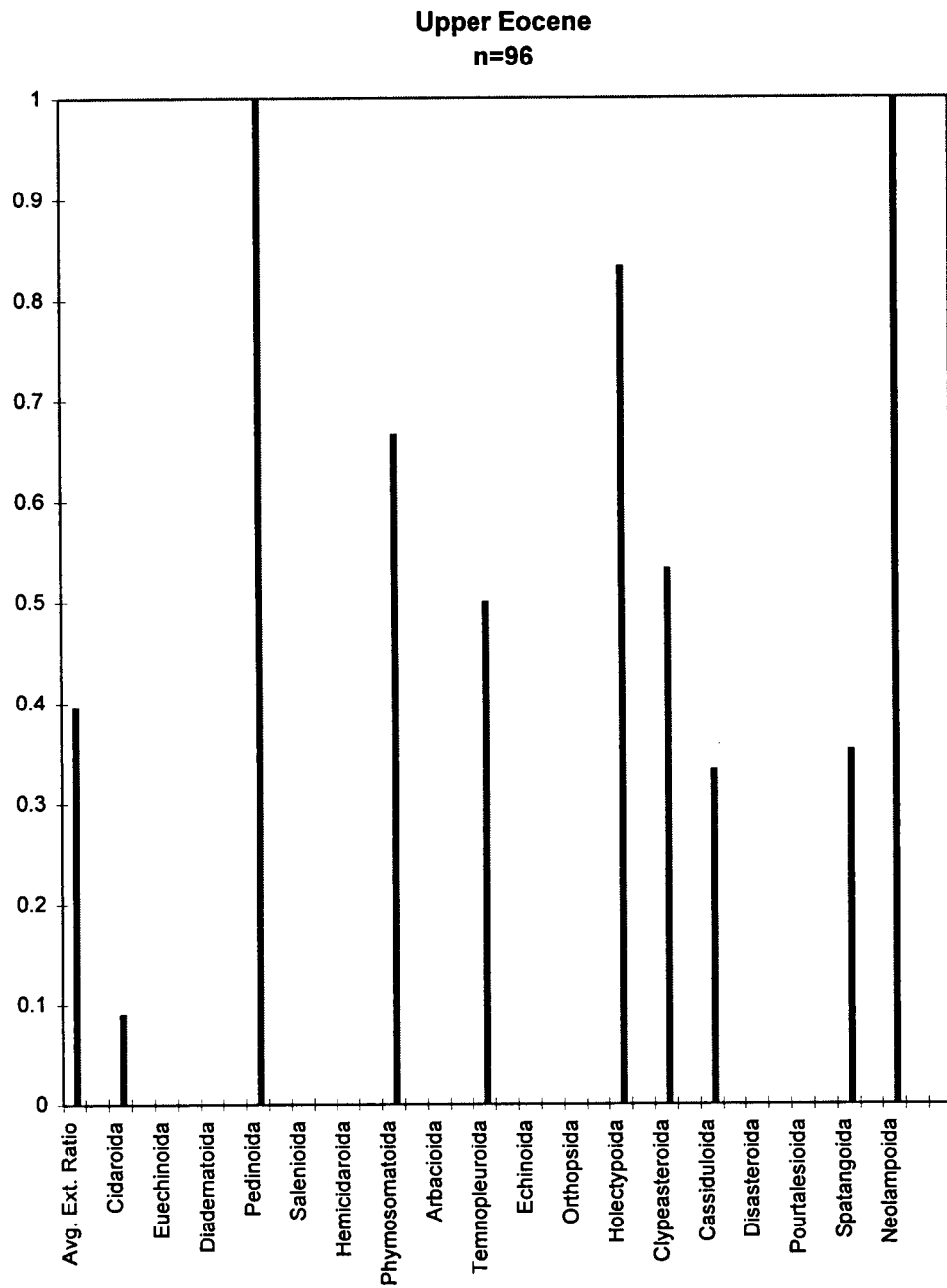


Figure D6. Bar graph representation of each ordinal extinction ratio compared to the weighted mean average extinction ratio for the Upper Eocene. The number of data entries is denoted by “n”. Orders without data for this time interval have values of zero.

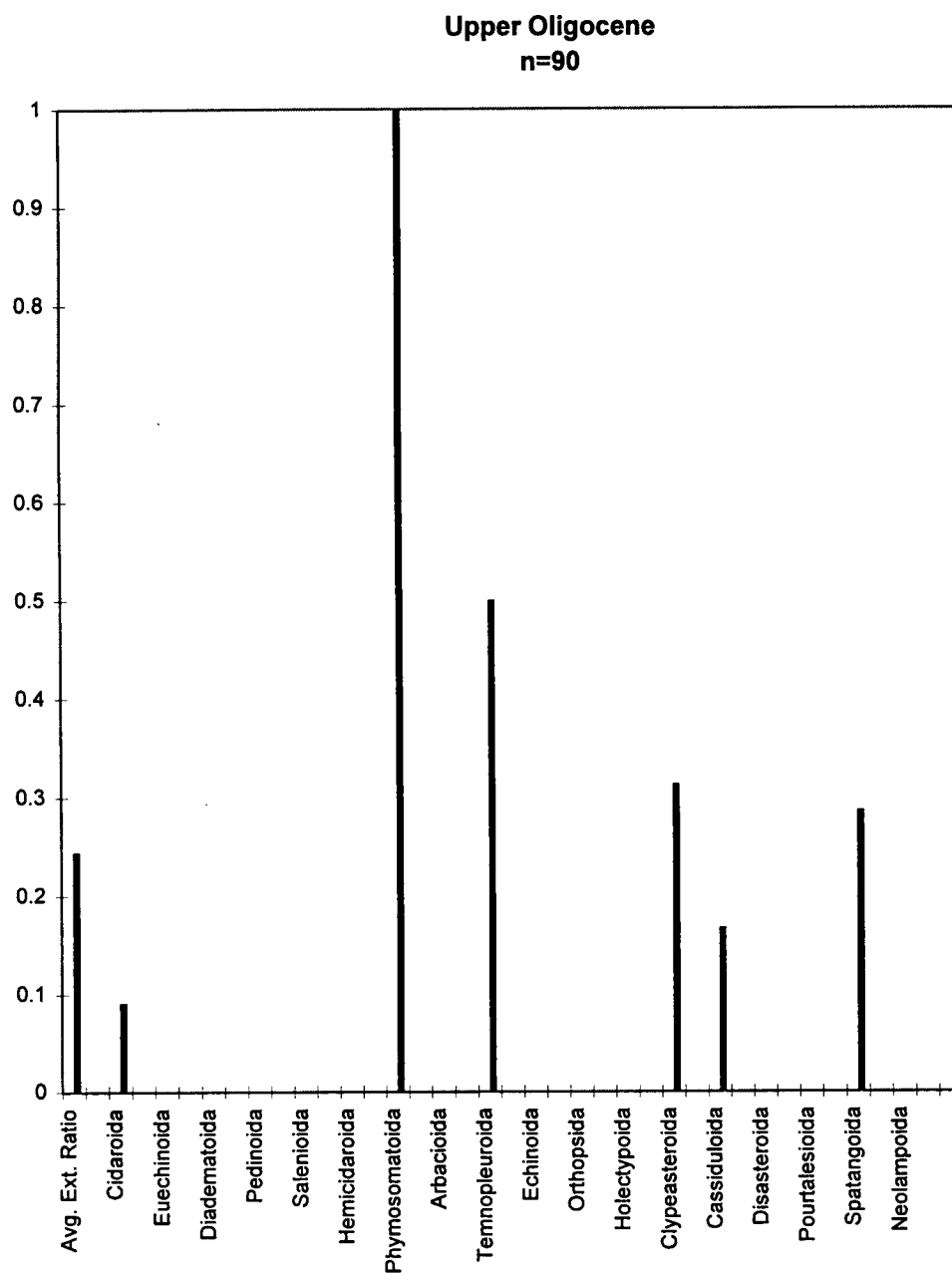


Figure D7. Bar graph representation of each ordinal extinction ratio compared to the weighted mean average extinction ratio for the Upper Oligocene. The number of data entries is denoted by “n”. Orders without data for this time interval have values of zero.

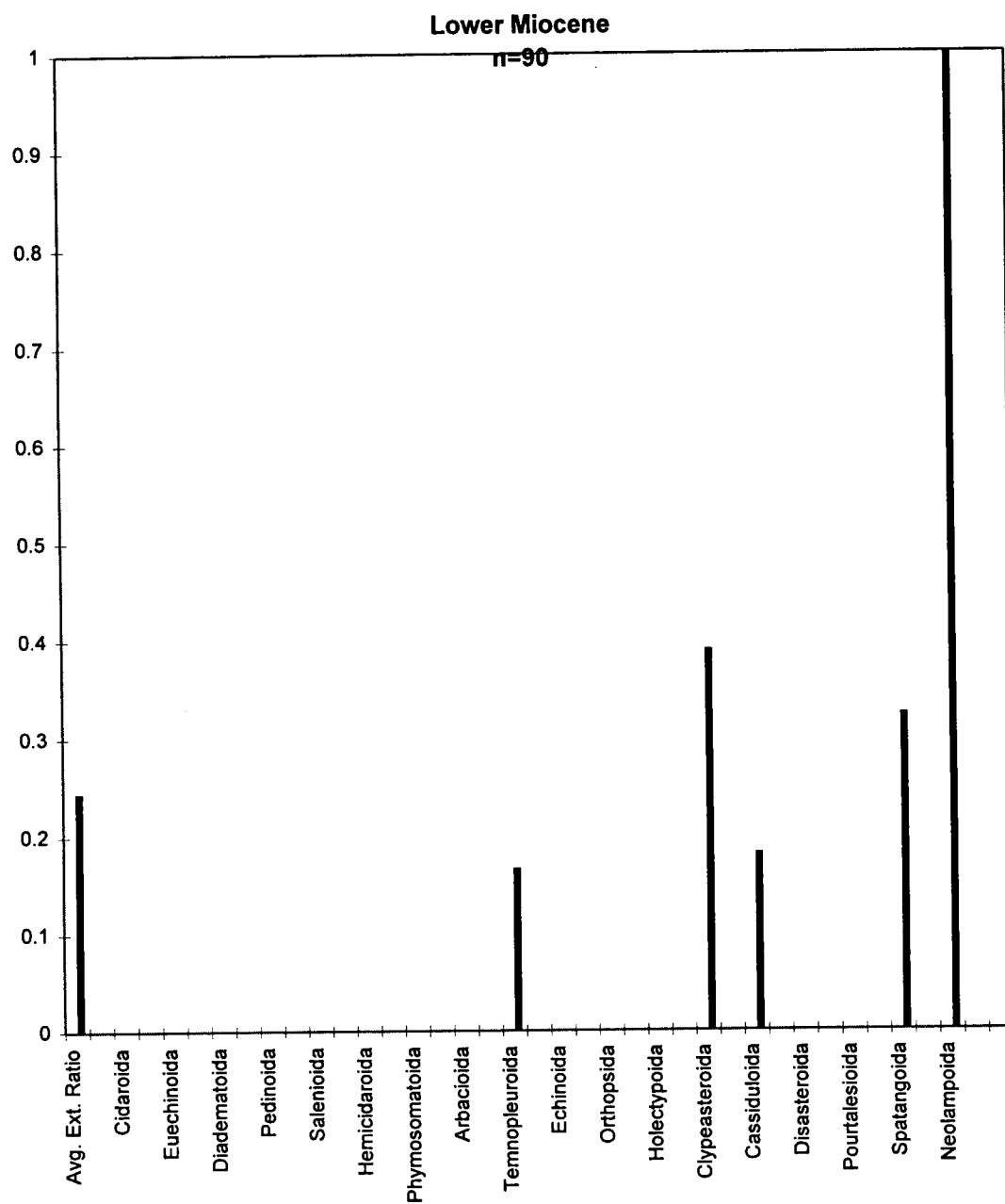


Figure D8. Bar graph representation of each ordinal extinction ratio compared to the weighted mean average extinction ratio for the Lower Miocene. The number of data entries is denoted by "n". Orders without data for this time interval have values of zero.

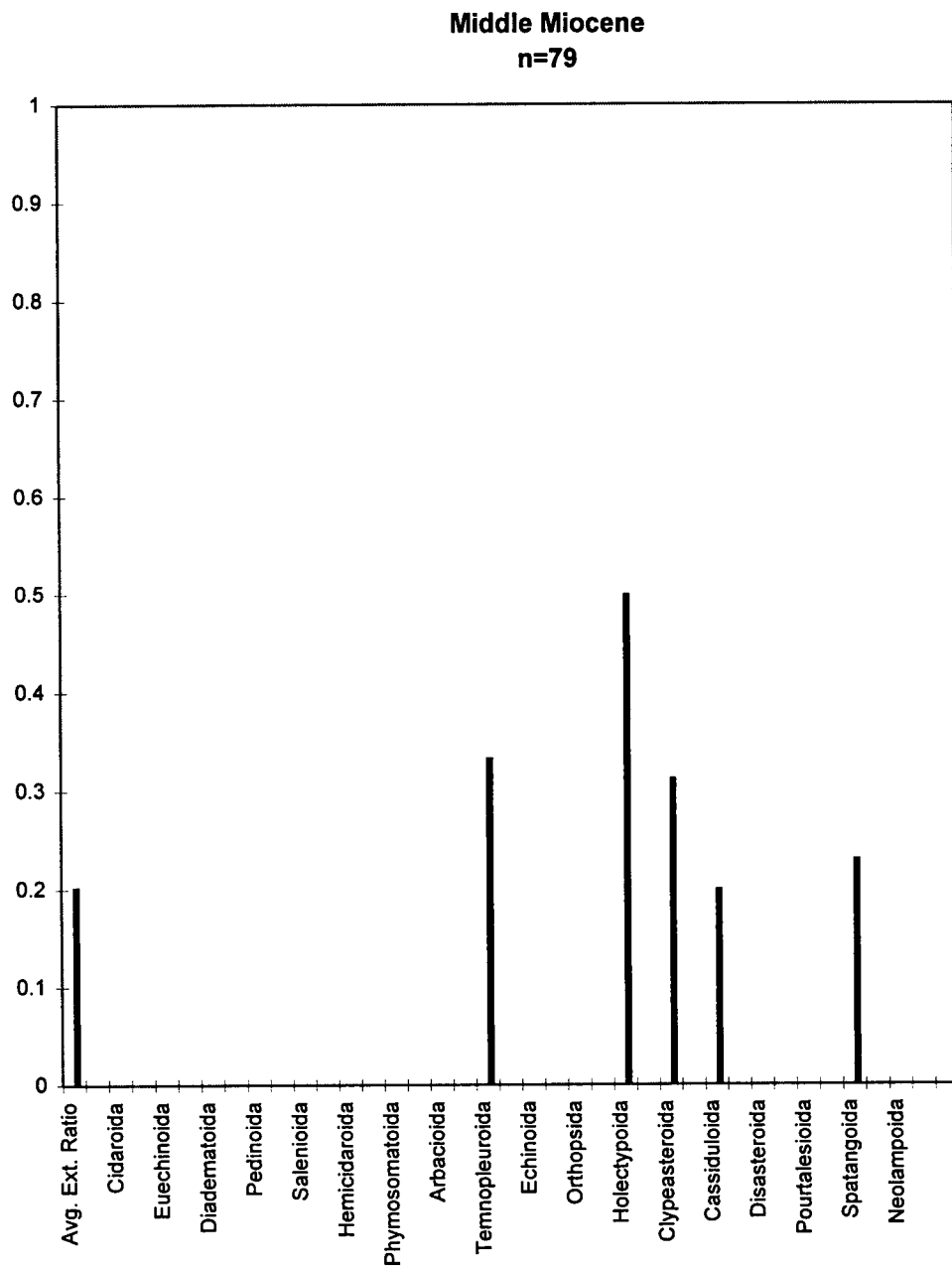


Figure D9. Bar graph representation of each ordinal extinction ratio compared to the weighted mean average extinction ratio for the Middle Miocene. The number of data entries is denoted by “n”. Orders without data for this time interval have values of zero.

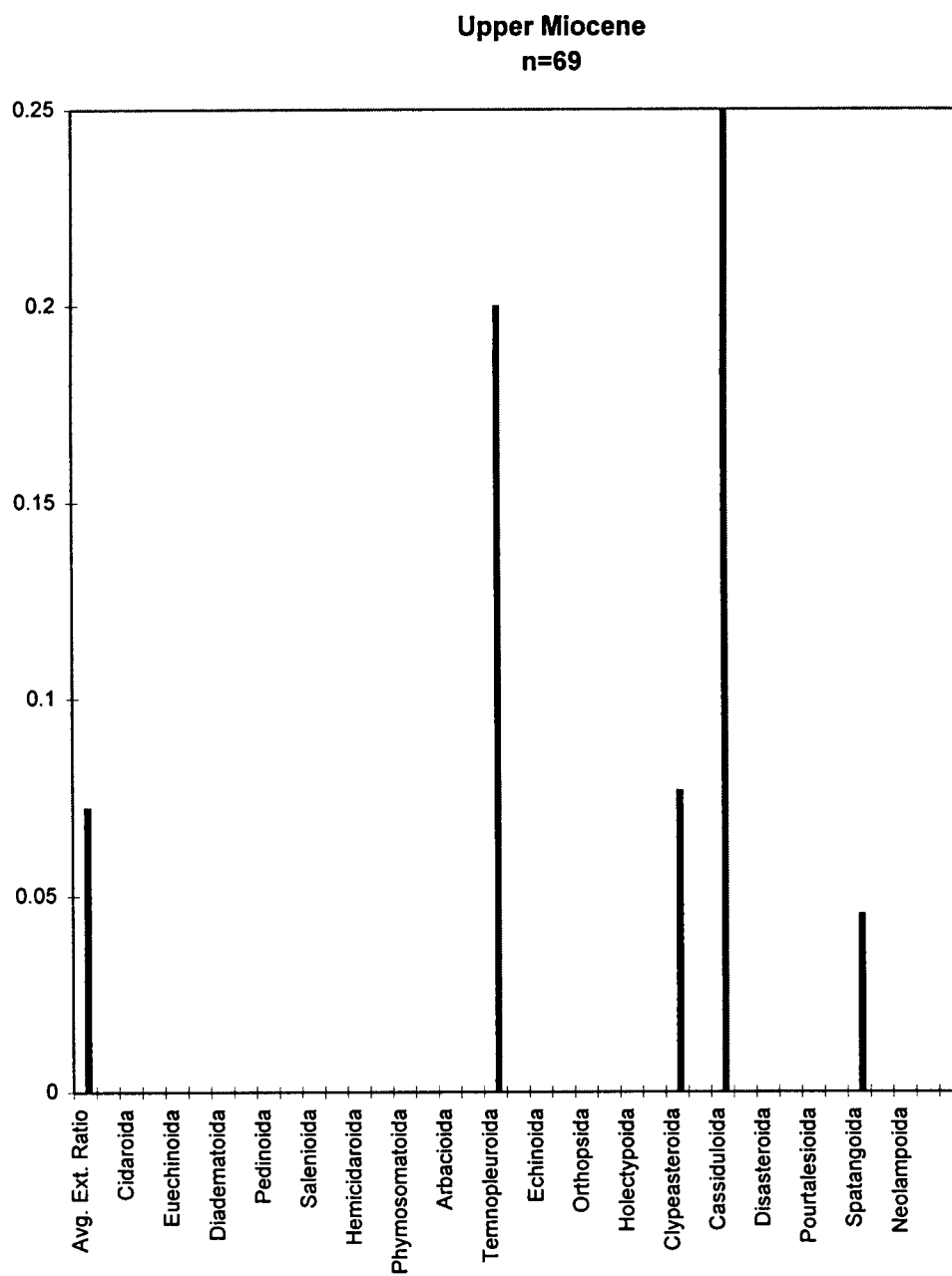


Figure D10. Bar graph representation of each ordinal extinction ratio compared to the weighted mean average extinction ratio for the Upper Miocene. The number of data entries is denoted by “n”. Orders without data for this time interval have values of zero.

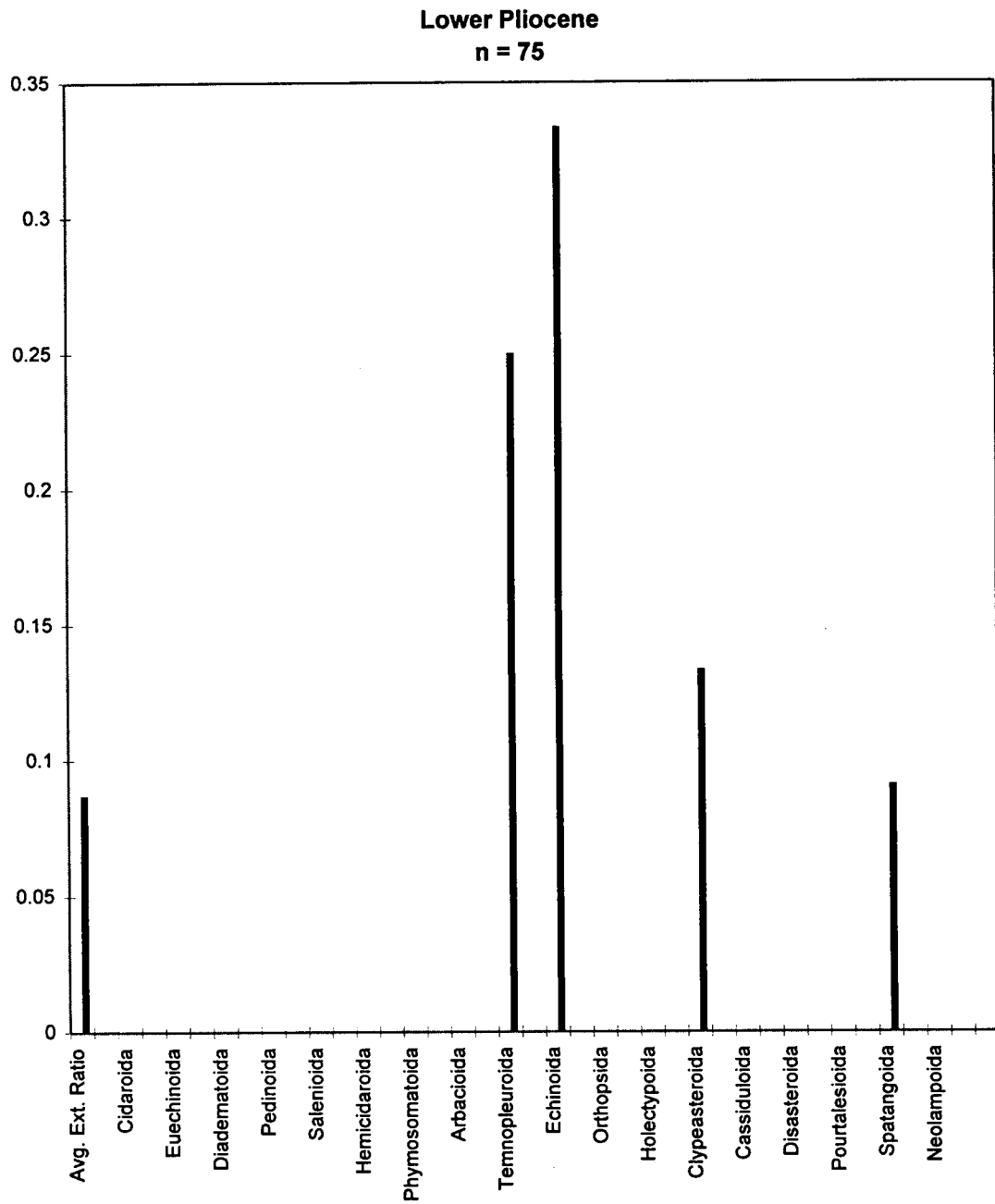


Figure D11. Bar graph representation of each ordinal extinction ratio compared to the weighted mean average extinction ratio for the Lower Pliocene. The number of data entries is denoted by “n”. Orders without data for this time interval have values of zero.

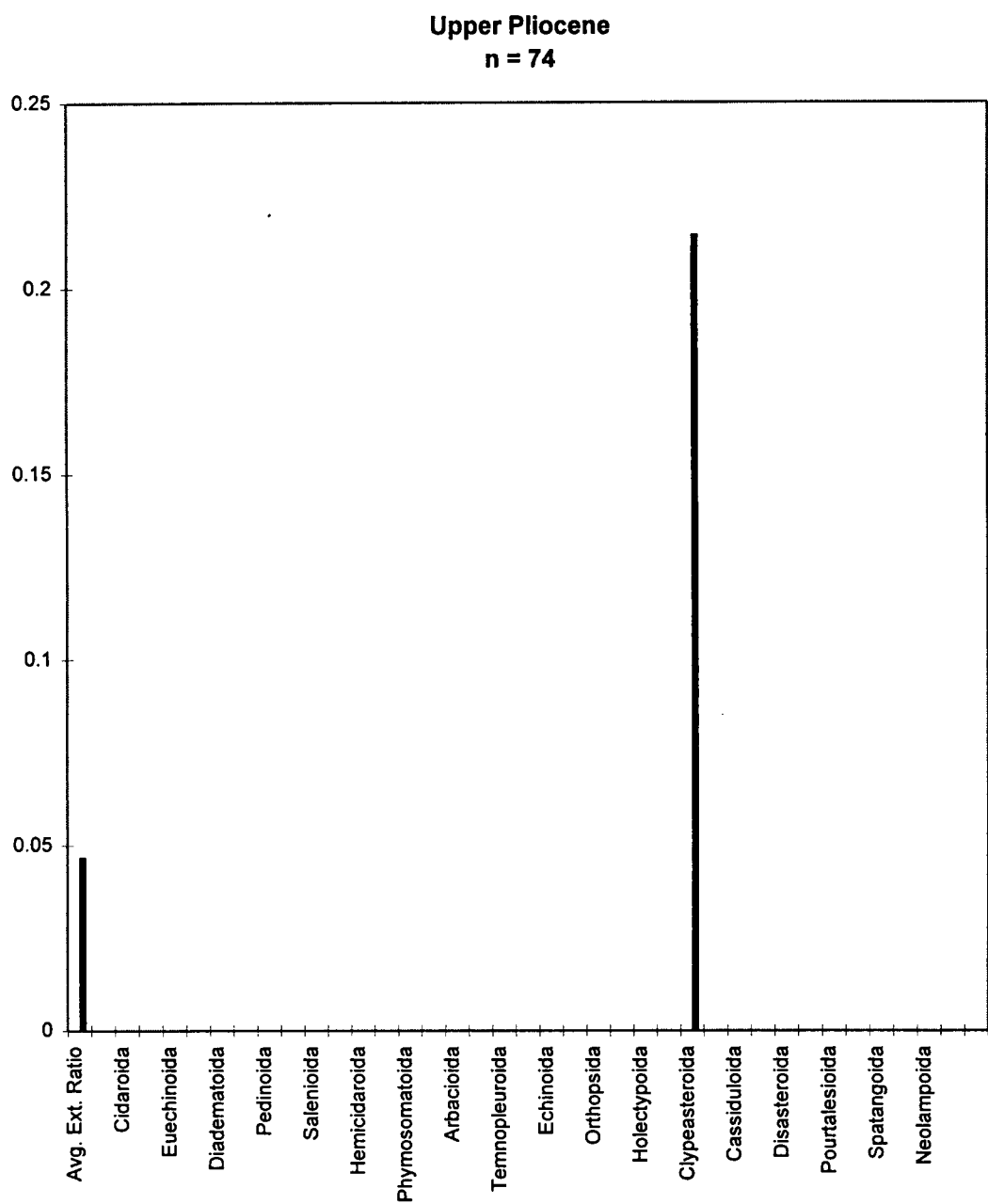


Figure D12. Bar graph representation of each ordinal extinction ratio compared to the weighted mean average extinction ratio for the Upper Pliocene. The number of data entries is denoted by “n”. Orders without data for this time interval have values of zero.

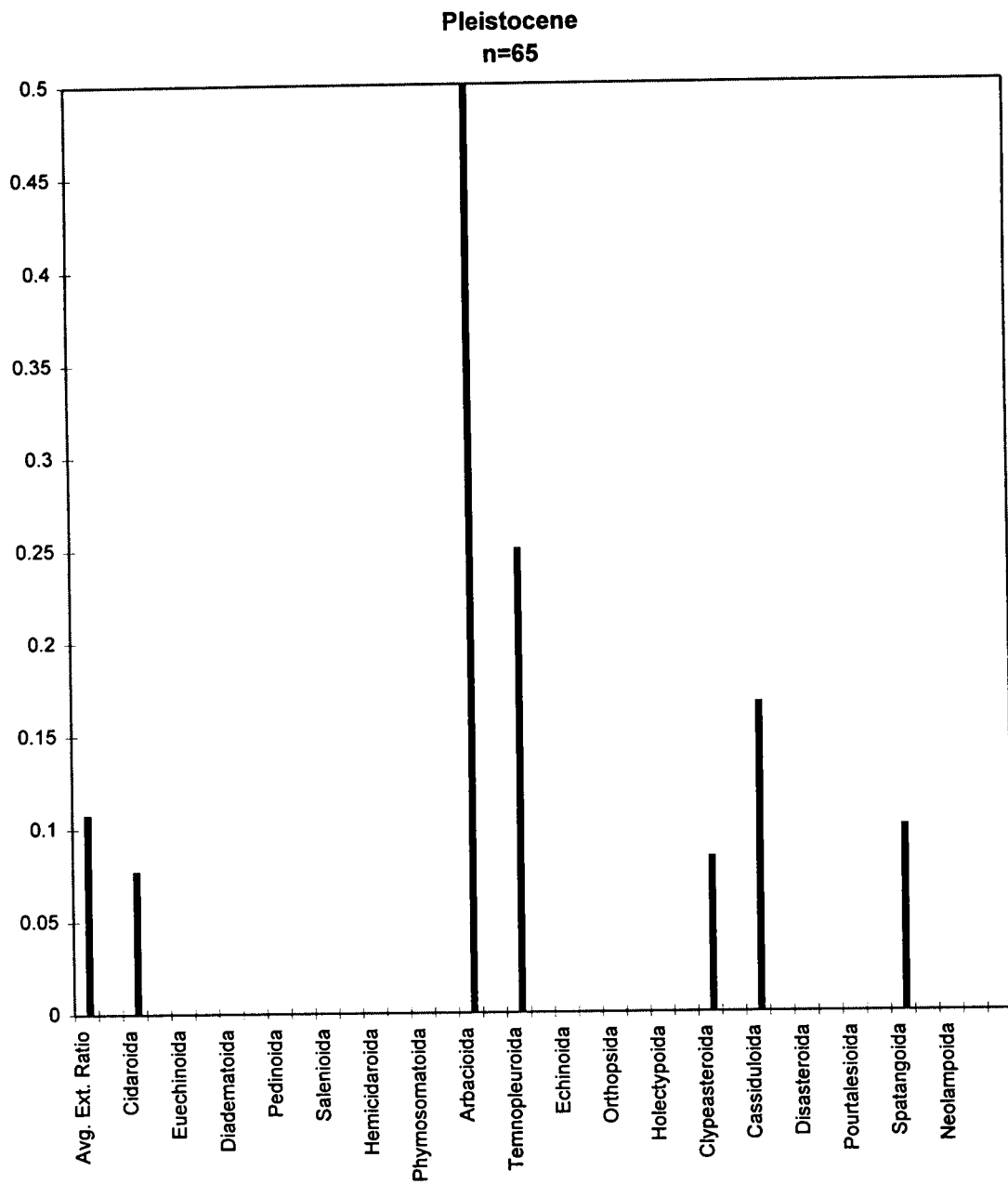


Figure D13. Bar graph representation of each ordinal extinction ratio compared to the weighted mean average extinction ratio for the Pleistocene. The number of data entries is denoted by “n”. Orders without data for this time interval have values of zero.

VITA

Gray Dean was born March 10, 1961. He graduated from McIntosh County Academy in 1979 and attended Georgia Institute of Technology and Brunswick College. He received a B.S. in Communication Arts from Georgia Southern University in 1987, after which he embarked upon a career of television production. He returned to the classroom in 1992 to obtain a B.S. degree in Geology which was conferred in 1994. Gray then began graduate studies at the University of Tennessee, Knoxville, where he received a Masters of Science in Geology, in 1997.

Currently, he has entered the Doctoral program at Tennessee, where he hopes to continue with his work in paleoevolutionary studies.