Heart Urchins at the Cretaceous/Tertiary Boundary: A Tale of Two Clades

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Abstract.—Previous estimates of the global generic diversity loss for echinoids at the Cretaceous/Tertiary boundary have been as high as 65%. However, these estimates are based on compilations of occurrence data from the existing literature and are plagued by problems of inconsistent taxonomic usage. Analysis of a taxonomically standardized, phylogenetically framed data set demonstrates that the generic extinction rate for heart urchins was 33%, and that the two constituent orders suffered markedly different fates. Whereas holasteroids lost 56% of their generic diversity at the end of the Cretaceous, only 17% of spatangoid genera became extinct. Correlation of extinction with a range of geographical, environmental, and biological factors has been explored. Survivorship is significantly correlated only with feeding strategy, implying that the extinctions of atelostomate echinoids at the Cretaceous/Tertiary boundary were nutrient driven. In addition, feeding strategy is correlated with atelostomate clade affinity, explaining the differential fates of holasteroids and spatangoids at the end of the Cretaceous.

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Introduction

Mass extinction events represent periods of rapid and statistically significant (Hubbard and Gilinsky 1992) loss of biological diversity on a global scale. They stand out as peaks against the more usual background extinction levels (Raup and Sepkoski 1982), and their sheer magnitude and apparently indiscriminate nature have long been considered indicative of the involvement of external factors. However, mass extinctions are nonrandom (Raup 1986). The survivors do not represent an arbitrary sample of the preextinction biota, and clues to the causes of mass extinction events can be gleaned from analysis of patterns of survivorship selectivity. To date, the detailed and systematic investigation of survivorship selectivity has been attempted only with molluscan faunas at the Cretaceous/Tertiary (K/T) boundary (Raup and Jablonski 1993; Jablonski and Raup 1995; McClure and Bohonak 1995), and as yet there is little consensus about recognized patterns. Analysis of other taxonomic groups will allow confirmation or qualification of the generalities currently drawn from fossil mollusks. In this paper I present an analysis of the survivorship patterns within the heart urchins (Echinoidea: Irregularia: Atelostomata) at the Cretaceous/Tertiary boundary.

Atelostomate echinoids are characterized by their ovate or heart-shaped horizontal outline, modified plates in the adoral portion of interambulacrum 5 forming a plastron, and ambulacrum III commonly differentiated from the paired ambulacra. The relationship of the Atelostomata to the remaining irregular echinoids is shown in Figure 1. Upper Cretaceous atelostomate echinoids are subdivided into Holasteroida and Spatangoida on the basis of differences in apical disk and plastron plating.

The heart urchins provide an ideal model organism on which to focus. They form an important and diverse component of the marine benthos before and after the Cretaceous/Tertiary boundary, and since the preservation potential of echinoids is comparatively high, especially amongst the irregulars (Kier 1977), fossil heart urchins are abundant in differing facies types from the poles to the equator in Late Cretaceous and Early Tertiary strata. Because of their morphological complexity, echinoids are relatively straightforward to classify taxonomically and phylogenetically. In addi-

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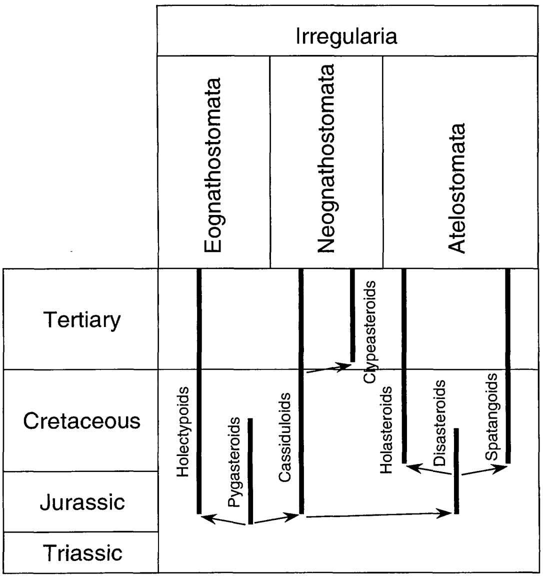

FIGURE 1. Phylogenetic relationships and stratigraphic ranges of irregular echinoids (after Smith 1984).

tion, there is good correlation between morphology and paleobiology (e.g., Kanazawa 1992), allowing the association between survivorship and key biological traits to be investigated. For example, mucus string feeding can be inferred from spatangoids with a deeply sunken frontal groove and modified spines and tubercles (Bromley et al. 1995). Perhaps most significantly, atelostomate echinoids encompass some clades that survived and others that became extinct at the end of the Cretaceous. In the extinction debate, the limelight has often been given to taxa, such as ammonites and dinosaurs, that were totally annihilated. Yet there is little that can be deduced about extinction processes if there are no surviving lineages, and the factors that are important in survival can be deduced only by looking at a group in which only some clades became extinct.

Previous Studies of Echinoids at the K/T Boundary

Compilations of echinoid species data (e.g., Lambert and Thiéry 1909–1925; Kier and Lawson 1978; Moskvin et al. 1980) have been used by a number of authors to assess diversity changes across the Cretaceous/Tertiary boundary. For example, Kier (1974) tallied only 108 species from Paleocene strata compared with 1137 from the Senonian in Lambert and Thiéry's (1909–1925) compilation. Combining data from Lambert and Thiéry (1909–1925), Moskvin and Poslavskaya (1959), Poslavskaya and Moskvin (1960), and Kier and Lawson (1978), Stokes (1979) concluded that spatangoids were hardly affected by the crisis at the end of the Cretaceous. He also established that the major faunal changes in heart urchins at the Cretaceous/Tertiary boundary, noted by Poslavskaya and Moskvin (1960), were due primarily to disappearances of holasteroid taxa. Moskvin et al. (1980) produced a compendium of Campanian to Paleocene occurrences for echinoid species from the former Soviet Union and for echinoid genera worldwide. They found significant losses in generic diversity at the end of the Maastrichtian for all orders except cidaroids and spatangoids. The same data were subsequently analyzed by Shimanskii and Solovjev (1982), who claimed that extinctions over this time period were progressive rather than abrupt, starting in the Upper Senonian. Roman (1984) employed the same data set and demonstrated that the K/T boundary coincided with the single most important event in post-Paleozoic echinoid history, with 83 out of 127 genera (65%) present for the last time during the Maastrichtian. Kier and Lawson's (1978) compilation of echinoid species includes only taxa described between 1925 and 1970 and does not take account of the many abundant species that had been previously described. From these data, McKinney (1995) estimated that 57% of Maastrichtian echinoid genera did not survive into the Tertiary.

Jeffery (1997a) produced an account of echinoid faunal changes in continuous Maastrichtian to Danian sections of the Mangyshlak Peninsula, Kazakhstan. This study demonstrated that although extinction levels within the sections were extremely high (82% at generic level), the inclusion of occurrence data for localities outside of Kazakhstan reduced the estimate to 25%, highlighting the difficulties associated with the extrapolation of local extinction patterns. The same pattern of local extinction and replacement was repeated in other K/T sections. In Denmark a 56% extinction across the Cretaceous/Tertiary boundary at the genus level was reduced to 25%, and in the Maastricht area, a loss of 68% of Maastrichtian genera dropped to 39%. Thus migration and changes in geographic range, rather than extinction, account for at least some of the perceived local loss of taxa at the Cretaceous/Tertiary boundary.

Eble's (1998) exploration of diversity and disparity patterns in Mesozoic atelostomate echinoids also covered the period spanning the K/T boundary. Stratigraphic ranges were taken mainly from Sepkoski's unpublished generic database with additions and modifications. Genera known only from poorly preserved or incomplete specimens were excluded from the study. Although the lower temporal resolution of this study may have inflated extinction estimates by effectively concentrating all Senonian extinctions at the K/T boundary, the resulting analysis found that losses were more severe among holasteroids than spatangoids, with 73% of holasteroids and 41% of spatangoids going extinct at the end of the Cretaceous.

Of the 43 heart urchin genera with Maastrichtian representatives compiled from the literature for this study (prior to taxonomic standardization), 28 have no post-Cretaceous record. This represents a global generic-level extinction of 65% at the K/T boundary for atelostomate echinoids. This value is similar to other estimates of marine macroinvertebrate extinction calculated from compendia of occurrences (Roman 1984; Raup and Jablonski 1993; McKinney 1995).

Approach Adopted for This Study

Taxonomic Revision

Artifacts of nomenclature, such as the naming of species solely on the basis of their occurrence in a particular geographic locality or stratigraphic horizon, as well as the idiosyncrasies of individual taxonomists, can lead to taxonomic disappearances (or pseudoextinction) and a subsequent inflation of extinction estimates. To produce a global database with a uniform taxonomy free from the problems of inconsistent taxonomic usage commonly encountered in the literature and consequently in compendia of occurrences (Wingard 1993), it is necessary to ensure that all morphologically identical taxa are synonymized, and to verify that taxa assigned the same name by different workers are morphologically consistent. To this end, a taxonomic revision of all the atelostomate echinoid species recorded in the literature from Maastrichtian and Paleocene strata worldwide was undertaken, based largely on museum holdings. Taxa were synonymized unless significant differences in test plating and structure could be consistently and unambiguously distinguished. Size and outline differences were not taken to be necessarily indicative of species boundaries. Some 307 nominal species of atelostomate echinoid from over 100 stratigraphic formations have been revised, including newly collected material from the type Danian (Stevns Klint, Denmark) and the type Maastrichtian. Fieldwork at several important Maastrichtian and Paleocene localities in Spain added a number of new species (Smith et al. 1999). Taxa previously regarded as subgenera of *Hemiaster* were considered to have sufficient morphological differences to be treated as genera in this analysis. This work together with a taxonomic revision of all other echinoids from this time interval is published elsewhere (Smith and Jeffery in press). Where possible, taxa were placed in an eightfold stratigraphic scheme that included four Maastrichtian and four Paleocene subdivisions.

TABLE 1. Effect of taxonomic standardization on Maastrichtian and Paleocene atelostomate echinoid data set.

	Pre-revision	Post-revision
Number of species	307	129
Number of genera	72	51

Taxonomic revision substantially reduced the size of the atelostomate data set. Even taking into account recent taxonomic revisions of this group (e.g., Kier 1972, 1984), 29% of generic names were found to be superfluous, while 58% of species names were removed (Table 1). Only those genera with Maastrichtian representatives (39 taxa after revision) were included in the subsequent survivorship analyses.

Phylogenetic Analysis

The presence of large numbers of nonmonophyletic taxa in the literature indicates that traditional taxonomy does not always reflect genuine biological groupings and processes and can conceal lineage continuity. The last appearance of a non-monophyletic taxon may correspond to a true biological extinction but equally may just reflect a change in nomenclature. Thorough phylogenetic analysis may lead to a reduction in the number of apparent extinctions by allowing inferences about the survival of clades to be made. For example, *Stegaster cotteaui*, which is found solely in Maastrichtian strata, has *Sanchezaster habanensis* as its Eocene sister group. In addition, phylogenetic analysis enables spurious patterns of preservation or collection bias to be distinguished from real evolutionary patterns in the fossil record. It is now widely recognized that the construction of robust phylogenies will allow the more reliable calculation of levels of mass extinction in the fossil record (Sepkoski and Kendrick 1993; MacLeod 1996; Jablonski 1997; Jeffery and Smith 1998), although many authors maintain that traditional taxonomic groupings may equally well capture the underlying pattern of shifts in biodiversity (Raup and Boyajian 1988; Sepkoski and Kendrick 1993).

As yet, no modern species or generic-level phylogenies are available for the Echinoidea, and so phylogenetic analyses of Maastrichtian and Paleocene atelostomate echinoids have been carried out to determine the relationships between taxa and thus ascertain which clades survived the K/T event. Cladistic analyses were performed using morphological characters compiled for all species examined as part of the taxonomic revision, as well as for those species where there are unambiguous descriptions and illustrations in the literature. Following David (1988) and Mooi and David (1996), the chosen characters were based, wherever possible, on structural differences in test architecture rather than on "softer" characters such as overall size. Generic-level analyses were performed on the holasteroids and spatangoid suborders Micrasterina and Hemiasterina in addition to more detailed species-level analyses on subsets (i.e., clades) identified by the generic analyses. Species-level analyses were carried out when coding intragenerically variable characters as question marks may have blurred any phylogenetic signal.

The phylogenetic analyses were carried out using the Macintosh application PAUP 3.1.1 (Swofford 1993). Accelerated transformation (ACCTRAN) was used for character-state optimization. Small data sets were subjected to branch-and-bound search, while 25 random addition sequence replicates of a heuristic search were used with larger data sets. Where multiple solutions were produced, characters were reweighted according to the rescaled consistency index derived from the original unweighted analysis, and the search repeated (Farris 1988). In all instances, except the generic-level analysis of the Hemiasterina, this approach resulted in one of the original trees being selected. Bootstrapping based on 1000 iterations was carried out to test the strength of the phylogenetic signal (Felsenstein 1985). Full details of the phylogenetic analyses are presented elsewhere (Jeffery 1997b, 1998).

For the Micrasterina, 52 characters were scored for nine Maastrichtian and Paleocene genera plus *Toxaster* as outgroup, and the Eocene *Habanaster*. A branch-and-bound search produced a single most parsimonious solution (CI = 0.892; RI = 0.858), identifying *Habanaster* as the sister group to the exclusively Maastrichtian *Ovulaster*. For the Hemiasterina, 26 Maastrichtian and Paleocene genera plus the outgroup *Toxaster* were included. Heuristic analysis of the 52-character data set produced 67 trees. By reweighting using the rescaled consistency index the number of solutions was reduced to two (CI = 0.658; RI = 0.800). One solution best fits the stratigraphy. For holasteroid genera, 35 characters were scored for 18 Maastrichtian and Paleocene taxa plus *Holaster nodulosus* as outgroup. Two most parsimonious solutions were identified by heuristic searching. One was chosen (CI = 0.674; RI = 0.834) by reweighting according to the rescaled consistency index and rerunning the analysis. A branch-and-bound species-level analysis of the stegasterid holasteroids with *Echinocorys* as outgroup (11 taxa, 29 characters) produced a single parsimonious solution (CI = 0.901; RI = 0.891) identifying the Eocene *Sanchezaster habanensis* as sister taxon to the Maastrichtian *Stegaster cotteaui*.

By plotting phylogeny against stratigraphy (Jeffery 1997b, 1998), heart urchin clades that survived the end-Cretaceous event were determined. The data are summarized in the Appendix. Errors on extinction estimates were calculated using the binomial standard deviation.

Selectivity Analysis

It has been suggested that the factors which influence survivorship during periods of background extinction are ineffective during mass extinctions (Jablonski 1986a). For example, although lineages containing small numbers of species are supposedly prone to higher extinction levels during normal times, it seems that species richness does not act as a significant buffer during mass extinction events (Jablonski 1986a, 1989, 1995). So are mass extinctions indiscriminate with respect to taxonomic position, or do some taxa possess biological or ecological traits that increase their chances of survival? Many patterns of survivorship selectivity have been proposed in the vast mass extinction literature but few have been tested empirically. Notable exceptions include work on K/T bivalve faunas (Raup and Jablonski 1993; Jablonski and Raup 1995; McClure and Bohonak 1995).

For this study, patterns of survivorship selectivity in end-Cretaceous heart urchins were examined using chi-squared tests of contingency tables at the 95% level. This approach has proved its worth in other investigations of extinction selectivity (McKinney 1985; McClure and Bohonak 1995; Lessa and Fariña 1996), although it has been suggested that the chi-squared test is somewhat liberal. In order to reduce Type 1 errors, the Cochran continuity correction (see Zar 1984) was used for contingency tables with one degree of freedom, and in addition, Fisher's exact test was used to determine probabilities for these tables. For continuous and ordered variables, the Kolmogorov-Smirnov two-sample test was applied. All possible correlates to survivorship at mass extinctions suggested in the literature (Table 2) were explored. All analyses focused on generic-level traits. Taxa used in the analysis plus details of possible correlative factors are tabulated in the Appendix. Two sets of analyses were carried out: the first cross-classifying each of the possible correlates with the extinction or survival of the genera, and the second testing for association between possible correlative factors and atelostomate higher taxonomy in order to explore why holasteroids were more severely depleted at the Cretaceous/Tertiary boundary. Sample sizes for the chi-squared tests ranged from 38 to 89 (larger numbers where a single genus was scored in several categories, such as sediment type). Where appropriate, categories were chosen to minimize the number of cells with expected values of less than five. Exact p-values for all statistics were found using Systat.

TABLE 2. Possible correlates to atelostomate echinoid survivorship at the end of the Cretaceous.

Geographic and environmental	Biological
Geographic range	Life position in sediment
Absolute geographic distribution	Larval strategy
Water depth	Feeding strategy
Sedimentary environment	

Determining Paleogeographic Ranges.—A number of different methods of estimating geographic range exist (see Emlet 1995). For this study geographic range during the Maastrichtian was determined as (1) the number of degrees of paleolongitude between a clade's two most distant occurrences plotted onto a paleogeographic reconstruction of the Maastrichtian (Scotese et al. 1988) (categories were single locality, 2–20 degrees, 21–60 degrees, and 61 or more degrees); (2) the number of degrees paleolatitude between a clade's most northerly and southerly occurrences (categories were single locality, 2–20 degrees, 21–60 degrees, and 61 or more degrees); (3) the number of regions (categories were single region, two, and three or more regions); and (4) the number of localities (categories were single locality, two to four, five to eight, and nine or more localities) in which a taxon occurred during the Maastrichtian. Regions were composed of smaller local areas that have been subject to monographic treatment and were chosen to be of approximately equal size. For chi-squared tests, range size was split into categories, chosen to minimize the number of cells in the contingency tables with expected values of less than five.

Determining Absolute Geographic Distribution.- All localities yielding fossil atelostomate echinoids were plotted onto a Maastrichtian paleogeographical reconstruction (Scotese et al. 1988), and paleolatitudes and paleolongitudes were calculated for each Maastrichtian clade. Limits of categories for chi-squared tests were chosen using gap analysis. Occurrence in two latitudinal or longitudinal categories was not taken as evidence of occurrence in intermediate categories. For the longitude analysis, categories were 90°W–5°W, 4°W–20°E, 21°E–50°E, and 51°E or more. In order to investigate the association between latitude and extinction intensity, northern and southern latitudes were combined. Categories for chi-squared tests were 0–25°, 26–43°, and 44° or more. In addition, the effect of latitudinal tolerance on extinction was explored. Latitudinal tolerance was defined as the paleolatitudinal range with northern and southern latitudes combined. Categories were single locality, 2–20°, and 21–50°.

Inferring Water Depth.—Independent data from general sedimentological and faunal studies were used to identify paleodepth preferences for Maastrichtian and Paleocene echinoid communities (see Jeffery 1997b). Water depth was divided into four categories: littoral, onshore, mid- to outer shelf, and deep water. Possible correlation of survivorship with bathymetric tolerance (number of depth zones occupied) was also explored.

Inferring Echinoid Substrate Preferences.—Recent and fossil echinoids are known from a wide range of marine habitats, from shallow coastal waters to the deep sea, and from rocky substrates to unconsolidated sediment. However, it is clear that individual echinoid species exhibit marked substrate preferences (Smith 1984; Carter et al. 1989; Carter and Hamza 1994), and the nature of the substratum is thought to strongly influence the local distribution of echinoid taxa (Smith 1984). Inspection of sediment within, and adhering to the outside of, echinoid tests is the easiest way of determining the substrate preferences of fossil echinoids. For atelostomates, sediment preferences may also be ascertained from the functional morphology of the adult test, since the presence and position of fascioles and the density of tuberculation give an indication of the grade of sediment in which the animal could live. Since the majority of specimens examined for this project come from well-characterized lithological units, the substratum preferences for each genus were gathered from general sedimentological and faunal studies of each stratigraphic unit (see Jeffery 1997b). Sediment type was divided into four categories based on grain size and calcareous content: chalk/marl, calcarenite/sandy limestone, sand/gravel, and silt/mud.

Inferring Burrowing Habit in Heart Urchins.—The burrowing habits of fossil and Recent heart urchins may be inferred in a number of ways. For spatangoids, the shape of the test in lateral profile gives an indication of the sediment type inhabited and depth of burial (Kanazawa 1992). For both holasteroids and spatangoids, the density of tuberculation on the aboral surface and the presence of large tubercles along the edges of the unpaired ambulacrum also provide information on the animal's ability to burrow (Smith 1980a), since dense spine cover prevents sediment from choking the test and larger spines along the frontal groove provide space for tunnel-building tube feet to function. Fascioles are made up of miliary spines that produce mucus, which is used to coat the upper surface of the test and prevent it from becoming clogged with sediment. Hence, the presence of aboral fascioles indicates an infaunal habit. Finally, large pores located in the unpaired ambulacrum for funnel-building tube feet or subanally for tunnel-building tube feet also provide evidence of a burrowing mode of life (Smith 1980b). For this study, taxa considered to be semi-infaunal and aborally exposed were included in the epifaunal category, since they would have been subject to similar levels of environmental stress to fully epifaunal taxa. Excluding semi-infaunal taxa or combining them with fully infaunal forms does not alter the result of the analysis.

Inferring Developmental Mode in Echinoids.—Developmental mode in marine invertebrates can be broadly divided into taxa that are dependent on particulate matter in the plankton for their nutrition until metamorphosis (planktotrophs) and those that do not feed but rely solely on the nutrient reserves in the eggs from which they hatch (lecithotrophs). The reproductive strategy of echinoids may be inferred in three different ways (Jeffery 1997c). First, the presence of depressed areas on the adult test, thought to be used as "marsupia" where offspring are sheltered, implies brooded development (Kier 1967, 1969; McNamara 1994). Second, since nonplanktotrophs typically produce far larger eggs than planktotrophs, extreme sexual dimorphism in gonopore size can be used to infer nonplanktotrophy in sea urchins (Kier 1967, 1969; Emlet 1989). Finally, developmental mode may be inferred from the orientations of crystallographic axes of apical disk plates (Emlet 1985, 1988, 1989), since the calcite skeletal rods of planktotrophic larvae determine the orientation of the calcite in the apical system of the adult echinoid. For this study, data on reproductive mode were deduced using the methods outlined above or collated from the published literature. Only one species, *Abatus pseudoviviparus* Lambert, which has been collected with juveniles within the deeply sunken petals of adult specimens, was considered to be marsupiate. Analysis tested for association between survivorship and planktotrophy versus nonplanktotrophy.

Inferring Feeding Strategy in Atelostomate Echinoids.—All irregular echinoids are deposit feeders that collect detritus from the seafloor. However, differences in oral morphology suggest that two different collection strategies are employed within the Atelostomata (see Fig. 4). The first group have a deep, sharp frontal groove leading directly to the mouth and no enlarged pores around the mouth. They are similar to modern deep-sea forms, reliant on the rain of phytodetritus from above, which funnel quantities of surface sediment directly into the mouth to extract the small amount of organic material. Taxa adopting this strategy, here called "surface sievers," are often associated with deep-sea, oligotrophic settings (Jeffery and Smith 1998) today and in the fossil record. The remaining atelostomate echinoids have specialized pencillate tube feet around the mouth that they use to pick up and manipulate small particles of detrital material (Smith 1980b). Large perioral pores are evidence of the existence of such tube feet in life. These taxa are here denoted "selective detritivores."

Finally, the size of Danian individuals in surviving clades relative to their Maastrichtian precursors may reveal details of nutrient stress at the K/T boundary. To assess relative size change at the end of the Cretaceous, the sizes (test lengths) of the largest available Maastrichtian and Danian individuals were measured and Danian maximum size was expressed as a percentage of Maastrichtian maximum size. Skewness and standard error of skewness were determined using Systat.

Results

Size of the Extinction Event

Range charts for Maastrichtian and Paleocene species of atelostomate echinoid (Smith and Jeffery 2000) illustrate that of the 94 species present in the upper Maastrichtian, only 27 survive into the Tertiary. This implies a species-level extinction rate of 71%. However, the dependence of individual species on the continuity of particular facies types, coupled with facies changes at the end of the Cretaceous, means that the proportion of apparent extinctions that represent sampling artifact rather than true lineage termination is uncertain. These difficulties may be minimized by looking instead at generic extinction rates.

Of the 39 genera of atelostomate echinoid present during the Maastrichtian, 13 (9 holasteroids and 4 spatangoids) have no post-Cretaceous representatives or descendants. This corresponds to a worldwide generic extinction level for atelostomate echinoids of 33% (±8 binomial SE) over this time period. If the two genera known only from lower Maastrichtian strata (*Offaster* and *Hagenowia*) are excluded, the extinction level is reduced to 30% (±8 binomial SE). These figures are comparable to the global generic extinction rate of 36% estimated from a standardized data set by Smith and Jeffery (1998) for all echinoids at the Cretaceous/Tertiary boundary, but are substantially lower than previous estimates (Roman

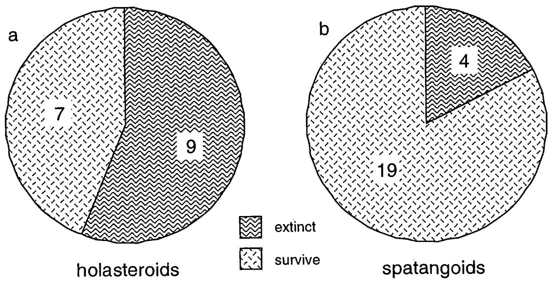

FIGURE 2. Generic extinction levels (in numbers of genera) at the Cretaceous/Tertiary boundary in holasteroids (A) and spatangoids (B).

1984; McKinney 1995; this study prior to taxonomic revision) calculated from global compilations of taxonomic occurrences.

Holasteroids versus Spatangoids.—Of the 16 holasteroid genera present during the Maastrichtian, only seven survive into the Paleocene. This corresponds to an extinction rate of 56% (±13 binomial SE). In contrast, 19 out of 23 Maastrichtian spatangoid generic-level clades are also present in Paleocene strata, representing an extinction rate of just 17% (±8 binomial SE). These differential extinction levels are shown diagrammatically in Figure 2. A chi-squared (χ^2) test for independence suggests that extinction is significantly correlated with higher taxonomic grouping (Table 3).

Since the taxonomic revision covered all species of Maastrichtian and Paleocene atelostomate echinoids, the data set also includes taxa with their first occurrence in the Paleocene. Twelve genera of heart urchin (3 holasteroids and 9 spatangoids) originated in the Paleocene. While spatangoids regained and even surpassed their preextinction generic diversity in the Paleogene, holasteroids never recovered from their mass extinction losses and have been in decline ever since their late Cretaceous zenith (Eble 1998). They are now confined almost exclusively to deep-sea habitats.

Although the contrast between holasteroid and spatangoid extinction levels has been noted by previous authors (Stokes 1979; Roman 1984; Eble 1998; Jeffery and Smith 1998; Smith and Jeffery 1998), it is still a surprising result that has not been adequately explained. Holasteroids and spatangoids are sister taxa with a broadly similar appearance and lifestyle. Because of their phylogenetic relationship and the fact that they suffered such different fates at the K/T boundary, holasteroids and spatangoids offer a means of testing hypotheses about end-Cretaceous scenarios.

Selectivity of the Extinction Event

Although revised extinction estimates are lower than those previously published, it still appears that a sizable proportion of atelostomate echinoids became extinct at the end of the Cretaceous. Could the extinction event itself be an artifact of taxonomic practice, with clades including the fewest Maastrichtian species most likely to disappear? Were taxa indiscriminately or selectively affected? Since a completely random pattern of biological loss would lead to lower extinction rates within species-rich clades, one way of determining selectivity in the data set is to test the association between extinction and species richness. A chi-squared test indicates that extinction is not significantly correlated with the number of Maastrichtian species included in a clade (categories were one species, two species, three or more species) (Table 3). This suggests that extinctions were not entirely random and that the species that perished had traits in common that made them more susceptible to the environmental stresses operating in the terminal Cretaceous (Raup 1995).

Chi-squared tests indicate that atelostomate survival into the Tertiary is independent of all geographical and environmental correlates

TABLE 3. Summary statistics of contingency tables testing the independence of extinction with regard to taxonomy. df represents degrees of freedom in chi-squared tests; p represents significance level found with chi-squared test; F represents significance level found with Fisher's exact test; KS represents significance level found with Kolmogorov-Smirnov two-sample test.

Factor	df	χ^2	p	F	KS
Higher taxonomic placement	1	5.842	0.016	0.017	
Number of species in a genus	2	2.007	0.367		1.000

TABLE 4. Summary statistics of contingency tables testing the independence of extinction with regard to possible geographical, environmental, and biological correlates. Abbreviations as in Table 3.

Factor	df	χ^2	p	F	KS
Total longitudinal range	3	0.391	0.942		0.836
Total latitudinal range	3	2.360	0.501		0.588
Number of regions	2	1.771	0.412		0.992
Number of localities	3	0.308	0.959		0.999
Absolute longitude	3	1.288	0.732		0.584
Absolute latitude	2	0.142	0.932		0.466
Latitudinal tolerance	2	2.028	0.363		0.422
Water depth	3	1.079	0.782		0.994
Number of depth zones	3	4.708	0.194		0.924
Sediment type	3	1.617	0.656		
Number of sediment types	2	0.169	0.919		0.999
Life position in sediment	1	1.463	0.226	0.129	
Larval strategy	1	1.254	0.263	0.281	
Feeding strategy	1	5.128	0.024	0.022	

(Table 4). There is no significant correlation between survivorship and size of geographic range (however measured), absolute geographic distribution, water depth, or sedimentary environment. Moreover, none of these factors are significantly associated with clade affinity (Table 5). Survivorship of heart urchins at the Cretaceous/Tertiary boundary is significantly correlated with feeding strategy but not with larval strategy or life position in the sediment (Table 4). Of these biological factors, both feeding strategy and life position in the sediment are associated with atelostomate higher taxonomy (Table 5).

Of the 17 generic-level clades for which Maastrichtian and Danian individuals exist and size data are available, 75% show a reduction in the size of individuals at the K/T boundary (Fig. 3). Analysis of skewness indicates that the distribution is significantly skewed.

Discussion

Size of the Extinction Event

It has been suggested that although the general pattern and tempo of biodiversity change through time can be gleaned from analysis of compilations of taxonomic data containing both monophyletic and paraphyletic taxa, clades may better reflect the magnitude of mass extinction events (Sepkoski and Kendrick 1993). Calculation of the global generic-level extinction of heart urchins at the Cretaceous/Tertiary boundary from an uncritical compilation of occurrences in the literature gives a value similar to previous estimates (Roman 1984; McKinney 1995). However, a

TABLE 5. Summary statistics of contingency tables testing the independence of atelostomate higher taxonomy with regard to possible geographical, environmental, and biological correlates. Abbreviations as in Table 3.

Factor	df	χ^2	p	F	KS
Total longitudinal range	3	3.323	0.344		0.624
Total latitudinal range	3	2.034	0.565		0.536
Number of regions	2	1.096	0.578		0.981
Number of localities	3	0.447	0.930		0.886
Absolute longitude	3	1.472	0.689		0.217
Absolute latitude	2	1.947	0.378		<0.001
Latitudinal tolerance	2	0.366	0.833		0.756
Water depth	3	2.541	0.468		0.798
Number of depth zones	3	2.490	0.477		0.863
Sediment type	3	2.346	0.504		
Number of sediment types	2	0.884	0.643		0.992
Life position in sediment	1	11.078	0.001	0.001	
Larval strategy	1	2.591	0.108	0.130	
Feeding strategy	1	18.759	<0.001	0.001	

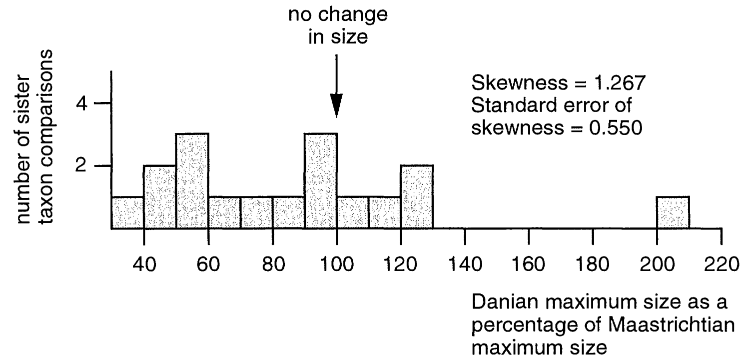

FIGURE 3. Histogram of Danian maximum test size as a percentage of Maastrichtian maximum test size for surviving clades of atelostomate echinoids.

nomenclatural revision and subsequent phylogenetic analysis virtually halves the estimated extinction rate. Although the "non-trivial problem of integrating local and synoptic databases" (Jablonski 1996: p. 3) has been recognized, its effects are grossly underestimated. This result underlines the amount of error that taxonomic inconsistencies can contribute to any regional or global analysis and suggests that similar treatment of other data sets could lead to analogous reductions in the magnitude of extinction level estimates for other groups.

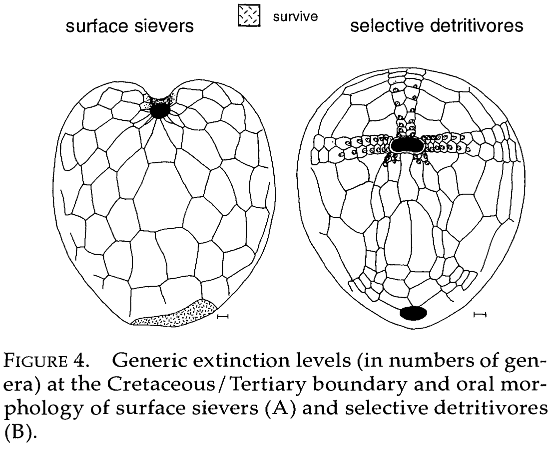

FIGURE 4. Generic extinction levels (in numbers of genera) at the Cretaceous/Tertiary boundary and oral morphology of surface sievers (A) and selective detritivores (B).

Selectivity of the Extinction Event

The lack of correlation between survivorship and species richness in heart urchins at the Cretaceous/Tertiary boundary attests to the nonrandom nature of the mass extinction event and corroborates previous work on extinctions of bivalves at the end of the Cretaceous (Jablonski 1989, 1991, 1995, 1996; McClure and Bohonak 1995), corals (Sorauf and Pedder 1986) and ammonoids (House 1985) in the Late Devonian, and trilobites at the end of the Cambrian (Westrop 1989). The end-Permian extinction event is the only documented exception to this general trend (Erwin 1989a, 1990). Rather than representing arbitrary samples of the preextinction biota, heart urchin survivors have biological, ecological, and geographical correlates in common.

Geographic Range.—Widespread taxa are commonly believed to be more resistant to extinction than those with narrow geographic ranges during periods of both background and mass extinction. This pattern has been documented for Cambrian trilobites (Westrop 1989, 1991), Late Ordovician taxa (Sheehan et al. 1996), end-Permian gastropods (Erwin 1989a,b, 1990), end-Cretaceous bivalves and gastropods (Jablonski 1986a, 1989, 1991, 1995; Jablonski and Raup 1995), foraminifera (Keller 1996), and other taxa at the K/T boundary (Sheehan et al. 1996). In marked contrast, a widespread geographic distribution does not appear to have acted as a buffer to extinction during the Late Devonian mass extinction (McGhee 1996). Presence in a large number of provinces is also an indicator of abundance, and it has been suggested that the most common taxa were also the most resilient (Keller 1996). However, this is not supported by analysis of bivalves at the end-Cretaceous mass extinction (McClure and Bohonak 1995), nor by this analysis of atelostomate echinoids, which indicates that survival into the Tertiary is independent of the size of geographic range (however measured). The difference between these results can be explained in terms of the data used for analysis (Smith and Jeffery 1998). In contrast to most previous work, this study uses a phylogenetic framework, identifying lineage rather than taxonomic continuity. All synoptic compilations contain a proportion of superfluous names of taxa often known only from a single locality or stratigraphic horizon. The exclusion of these taxa through taxonomic standardization combined with the construction of a phylogenetically based data set reduces the number of endemic pseudoextinctions. In addition, the pattern of selectivity revealed by other studies could be an artifact since widespread taxa are likely to be more common and thus better sampled on both sides of the boundary.

Absolute Geographic Distribution.—It has been suggested that taxa show different levels of extinction susceptibility at times of mass extinction depending on their absolute geographic distribution, with low-latitude faunas generally considered to be the least resilient. This pattern has been demonstrated for foraminifera (Keller et al. 1993; MacLeod and Keller 1994; Keller 1996), dinoflagellates (Elliot et al. 1994), and corals (Rosen and Turnsek 1989) at the K/T boundary and for taxa during the Late Devonian mass extinction (McGhee 1996). The opposite pattern of high extinction levels in high latitudes is documented for the Late Ordovician extinction, which is thought to have been caused by a glaciation event (Sheehan et al. 1996). Calcareous nannoplankton extinctions, on the other hand, show no latitudinal bias at the end of the Cretaceous (Pospichal 1996). Bivalves too show fairly uniform extinction intensities at all paleolatitudes (and paleolongitudes) if rudists are excluded from the analysis (Raup and Jablonski 1993). Including the rudists, which are restricted to tropical carbonate platform facies, produces a pattern of elevated extinction in low latitudes (and west of 30° W) (Raup and Jablonski 1993), supporting the suggestion that the preponderance of endemic taxa in the Tropics could in itself explain the latitudinal patterns (Jablonski 1995). Atelostomate survivorship at the end of the Cretaceous is not significantly correlated with absolute paleolatitude, paleolongitude, or latitudinal tolerance, corroborating claims that extinction at that time was globally uniform (Raup and Jablonski 1993) and attesting to the global scale of the mass extinction event (Jablonski and Raup 1995).

Water Depth.—A number of studies indicate that deep-water taxa experienced lower levels of extinction than shallow-water taxa (Sorauf and Pedder 1986; McGhee 1996 for the Late Devonian; Erwin 1996 for the Permian/Triassic boundary; Kaiho 1994 for K/T foraminifera) and that genera with broad depth ranges were less severely effected (Westrop 1989 for end-Cambrian trilobites; Erwin 1989a,b, 1990 for end-Permian gastropods) during times of mass extinction. For the Frasnian/Famennian event, the increased levels of extinction in shallower-water taxa have been ascribed to "a massive disruption of the upper oceanic water habitat" (McGhee 1996: p. 121), perhaps caused by an asteroid impact (Sorauf and Pedder 1986; McGhee 1996) or a rapid decline in ocean temperature (Sorauf and Pedder 1986). At the Permian/Triassic boundary, major sea level fluctuations combined with large-scale vulcanism could have led to the preferential survival of deep-sea and depth-tolerant taxa (Erwin 1996). In contrast, no correlation between extinction level and bathymetric distribution has been found in bivalves at the Cretaceous/Tertiary boundary (Jablonski and Raup 1995; Jablonski 1996; McClure and Bohonak 1995) or for marine invertebrates during the Paleozoic mass extinctions (Sepkoski 1987). Heart urchin survivorship at the end of the Cretaceous was independent of both paleodepth inhabited and breadth of bathymetric range, corroborating the results of previous analyses of the marine invertebrate macrofauna at the Cretaceous/Tertiary boundary.

Sedimentary Environment.—There has been no previous work on survivorship selectivity and substrate preferences of pre–mass-extinction faunas per se. This is surprising since many marine invertebrates require specific sedimentary habitats (Koch 1995). However, since substrate type is generally linked to water depth and latitude, tests for association between survivorship and latitude or depth also provide indirect information on correlation between sedimentary environments and extinction intensities. For example, Raup and Jablonski (1993) found that by excluding carbonate-platform-dwelling rudists from their analysis there was no significant difference between extinction intensities at different latitudes. Low-latitude extinctions amongst echinoids can also be largely explained by the virtual disappearance of carbonate platform facies in the Danian (Smith and Jeffery 1998). Analysis of the Cretaceous/Tertiary boundary heart urchin data set reveals that survival is not associated with either substrate preference or sedimentary tolerance (number of lithofacies occupied). Although these results appear to contradict previous studies that have shown end-Cretaceous marine invertebrate extinctions to be concentrated in carbonate platform habitats (Sohl 1987; Rosen and Turnsek 1989; Raup and Jablonski 1993; Jablonski 1995, 1996; Smith and Jeffery 1998), very few Maastrichtian atelostomate echinoids are known from carbonate platform settings. The one genus known exclusively from this habitat (*Hemipneustes*) does go extinct.

Life Position in the Sediment.—A number of studies have indicated that infaunal taxa are more resistant to extinction during background times than those living epifaunally since they are buffered against environmental stresses and perturbations (Kauffman 1978; Stanley 1986). It has also been suggested that the ability of spatangoids to burrow to greater depths than holasteroids contributed to their survival at the end of the Cretaceous (Roman 1984; Eble 1998). In contrast, no significant difference in extinction rates between infauna and epifauna has been found for end-Cretaceous bivalves (Jablonski and Raup 1995; McClure and Bohonak 1995), though it should be noted that Jablonski and Raup (1995) excluded rudists from their global analysis. Atelostomate survival at the end of the Cretaceous is not correlated with life position in the sediment. However, there is a significant correlation between burrowing habit and atelostomate higher taxonomy (i.e., significantly more holasteroids are epifaunal than is expected). This result goes some way toward explaining why ability to burrow has often been cited as the reason that spatangoids preferentially survived the K/T event.

Larval Strategy.—In instances where adults could not survive a prolonged (i.e., more than one reproductive season) loss of oceanic productivity, taxa with lecithotrophic larvae are thought to be less susceptible to extinction. In fact, larval strategy has been proposed as the explanation for the survival of the nautiloids (with a lecithotrophic larval stage) and the demise of the ammonites (with a planktotrophic larval stage) at the end of the Cretaceous (Landman 1984; Kennedy 1989, 1993; Gallagher 1991; Sheehan et al. 1996), the persistence of trilobites with a benthonic larval stage during the Late Ordovician (Chatterton and Speyer 1989), and the decimation of bivalves and brachiopods at the end-Permian mass extinction (Erwin 1990). However, no correlation between survivorship and larval type has been found for taxa during the Late Devonian (McGhee 1996), for gastropod mollusks at the K/T boundary (Jablonski 1986a,b; Valentine and Jablonski 1986), or for heart urchins at the end of the Cretaceous (this study) despite the fact that all four atelostomate clades with nonplanktotrophic development survived. The nonsignificant result could be related to the very small number of nonplanktotrophic echinoids present in the Maastrichtian (Jeffery 1997c). Regardless, the ability of adult echinoids to withstand prolonged periods without food (Giese 1966) may make this analysis of developmental mode and preferential survivorship irrelevant.

Feeding Strategy.—Feeding strategy is often cited as a correlate to preferential survivorship at the Cretaceous/Tertiary boundary, with detritivores showing significantly lower extinction rates than those taxa that rely on primary productivity (McKinney 1985, 1987; Sheehan and Hansen 1986; Rhodes and Thayer 1991; Ward et al. 1991; Hansen et al. 1993; Jablonski and Raup 1995; Jablonski 1996; Sheehan et al. 1996). A similar pattern is evident during the end-Permian mass extinction (Erwin 1989a, 1996). The correlation between extinction level and deposit or suspension feeding at the end of the Cretaceous is often explained in terms of a catastrophic collapse of phytoplankton production brought about by global darkness following a bolide impact (Sheehan and Hansen 1986; Paul and Mitchell 1994; Sheehan et al. 1996). However, deposit feeders are more dependent on the input of organic matter from surface waters than commonly recognized (Jablonski and Raup 1995; Levinton 1996), since they rely on the fall of phytodetritus to the seafloor for their nutrition. In fact, many detritivores live in environments that are nutrient stressed for much of the year as nutrient supply to the seafloor fluctuates with the seasonality of phytoplankton production. Among deposit-feeding bivalves the low overall extinction rate is due to extremely low extinction levels in just two groups, the Nuculoida and the Lucinoidea (Jablonski and Raup 1995). Thus preferential survivorship is attributable to factors other than, or in addition to, the dichotomy between deposit and suspension feeding (Jablonski 1996; Levinton 1996).

All atelostomate echinoids are deposit feeders, but they practice two different food collection strategies. The spatangoids included in this study all possess the large perioral pores characteristic of selective feeding. By contrast, a large proportion of the holasteroids have a deep, sharp frontal groove and no enlarged pores around the peristome, characteristic of surface sievers. Oral morphology, and therefore feeding strategy, is significantly correlated with atelostomate higher taxonomy. Within the atelostomate echinoids, surface sievers (and thus holasteroids) were more severely affected at the Cretaceous/Tertiary boundary (Figure 4).

In general, the assimilation efficiency of selective detritivores is far greater than for many other detritus-feeding species (Barnes and Hughes 1988). In addition to the organic material found on the surface of the sediment, much larger quantities of organic matter are preserved within the sediment. Typically this resource is difficult to access because it is composed of reduced organic matter, resistant to metabolic processes (Barnes and Hughes 1988). Today, several spatangoid taxa with the characteristic morphology of selective detritivores also possess an intestinal cecum containing sulfide-oxidizing bacterial symbionts, allowing them to utilize the reduced organic matter as a source of nutrition (Bromley et al. 1995) and enabling them to survive at greater depths in the sediment. It has been suggested that the adoption of this strategy by spatangoids may have allowed them to preferentially survive the Cretaceous/Tertiary boundary (Eble 1998). Irrespective of these speculations, elevated extinction rates among surface sievers would have accompanied a decrease in nutrient supply to deep-sea oligotrophic environments and are consistent with a collapse of primary productivity at the K/T boundary. In addition, since echinoids drastically curtail growth when faced with extrinsic food limitation (Lawrence 1987), the observation that most Danian echinoids are substantially smaller than their Maastrichtian precursors supports this conclusion. This result concurs with the prediction that the survivors of a nutrient-driven extinction event will be small (Paul and Mitchell 1994) and parallels the reduction in shell size in bivalves at the K/T boundary (Hayami 1997). Claims of a nutrient crisis at the K/T boundary are further bolstered by evidence of a decrease in primary productivity (Arthur et al. 1987; Margolis et al. 1987; Zachos et al. 1989) and the lower-than-expected extinction levels in low-energy, starvation-resistant taxa such as brachiopods (Rhodes and Thayer 1991).

These conclusions appear to be at odds with the fact that extinction is not significantly correlated with larval feeding strategy (i.e., planktotrophy vs. nonplanktotrophy). However, since adult echinoids are able to withstand complete starvation for prolonged periods of time (Giese 1966), it is conceivable that they could have weathered the drought in productivity and reproduced once conditions became more amenable. Alternatively, because the quantity of phytodetritus within the water column decreases with depth, a reduction in phytoplankton abundance that would be of insufficient proportions to decimate planktotrophic larvae in the upper water column could still lead to the curtailment of the rain of phytodetrital material to the seafloor and the subsequent starvation of detritivores in oligotrophic settings such as the deep sea or shallow carbonate platforms, explaining the observed pattern of selective extinction in the benthic adult rather than the planktonic larval stage. Finally, inspection of the raw data reveals that although there is no significant correlation, all four nonplanktotrophic taxa survived the K/T extinction event, a result that is entirely compatible with the proposed nutrient crisis in the terminal Cretaceous.

Conclusions

Deducing the causes of extinction events in the fossil record is fundamental to the understanding of evolutionary processes and the long-term dynamics of biodiversity (Banerjee and Boyajian 1996). Recent syntheses have moved away from explaining individual aspects of extinction events (e.g., Cys 1967 on the inability of dinosaurs to hibernate) toward interpretations that account for the whole pattern of biotic collapse. Even so, a plethora of "killing mechanisms" have been proposed as causes of mass extinctions, and the K/T boundary event in particular, but linking extinction patterns to potential forcing factors is complicated by the nature of complex biological systems (Jablonski 1996, 1997). For example, "a single 'forcing factor' might have radically different effects depending on the state of the system at the time of perturbation, and a single extinction pattern might be equally consistent with a host of potential forcing factors" (Jablonski 1997: p. 354). Despite these pitfalls, the recognition of patterns of survivorship selectivity can provide clues to the causes of mass extinctions (Raup 1986; Raup and Jablonski 1993; Jablonski and Raup 1995). For example, the globally uniform intensity of the K/T event, demonstrated by the lack of geographical selectivity patterns, attests to its magnitude and rules out the involvement of mechanisms with purely latitudinal or regional effects (Raup and Jablonski 1993).

Analysis of preferential survivorship in atelostomate echinoids at the Cretaceous/Tertiary boundary indicates that nonselective detritivores inhabiting already stressed oligotrophic settings were more severely affected, suggesting that the extinctions were nutrient driven. This pattern of survivorship selectivity is entirely compatible with a collapse in primary productivity brought about by a bolide impact. However, it is equally consistent with other extinction scenarios that invoke a breakdown of the food chain. Until finer stratigraphic resolution and the application of confidence intervals to stratigraphic ranges (e.g., Marshall 1995; Marshall and Ward 1996; Solow 1996) allow a more precise determination of the tempo of extinction patterns and until robust patterns of selectivity are known for other taxonomic groups, it will not be possible to say with certainty what role each of the possible multiple causes played in the biotic collapse at the end of the Cretaceous.

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Appendix

This appendix comprises data on the fate of Maastrichtian atelostomate echinoid clades at the Cretaceous / Tertiary boundary along with details of possible taxonomic, geographical, environmental, and biological correlates. Where survival is inferred by the identification of a post-Paleocene sister taxon, the sister taxon is parenthesized.

Key to column headings: A, Extinction or survival of clade at the K/T boundary. B, Higher taxonomic placement (hol = holasteroid; spat = spatangoid). C, Number of Maastrichtian species in clade. D, Maastrichtian regions known from (am = Americas; eu = Eurasia; t = Tethys (Africa and Middle East); ip = Indo-Pacific (Madagascar, Far East, and Australasia). E, Number of Maastrichtian localities. F, Absolute latitudinal range of Maastrichtian members of clade. G, absolute longitudinal range of Maastrichtian members of clade. H, Size of latitudinal range (in number of degrees), with latitudinal tolerance (i.e., northern and southern latitude combined) in parentheses. I, Size of longitudinal range (in number of degrees). J, Maastrichtian bathymetric depth (lit = littoral; on = onshore; mid = mid-outer shelf; deep). K, Maastrichtian sediment type (ch = chalk / marl; ca = calcarenite / sandy limestone; sa = sand / gravel; si = silt / mud). L, Life position in sediment (in = infaunal; epi = epifaunal). M, Larval strategy (plank = planktotroph; lec = lecithotroph; brood = brooder). N, Feeding strategy (siever = surface siever; select = selective detritivore).

Taxon	A	B	C	D	E	F	G	H	I	J	K	L	M	N
Galeaster	survive	hol	1	eu	7	29–41N	35–58E	12	23	mid, deep	ch	in	plank	siever
Basseaster	survive	hol	1	ip	2	35–37S	46–53E	2	7	deep	ch, ca	in	plank	siever
Stegaster I	extinct	hol	3	eu, t	12	29–41N	1W–58E	12	59	deep	ch	epi	plank	siever
Stegaster II (Sanchezaster)	survive	hol	1	eu, t	4	7–35N	15W–2E	28	17	deep	ch, ca	epi	plank	siever
Tholaster	extinct	hol	1	eu	2	35N	1W–2E	1	3	deep	ch	epi	plank	siever
Pseudoffaster	extinct	hol	1	eu	6	29–41N	2W–58E	12	60	on, mid, deep	ch, ca	epi	plank	siever
Rispolia	survive	hol	2	eu, t	4	22–58N	19W–3E	36	22	mid, deep	ch, ca	epi	plank	siever
Guettaria	extinct	hol	2	eu, t, ip	7	23–41N; 25S	1W–58E	66 (18)	59	deep	ch	epi	plank	siever
Echinocorys	survive	hol	1	eu, t, ip	19	31–48N; 28–50S	2W–101E	98 (22)	103	on, mid, deep	ch, ca	epi	plank	siever
Offaster	extinct	hol	2	eu	3	34–48N	2W–11E	14	13	on, mid, deep	ch, ca	epi	plank	select
Cardiaster	extinct	hol	5	am, eu, ip	14	18–52N	71W–135E	34	206	on, mid, deep	ch, ca	in	plank	siever
Cardiotaxis	extinct	hol	1	eu	5	41–48N	3–53E	7	50	deep	ch, ca	in	plank	siever
Hagenowia	extinct	hol	1	eu	3	47–48N	8–11E	1	3	deep	ch	in	plank	siever
Holaster	survive	hol	0*									in	plank	select
Giraliaster	survive	hol	1	ip	1	50S	101E	1	1	mid	ch	in	plank	select
Hemipneustes	extinct	hol	7	eu, t, ip	19	8–45N; 8–37S	2W–95E	82 (37)	97	lit, on, mid, deep	ch, ca, sa	in	plank	select
Micraster	survive	spat	3	eu	6	31–47N	1–46E	16	45	mid, deep	ch, ca	in	plank	select
Mokotibaster	survive	spat	4	t, ip	5	21N; 28–40S	12–73E	61 (19)	61	deep	ch, ca	epi	plank	select
Diplodetus	survive	spat	7	am, eu, ip	8	29–45N; 28–37S	71W–53E	82 (17)	124	lit, on, mid, deep	ch, ca, sa, si	in	lec	select
Ovulaster (Habanaster)	survive	spat	2	eu, t	4	23–40N	1W–48E	17	49	on, deep	ch	in	plank	select
Cyclaster	survive	spat	7	eu, ip	12	31–48N; 28S	2W–57E	76 (20)	59	on, mid, deep	ch, ca	in	lec	select
Isaster	survive	spat	1	eu	2	31–35N	2W–1E	4	3	mid, deep	ch, ca	in	plank	select
Hemiaster	survive	spat	9	am, eu, t, ip	22	8–52N; 18–40S	78W–135E	92 (44)	213	lit, on, mid, deep	ch, ca, sa, si	in	plank	select
Leiostomaster	extinct	spat	2	t	2	23N	1W–3E	1	4	deep	ch	in	plank	select
Leymeriaster	extinct	spat	3	eu, t, ip	3	32–45N; 30S	5–73E	75 (15)	68	lit, on, mid	ch, ca	in	plank	select
Mecaster	extinct	spat	2	am, t	6	8–32N; 12S	18W–48E	44 (24)	66	lit, on, mid, deep	ch, ca	in	plank	select
Gregoryaster	survive	spat	1	t, ip	2	28–40S	25–45E	12	20	deep	ch	in	plank	select
Linthia	survive	spat	3	am, t	6	7–23N	63W–47E	16	110	on, mid, deep	ch, ca	in	plank	select

**Holaster* has no Maastrichtian representative but is known from older and younger strata.

Appendix. Continued.

Taxon	A	B	C	D	E	F	G	H	I	J	K	L	M	N
Paraster	survive	spat	6	am, eu, t, ip	10	18–36N; 12–30S	71W–73E	66 (18)	144	lit, on, mid, deep	ch, ca, sa, si	in	plank	select
Tessieria	extinct	spat	1	t	1	7N	15W	1	1	on	ca	in	plank	select
Proraster	survive	spat	3	am, eu, t, ip	11	8–41N; 30–35S	71W–73E	76 (33)	144	lit, on, mid, deep	ch, ca	in	plank	select
Trachyaster	survive	spat	1	eu, ip	2	58N; 8S	19W–68E	66 (50)	87	on, mid	ca	in	plank	select
Holcopneustes	survive	spat	2	ip	3	8–30S	45–73E	22	28	on, mid, deep	ch, ca	in	plank	select
Mauritanaster	survive	spat	1	t	1	23N	3E	1	1	mid, deep	ch	in	lec	select
Abatus	survive	spat	1	ip	1	28S	45E	1	1	deep	ch	in	brood	select
Coraster	survive	spat	1	eu, t	7	31–41N	1–57E	10	56	deep	ch	in	plank	select
Orthaster	survive	spat	1	eu	2	29–41N	46–58E	12	12	deep	ch	in	plank	select
Homoeaster	survive	spat	3	eu, t, ip	13	7–52N; 27S	15W–135E	79 (45)	150	on, mid, deep	ch	in	plank	select
Iraniaster	survive	spat	3	t	3	8–12N; 3S	40–56E	15 (9)	16	mid	ch	in	plank	select