

# Estimating extinction levels for echinoids across the Cretaceous-Tertiary boundary

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**ABSTRACT:** Estimates of taxonomic turnover derived from compilations of published records have suggested that as many as 70% of genera became extinct at the K-T boundary. However, errors arising primarily from nomenclatural inconsistency have inflated these estimates. We have revised Maastrichtian and Palaeocene records at species level, restudying type material wherever possible, and have carried out cladistic analyses at species and genus level. From this we estimate that between 33 and 37% of clades at generic level have their last appearance in the Maastrichtian. Furthermore, we recognize a clear taxonomic bias in survivorship, with major clades of echinoid showing marked differences in extinction levels. Understanding the nature of this selectivity provides critical data that can test causative factors proposed to explain the K-T extinction.

## 1 INTRODUCTION

No period of geological time has been so extensively studied in terms of biological turn-over as the Cretaceous-Tertiary (K-T) boundary. Since it became popular to attribute the extinction at this time to the impact of a meteorite, a huge amount of research has gone into documenting the nature of the faunal and floral changes across this time interval (e.g. MacLeod *et al.* 1997). Yet despite all this work there remains no broad consensus as to how precisely the K-T extinctions were brought about or what patterns of preferential survivorship exist. Evidence amassed so far has come from the micropalaeontological record of deep-sea cores and onshore near-complete boundary sections, and from global studies of molluscs (Jablonski 1996).

Several workers have suggested that there was a collapse in primary productivity at this time, possibly brought about by impact-generated debris in the atmosphere, and that the effects of this event cascaded down the food chain (Hansen *et al.* 1984; Sheehan & Hansen 1986, Sheehan *et al.* 1996). This explains the preferential survival of foraminiferans living below the euphotic zone (Kaiho 1994), and the preferential survival of phytoplankton such as dinoflagellates that have the capability of surviving as cysts under harsh conditions (Habib *et al.* 1992; Paul & Mitchell 1994). It has also been proposed as the reason why ammonites became extinct whereas nautiloids with larger yolky eggs survived (Kennedy 1989, 1993, Gallacher 1991). However, other possible proximal causes have been suggested, such as surface-water acidification (D'Hondt *et al.* 1994, Robinson 1995) or marine regression with expansion of the oxygen-minimum zone (Rohling *et al.* 1991).

Irrespective of the precise driving mechanism invoked, there are three aspects of the K-T extinction event that need addressing:-

1. What was the size of the event (i.e. what percentage of taxa became extinct and how does that compare with extinction levels at other periods in the geological past)?

2. How prolonged was the event (i.e. were the majority of extinctions synchronous and geologically instantaneous or were extinctions extended over a long time interval)?

3. What factors correlate with extinction or survival of lineages? Is there a pattern to which lineages survived and which were driven to extinction based on geographic range or biological attributes and which might give clues as to the proximal cause of the extinction?

Studies that tackle the question of the time scale involved in the faunal transition have tried to turn to complete sequences and abundant fossils, and have thus explored the microfossil record through a few key sections. Macrofossil groups such as echinoids clearly have little to contribute to this discussion, since they are generally too rare in stratigraphic sections to be of use. However, the other two questions are clearly answerable from the fossil record of echinoids. In this paper we document what proportion of the late Cretaceous fauna went extinct, and what evidence there is for taxonomic selectivity.

## 2 PREVIOUS WORK

Echinoids have been surprisingly neglected in K-T boundary studies. In his pioneering study Kier (1974)

found a substantial drop in the number of echinoids described from the Palaeocene as opposed to the late Cretaceous. He identified only 108 Palaeocene species as opposed to 1137 Senonian species based on the Lambert & Thiéry's (1911-1925) compilation. Roman (1984) subsequently estimated that this change represented more than a five-fold decrease in the numbers of species.

Gravesen (1979) and Asgaard (1979) provided an account of the echinoid changes across the classic Maastrichtian-Danian sections in Denmark. Gravesen found that, although there were changes at species level in regular echinoids, genera all appeared to cross the boundary. Asgaard noted that the changes in irregular echinoid fauna largely reflected changes in facies, although she pointed out that infaunal holasteroids were more affected than ploughing forms. In the same volume Stokes (1979) analyzed changes in spatangoids and concluded that the K-T boundary event made little impact on this group. He found that there was a more profound change at the Campanian - Maastrichtian and Palaeocene-Eocene boundaries than at the end Maastrichtian.

A compilation of the species of the former Soviet Union and genera worldwide from the Campanian to early Eocene was published by Moskvina *et al.* (1980) and subsequently this data was used to construct patterns of survivorship and extinction by Shimanskii & Solovyev (1982) and Roman (1984). Roman found the K-T boundary coincided with a major extinction in echinoids, with two out of 14 orders (14%), 9 out of 38 families (24%), and 83 out of 127 genera (70%) present for the last time in the Maastrichtian.

Most recently van der Ham *et al.* (1987) have revised and compiled a complete faunal list for the Maastrichtian and Danian of the Maastricht district. The Danian fauna (26 species) is almost as large as that known from the latest Maastrichtian Meerssen Member of the Maastricht Formation (27 species), although only six species are in common, implying at the very least, a major faunal change.

How do echinoids compare with other taxa? Global extinction rates based on taxon counts over all major marine invertebrate groups with a reasonable fossil record suggest about 50% extinction at generic level and maybe 70-80% species extinction (Sepkoski 1989, Jablonski 1995), while Raup & Jablonski (1993) found that 63% of Maastrichtian bivalve genera did not pass through into the Tertiary. Thus Roman's (1984) estimate of ca. 70% extinction at generic level in echinoids is a little high, but not wildly different from that estimated for other groups.

### 3 PROBLEMS ASSOCIATED WITH ESTIMATING THE SIZE OF THE K-T EXTINCTION EVENT

Raw data counts of global generic diversity reported from the Maastrichtian and Palaeocene, such as those of Moskvina *et al.* (1980, 1982), and Roman (1984) imply a massive drop in biodiversity (70% of genera) at around the end of the Cretaceous. Yet when raw species counts are compiled for countries of the

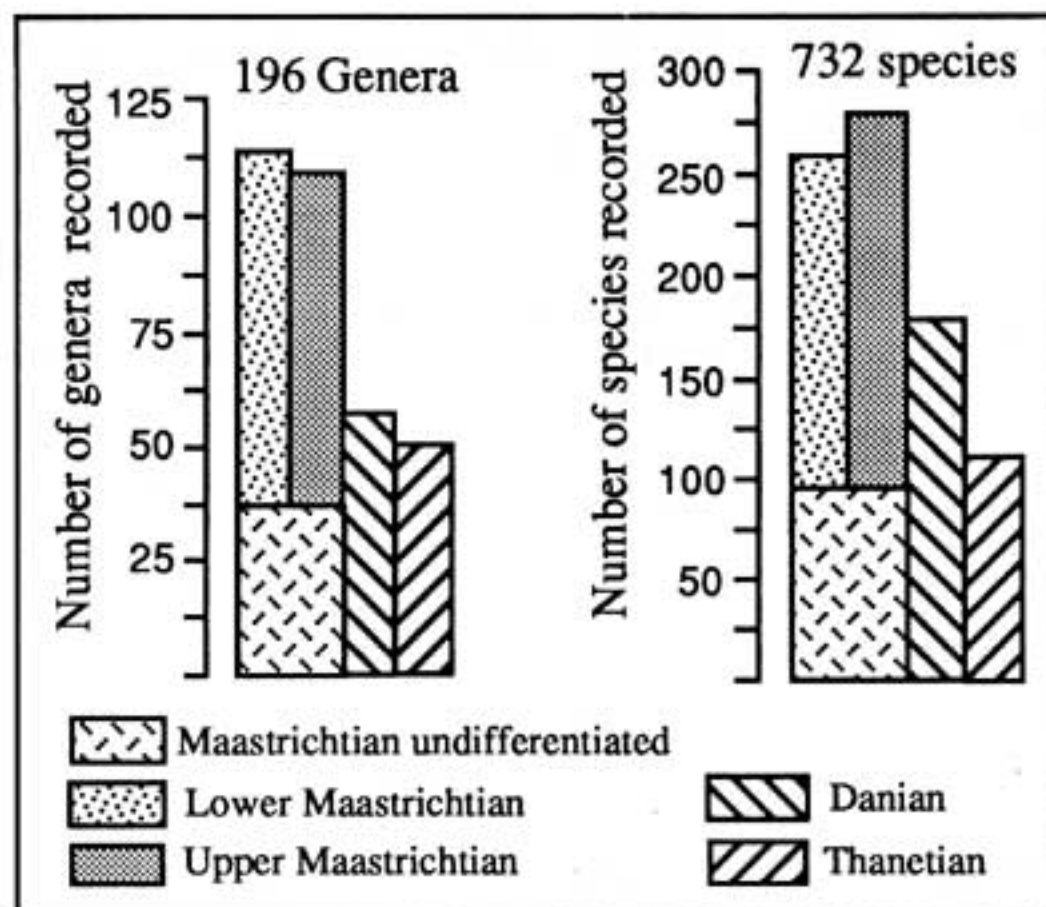


Figure 1. Diversity of Maastrichtian and Palaeocene echinoids as estimated from the published literature as of 1995.

Former Soviet Union (FSU), species numbers drop much less substantially, from 87 to 56, and drop again from the Danian into the Thanetian to 27. Our compilation of taxa recorded in the literature from Maastrichtian and Palaeocene deposits worldwide, undertaken for this study, shows a broadly similar pattern (Fig. 1). No taxonomic standardization has been applied to this data set, although obvious synonyms have been removed: it is the pattern deduced from an uncritical acceptance of the published literature.

However, there are four biases that might affect our perception of biological diversity change at this time.

**3.1 Sampling bias.** The major problem faced by anyone wanting to turn to the fossil record to document patterns of change across the K-T boundary is that continuous sections in fossiliferous shallow water settings basically do not exist. There was a marked drop in sea-level during the late Cretaceous, culminating more or less at the K-T boundary, followed by a rapid sea-level rise that may have been as great as 130 m (Keller *et al.* 1993). This resulted in platform drowning and brought about a major reorganization of facies across the marine shelf generating major sampling problems for K-T studies.

For example, in the North Oman Mountains the high diversity late Maastrichtian carbonate shelf deposits are succeeded by a coarse conglomerate of reworked limestone boulders and then by deep-water Palaeocene turbiditic beds, recording a history of exposure and subsequent platform drowning (Smith *et al.* 1995). Although deeper-water settings were less affected by facies shift, they preserve a much sparser benthic fauna and are thus less informative.

Is the decrease in numbers of recorded species therefore simply a reflection of the smaller number of Palaeocene outcrops preserving echinoid faunas? Before we can decide whether there is a greater than

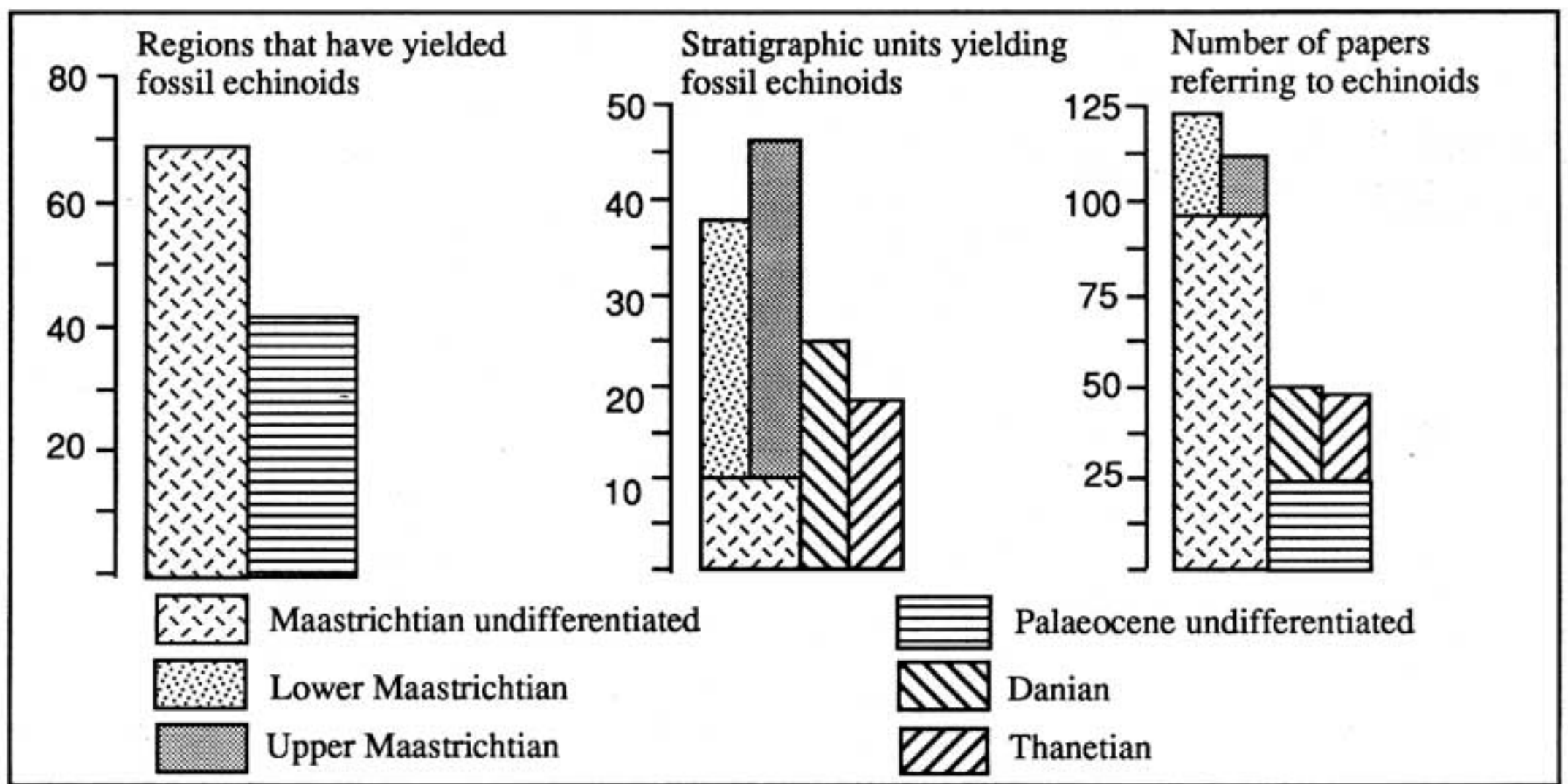


Figure 2. Possible biases that could be influencing the recorded diversity of echinoids across the K-T boundary.

expected drop in taxonomic diversity at this time we need to have some idea of how even our sampling is.

We have used two indirect methods of assessing sampling intensity. (i) Numbers of regions with rocks of a given age yielding echinoids; and (ii) numbers of named stratigraphical formations of a given age yielding echinoids. The latter probably gives a more accurate assessment. For example, in the Maastricht district there are eleven stratigraphical units of Maastrichtian age which have yielded echinoid faunas, yet only one of Danian age (van der Ham *et al.* 1987). Clearly even if there was no extinction of echinoids, the much more extensive sampling of Maastrichtian lithofacies alone would create an apparent decrease in diversity over the K-T boundary. A further measure employed is the number of publications dealing with Maastrichtian or Palaeocene taxa. This provides an index of how-well studied the faunas are.

All three approaches (Fig. 2) show that Maastrichtian deposits with echinoid faunas are much better sampled than Palaeocene ones. There are about 50% more regions where Maastrichtian deposits yield echinoids as opposed to Palaeocene deposits, largely because of the absence of suitable outcrop, at least in the better studied regions of the world. Thus the perceived drop in diversity between the Maastrichtian and Palaeocene could simply be a result of poorer sampling. This correspondence, of course does not imply that the pattern IS due to sampling bias (the drop in diversity could be real making echinoid faunas genuinely sparser in the Palaeocene), but it does mean that methods of analysis that compensate for uneven sampling need to be adopted.

Geographic bias in sampling might also affect perceived patterns. For example, if Palaeocene deposits with echinoids are rarer in well-studied geographical regions such as western Europe and

North America compared to Maastrichtian deposits, then this too could create a spurious drop in diversity after the Maastrichtian. In the U.K. Maastrichtian deposits of Norfolk have been intensively studied over many years, but Danian marine deposits are absent and Thanetian beds of the wrong facies for echinoids. Eighty-eight regions (broadly speaking local sedimentary basins) yield echinoids of this time interval. However, their distribution shows a very strong bias towards the northern hemisphere, with western Europe the most densely sampled, as might be expected.

**3.2 Nomenclatural inconsistency.** This represents a major source of error in any global analysis that has to deal with taxonomic studies carried out by different workers publishing at different times and with different background experience. It is absolutely essential that the alpha taxonomic framework employed is standardized to (i) remove those forms that are morphologically indistinguishable but given different names where they have been found in different countries or different stratigraphic intervals and described by different workers; and (ii) ensure that taxa referred to by the same name by different workers fall within reasonable morphological limits.

A good example of the problem is presented by the form described by Agassiz (1854) as *Nucleolites analis*. This species has a checkered history, being mistakenly recorded from the Maastrichtian instead of the Danian of the Maastricht district by Smiser (1935) and misidentified as *Lychnidius* (= *Nucleopygus*) *scrobiculatus* by Lambert (1898). Van der Ham (1988) clarified the taxonomy and biostratigraphy of this species in the Maastricht district. All, however, accepted it as a cassiduloid. However, a virtually identical form was described from the Danian of



**3.3 Pseudoextinctions.** Nomenclatural changes separating Cretaceous and Tertiary forms mask the fact that there is lineage continuity across the boundary. For example, the genus *Thylechinus* (a Cretaceous taxon) is recognized from the Maastrichtian and *Arbacina* (a Tertiary taxon) from the late Danian. Yet cladistic analysis identifies them as sister taxa, and indeed they are so similar morphologically that they could even be synonymized at species level. *Arbacina* clearly represents a direct continuation of the Maastrichtian *Thylechinus* clade, and consequently, the last occurrence of *Thylechinus* in the Maastrichtian is a pseudoextinction. Pseudoextinctions inflate estimates of the size of the K-T event.

**3.4 Lazarus taxa.** Some taxa have such a patchy fossil record that they simply disappear for long intervals of time. If only a narrow time interval is examined then some surviving taxa may be overlooked. For example, the regular echinoid *Hyposalenia* appears in abundance in the shallow subtidal middle to upper Danian facies in the Maastricht district and in Mangyshlak, Kazakhstan. Although it has never been recorded from any Maastrichtian or early Danian deposit, its sister species in the same genus are widespread and common in the Albian and Cenomanian. *Hyposalenia* must have existed during the Maastrichtian and early Danian even though it has not yet been found. The construction of cladograms allows us to compensate for sampling deficiencies by identifying lineages that must have existed but which have yet to be found in the fossil record.

#### 4 APPROACH ADOPTED IN THIS STUDY

Our study attempts to provide a uniform taxonomic framework for the study of Maastrichtian - Palaeocene echinoids and to set this in a solid phylogenetic framework. So far we have encountered published references to about 160 genera and 730 species attributed to the Maastrichtian-Palaeocene. Correlation and dating is relatively straight-forward for well-studied areas such as northwestern Europe, but becomes progressively more difficult elsewhere, especially for Tethyan carbonate platforms where both distinctive ammonite or planktonic foraminiferans are generally lacking. Wherever possible faunas are placed within an eight-fold subdivision (four Maastrichtian and four Palaeocene units). However, for many regions it is often not possible to be more precise than 'Maastrichtian' or 'Palaeocene' about the age of deposits.

We have restudied many of the important collections of Maastrichtian - Palaeocene echinoids, examining the type material wherever possible in order to standardize nomenclature. Special attention has been paid to establishing plating details for less well known species. So far we have been able to examine specimens of about 95% of the named genera, and maybe two-thirds of the nominal species. We have synonymized species unless there is a significant difference in test structure and appearance. Small

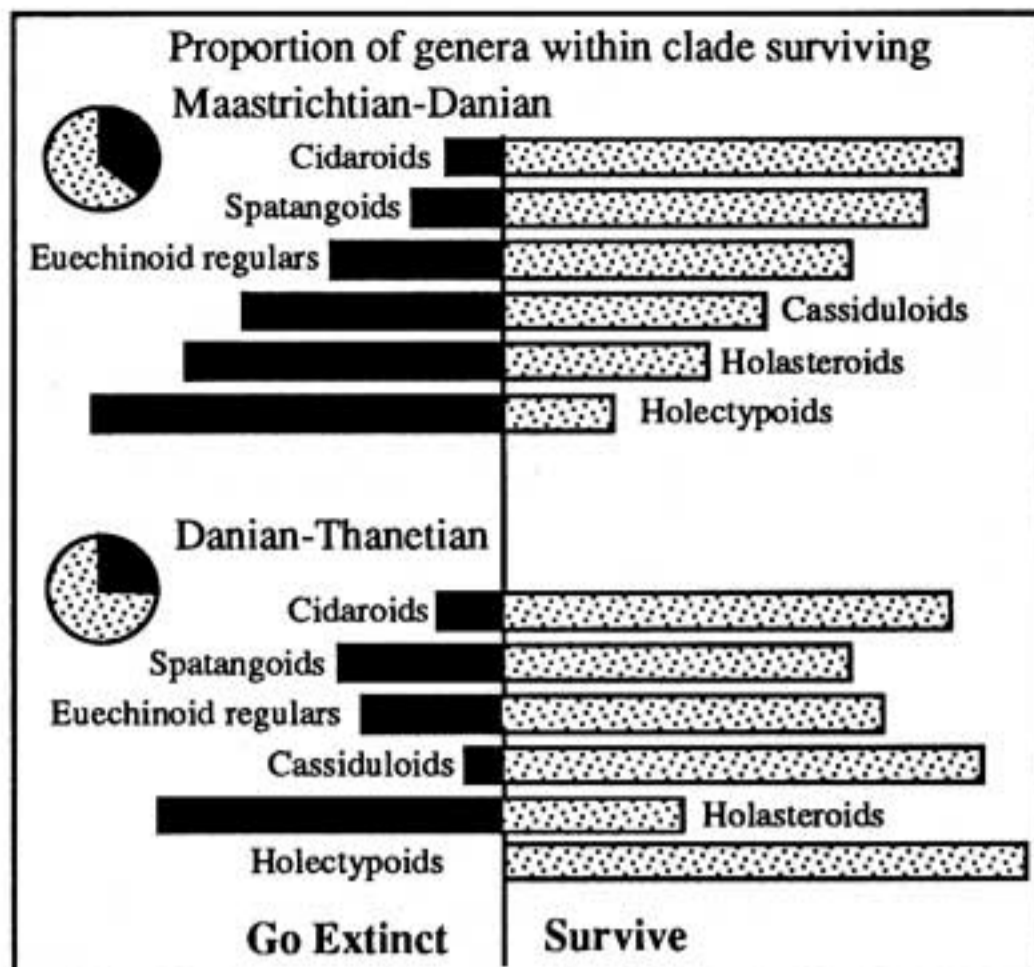


Figure 3. Comparative levels of extinction for major echinoid clades at the end Cretaceous.

differences in outline or profile are not considered enough to justify nomenclatural separation at species level. Morphological characters for cladistic analysis are being compiled for all species that we have examined personally and for other taxa where high-quality illustrations and descriptions exist. An example of our approach at species level is given in Jeffery (1997).

#### 5 RESULTS AND DISCUSSION

A list of taxa that we have examined or infer to have existed in Maastrichtian deposits is given in Table 1. Although our analyses are not yet complete and cladistic analyses in progress will undoubtedly add to the picture, we present our provisional findings. Overall, of the 116 clades that we currently recognize as occurring in Maastrichtian, 37% have no post-Cretaceous representatives. Some of these extinctions, such as the disappearance of the holasteroid *Hagenowia*, almost certainly predate the end Maastrichtian, since the clades are known only from early Lower Maastrichtian strata. Unfortunately, the problems of accurate dating within the Maastrichtian in shallow marine carbonate facies, preclude a more refined stratigraphic resolution for many deposits. Removing taxa recorded only from the Lower Maastrichtian, while leaving taxa of definite Upper Maastrichtian or Maastrichtian undifferentiated, reduces extinction to 33%. This is still a substantial drop in diversity, but is considerably less than the 70% estimated from raw taxonomic counts in the literature (Roman 1984).

Two other points are worth emphasising here. Firstly, there is a clear systematic bias to the taxa that are being affected by the K-T event (Fig. 3). Low levels of extinction were suffered by cidaroids,

spatangoids, calycinids and phymosomatids, whereas holoctypoids, cassiduloids and holasteroids were much more severely affected. Understanding the biological differences between these groups can shed light on the driving force involved (Smith & Jeffery, in prep.). For example, extinction in holasteroids is largely confined to one major clade. This clade is exclusively deep-sea (outer shelf settings) and fed by gleaning phytodetritus from the surface sediment in these oligotrophic settings. Starvation seems the most likely cause of extinction in this group. Spatangoids and other holasteroids such as *Echinocorys*, by comparison, are remarkably resistant to extinction at the K-T boundary, correlated with their preferred distribution in somewhat more onshore environments where there was significant terrigenous input.

Secondly, although the end Cretaceous extinction is a major event, there is a sizeable proportion of taxa (25%) that survive into the Danian but then become extinct. Interestingly spatangoids suffered much greater extinction at this period, while most of the remaining holasteroids also disappeared. The taxa affected by this event are predominantly chalk-dwellers, and it is the disappearance of chalk deposition at the end of the Danian that is the most likely correlative factor.

This, together with evidence that life in the plankton was becoming less predictable towards the end of the Cretaceous (Jeffery, submitted), implies that several factors combined to drive the faunal changes at the end of the Cretaceous.

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