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Selectivity of extinction among sea urchins at the end of the Cretaceous period

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By compiling large databases and searching for environmental and palaeobiological correlates associated with survival, insight can be gained into the driving mechanisms involved in mass extinctions[1–4]. Although this approach lacks precise temporal resolution and thus cannot be used to investigate how rapidly extinction took place, it provides a broad overview, less plagued by sampling problems caused by shifting facies. Here we present a global analysis of a major marine invertebrate group, the sea urchins, which suffered 36% extinction at genus level in the late Maastrichtian age and continuing high levels of extinction in the Danian age. No preferential survivorship was found for clades with widespread distribution, but there was a strong correlation between feeding strategy and survivorship at the end of the Cretaceous period. Surprisingly, however, clades whose larvae must feed to reach metamorphosis were not significantly harder hit than those with non-feeding larval development. Our results indicate that nutrient supply was a crucial factor in driving K/T-boundary extinctions, with selection more strongly focused on benthic adult than on larval planktotrophic stages.

We have revised and standardized the taxonomy of Maastrichtian and Palaeocene echinoids worldwide to generate a cladistic phylogeny for the group at species level[5]. We recognize ~250 Maastrichtian echinoid species, placed into 115 approximately genus-level clades. Of 92 clades that are definitely recorded from late Maastrichtian strata, 36% have no post-Maastrichtian record. Further significant extinction occurred during the Danian (early Palaeocene), however, with 26% of the 55 clades present making their last appearance (Fig. 1). We collected environmental data on substrate, inferred water depth and palaeogeographic distribution, and palaeobiological data on maximum size, mode of life, feeding strategy and diversity for each occurrence. Evidence for selectivity of extinction was sought by testing for correlation between survivorship and these biological and geographical factors (Fig. 2). Box 1 summarizes our findings.

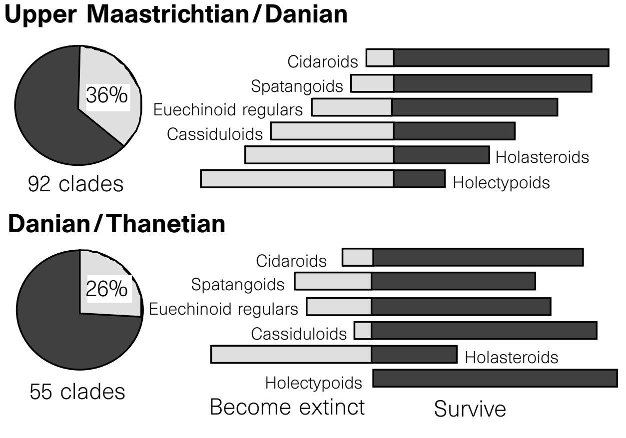

Figure 1 Genera of echinoids with last occurrences in the late Maastrichtian and Danian. Extinctions as proportions of total diversity (pie charts) and relative extinction levels for major higher taxa (bar charts) are shown.

Box 1 Correlates of survivorship for echinoids at the end of the Cretaceous period

Statistically significant correlation links survival with:
- Taxonomic structure (Fig. 2a)
- Feeding strategy (Fig. 2b)
- Palaeogeographic region (endemics only), with extinction levels highest in the Americas and lowest in the Indo-Pacific (Fig. 2c)

Survivorship weakly correlated with:
- Absolute palaeolatitude (in degrees away from the equator), with higher extinction levels encountered at low palaeolatitudes (Fig. 2e)
- Absolute palaeolongitude, with extinction levels lowest to the east (Fig. 2o)
- Water depth (Fig. 2d), with shallow-water faunas harder hit than deeper-water faunas. Analysis suggests that extinction in shallow water is concentrated in carbonate-platform facies
- Larval strategy: whether the organism is planktotrophic (and obliged to feed in the plankton before metamorphosis) or non-planktotrophic (Fig. 2g)

Survivorship independent of:
- Numbers of Maastrichtian morphospecies included in genus (Fig. 2j)
- Geographical distribution before the K/T event, measured by palaeogeographic range (Fig. 2i, l) and the numbers of discrete localities (Fig. 2k) or large-scale provinces (Fig. 2m) in which a clade is recorded
- Whether species were epifaunal or infaunal (Fig. 2f)
- Whether food was collected by grazing/scavenging or by deposit feeding (Fig. 2h)

Survival was independent of species diversity within each clade (Fig. 2j) and thus is not a taxonomic artefact determined by the size of the taxonomic units termed ‘genus’. It was also largely independent of the geographical range occupied during the Maastrichtian (Fig. 2i, l and m). It has previously been suggested that widespread genera preferentially survive at mass-extinction events[1,6]. Our data differ, however, probably because we have constructed an explicitly phylogenetic framework that identifies clade survival independently of taxonomic names. In our raw data we found many wrongly identified taxa recorded from single formations, inflating the estimate of ‘endemic’ extinctions.

Slight preferential losses of low-latitude faunas (Fig. 2e) and of shallow-water faunas (Fig. 2d) are inextricably linked, as deep-water sediments containing echinoid faunas from low latitudes are rare. Low-latitude extinctions are largely explained by the virtual disappearance of shallow carbonate-platform facies in the Danian, as is the difference in survivorship between Western Tethyan and Eurasian faunas (Fig. 2c). Loss from shallow-water carbonate settings took place across all habitats (Fig. 2n) and is not simply restricted to perireefal settings.

There is statistical support for extinction having been most intense in the Americas and lowest in the Indo-Pacific (Fig. 2c, o) when considering endemic species, but our numbers are extremely low and there are two confounding problems: a dearth of Danian echinoid faunas from the Americas, and uncertainty over the precise

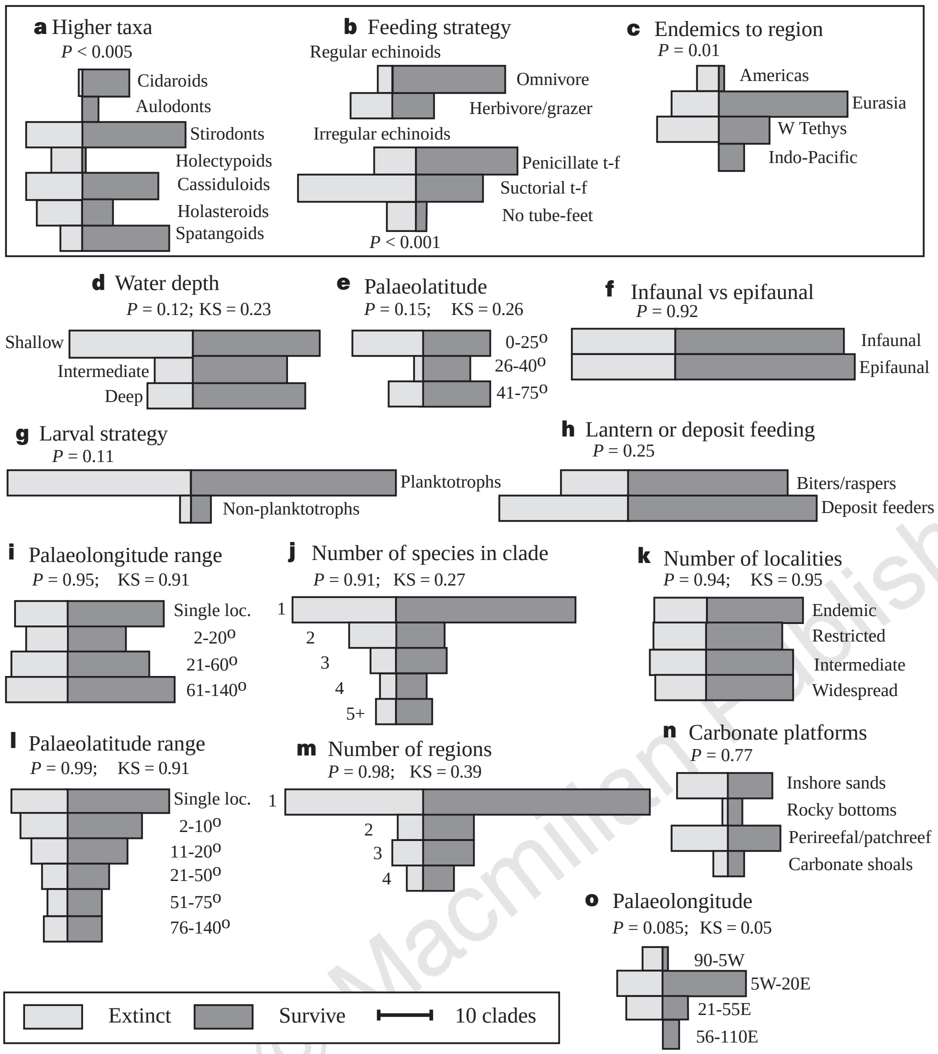

Figure 2 Proportions of Maastrichtian clades surviving into the Danian or becoming extinct. They have been partitioned according to: **a**, higher taxonomic grouping; **b**, feeding strategy, as reflected by the structure and arrangement of tube-feet (t-f) around the mouth; **c**, taxa restricted to a single geographic region; **d**, inferred water depth occupied ('shallow' corresponds to within fair-weather wave base; 'intermediate' corresponds to within storm wave base; 'deep' corresponds to basinal muds and chalks); **e**, palaeolatitude (taxa restricted to one band only) (in degrees away from palaeo-equator); **f**, infaunal or epifaunal habit; **g**, planktotrophic or non-planktotrophic larval stage; **h**, grazing or deposit feeding; **i**, palaeolongitudinal range (in degrees) ('single loc.' represents taxa recorded from one locality only); **j**, number of species in each clade; **k**, number of localities the clade is reported from (an endemic clade is present in 1 locality, a restricted clade in 2–4 localities, an intermediate clade in 5–8 localities and a widespread clade in more than 8 localities); **l**, palaeolatitudinal range (in degrees); **m**, number of regions (Americas, Eurasia, Western Tethys, Indo-Pacific) the clade occurs in; **n**, habitat for carbonate platform taxa; **o**, palaeolongitude (taxa restricted to one band only). *P* represents significance level found with a chi-squared test; KS represents the significance level found in a Kolmogorov–Smirnov test.

age of Cuban late Cretaceous endemic species (here treated as Maastrichtian). Further data are needed to decide whether this pattern is genuine or an artefact of sampling.

Where facies continuity exists across the K/T boundary, as in Eurasian chalk facies, there was considerably less extinction. Although it has been suggested[6,7] that chalk faunas were severely affected at the end of the Cretaceous, our evidence suggests that the main bout of extinction for chalk echinoids took place towards the end of the Danian when chalk deposition ended.

Levels of extinction at or near the end of the Cretaceous vary significantly amongst higher taxa (Fig. 2a), suggesting that differences in palaeobiology may have been important. We found that feeding strategy was highly correlated with survival (Fig. 2b). All irregular echinoids are deposit feeders, collecting detritus from the sea floor either by directly funnelling sediment into the peristome without the aid of tube feet or by selectively picking up particles from the sea floor using perioral tube feet[8]. Holasteroids and spatangoids have highly specialized penicillate tube feet that allow them to manipulate fine detrital material (of $<200\,\mu m$ in size) (refs 8, 9). Cassiduloids and holectypoids have only simple, suckered tube feet and are restricted to feeding on larger particles (of $\sim$500–1,500 μm in size) (refs 10, 11). Echinoids lacking tube feet continuously ingest the surface layer of sediment in nutrient-poor settings, passing large quantities through their gut to obtain adequate nutrition. Deposit feeders possessing penicillate tube feet and able to select fine organodetritus show significantly enhanced survivorship compared with the other types of feeders (Fig. 2b), with extinctions concentrated in nutrient-starved inner-shelf carbonate-platform settings.

It is more difficult to recognize discrete feeding strategies among regular echinoids, all of which feed by means of their lantern. Most are opportunistic, capable of feeding on various substrates[8]. Those with distinct phyllodes and keeled teeth are specialist raspers and grazing herbivores, however, and suffered significantly higher levels of extinction at the end of the Cretaceous than generalist omnivores without phyllodes. Deposit feeders as a whole were hardly more affected than lantern feeders (Fig. 2h).

Surprisingly, although clades with planktotrophic larvae appear somewhat more prone to extinction than clades with non-feeding (non-planktotrophic) larvae (Fig. 2g), the difference is not statistically significant, as was also found for gastropods[12]. As the majority of echinoids and gastropods with obligate planktotrophic larvae survived into the Tertiary period, it seems unlikely that the differential fates of ammonites and nautiloids at the K/T boundary can be ascribed directly to a difference in their larval development, as has previously been suggested[6]. These results also discredit bolide scenarios that invoke an instantaneous catastrophe involving the wholesale selective extermination of planktotrophs.

The correlation between feeding strategy and survival at the end of the Cretaceous is *prima facie* evidence that extinction of echinoids was in some way nutrient-driven, but why should such extinction be focused more strongly on benthic adults than on their planktonic larvae? The food supply for deposit feeders fluctuates because of seasonality of the phytoplankton, leading to

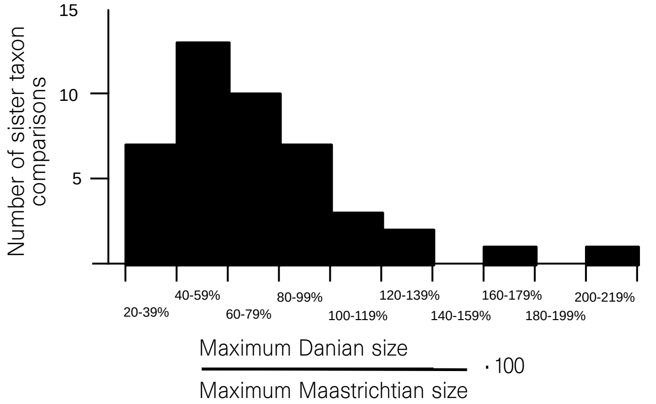

Figure 3 Difference in maximum organism sizes between Maastrichtian and Danian sister taxa.

nutrient stress throughout much of the year[13,14]. Furthermore, the proportion of phytodetritus reaching the sea floor rapidly decreases below the euphotic zone[14]. The observed pattern could, therefore, have been produced by a decrease in phytoplankton abundance at the end of the Cretaceous that was not so large as seriously to affect plankotrophic larvae living and feeding in the euphotic zone, but which reduced the organic matter reaching the sea floor sufficiently to trigger widespread extinction of already nutrient-stressed deposit feeders.

It is possible that the final blow was dealt by asteroid impact, but there is indirect evidence that conditions for plankton were becoming less favourable immediately before the K/T boundary. Climate was rapidly deteriorating[15] and extinction of several major molluscan groups had already taken place[16]. Furthermore, numerous lineages of echinoids independently switched to nonplanktotrophic development in the Maastrichtian, regardless of palaeolatitude and water depth[17], implying that survival for planktonic feeding larvae was becoming markedly less predictable. Furthermore, the fact that high levels of extinction continued into the Danian suggests a slow squeeze rather than an instantaneous catastrophe.

Finally, we note a dramatic decrease in size of post-Cretaceous survivors. Almost all Danian echinoids are significantly smaller than their Maastrichtian antecedents (Fig. 3) and apparently remained so until the latter half of the Danian. Early Danian echinoids either grew much more slowly or became more opportunistic, achieving sexual maturity at a much earlier stage. In either case, the small size of Danian survivors is consistent with nutrient supply remaining unpredictable and a limiting factor to growth for a considerable time interval following the K/T event, as postulated previously[18]. ☐

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A molecular evolutionary framework for the phylum Nematoda

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Nematodes are important: parasitic nematodes threaten the health of plants, animals and humans on a global scale[1,2]; interstitial nematodes pervade sediment and soil ecosystems in overwhelming numbers[3]; and *Caenorhabditis elegans* is a favourite experimental model system[4]. A lack of clearly homologous characters and the absence of an informative fossil record have prevented us from deriving a consistent evolutionary framework for the phylum. Here we present a phylogenetic analysis, using 53 small subunit ribosomal DNA sequences from a wide range of nematodes. With this analysis, we can compare animal-parasitic, plant-parasitic and free-living taxa using a common measurement. Our results indicate that convergent morphological evolution may be extensive and that present higher-level classification of the Nematoda will need revision. We identify five major clades within the phylum, all of which include parasitic species. We suggest that animal parasitism arose independently at least four times, and plant parasitism three times. We clarify the relationship of *C. elegans* to major parasitic groups; this will allow more effective exploitation of our genetic and biological knowledge of this model species.

To study the evolutionary relationships within the phylum, we constructed a database of small subunit (SSU) sequences from 53 taxa, including 41 new sequences[5–9]. Species were chosen to cover all the major parasitic and free-living taxonomic groups. Sequences were aligned with reference to a secondary-structure model[5] and on the basis of similarity[8]. Model phylogenies were evaluated under the criteria of maximum parsimony (MP), maximum likelihood (ML)