

# END-CRETACEOUS EXTINCTIONS

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The end-Cretaceous, Cretaceous-Tertiary (K-T), or Cretaceous-Paleogene (K-P) extinction event comprises all organismal extinctions that occurred the uppermost or Maastrichtian stage of the Cretaceous Period/System. During this time it is estimated that between 40 and 65 percent of marine species disappeared from the Earth's ecosystems. Prominent victims of this extinction include coccoliths, planktonic foraminifera, sponges, ammonites, gastropods, marine reptiles (e.g., mosasaurs, plesiosaurs), dinosaurs, and mammals. Groups comparatively unaffected by this event include diatoms, dinoflagellates, corals, brachiopods, echinoderms, marine arthropods, freshwater and terrestrial invertebrates (e.g., molluscs, arthropods), fish (marine and freshwater), and amphibians. The record of these groups within the Maastrichtian is of variable quality for a variety of reasons (discussed below). Moreover, interpretation of these patterns has suffered from and extreme focus on the Maastrichtian-Danian boundary interval itself, to the exclusion of efforts to establish the appropriate geographic and long-term temporal context within which individual group histories should be viewed. When this context is established many of the traditional interpretations of the end-Cretaceous extinction, including relative scaling of extinction magnitudes among various ecological groups, turn out to be at odds with available data. Three prominent single-cause mechanisms have been popular in accounting for this extinction, including sea-level change, a large igneous province (LIP) volcanic eruption on what is now the Indian sub-continent, and the impact of an ~ 10 km bolide on Mexico's Yucatan Peninsula. The ecological complexity of the end-Cretaceous extinctions, the time over which they took place and the record of historical association between these mechanisms and extinctions over the last 250 m.y. suggests that no single mechanism can reasonably account for the patterns seen in the fossil record unless that record is assumed to be so strongly biased that the basis for recognizing the Maastrichtian as a time of widespread extinction is itself called into question. Accordingly, most palaeontologists favour a multiple-cause explanation for the end-Cretaceous extinctions, though non-paleontological geologists continue to favour the bolide impact model.

## Introduction

Although the end-Cretaceous extinction event goes by a variety of names in both the technical and popular literature (e.g., Cretaceous-Tertiary

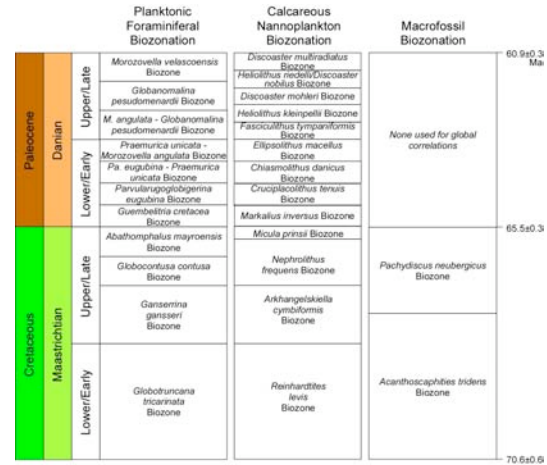


Figure 1. Chronostratigraphy, biostratigraphy, and geochronology of the (Cretaceous) Maastrichtian through (Paleogene, Paleocene) Danian interval. Boundaries between early/lower and late/upper Maastrichtian and Danian represent undated, informal units based on biostratigraphic zones.

[K-T] mass extinction, K-T boundary extinction, Cretaceous-Paleogene [K-P] mass extinction, Cretaceous-Paleogene [K-P] extinction), it is most closely associated with the uppermost Cretaceous Period/Stage—the Maastrichtian—and, to a lesser extent, the lowermost Paleogene Epoch/Age—the Danian (Figure 1). As such, any review of effects and causes that may (or may not) have occurred during this episode of Earth history must begin with a review of the stratigraphy of these two intervals, not only because they provide the temporal, environmental, geographic, and tectonic context within which such phenomena must be understood, but also because the study cause-effect associations in Earth history is, by definition, a largely stratigraphic exercise.

Dumont first defined the Maastrichtian in 1850 as a distinct stratigraphic subdivision of the Upper Cretaceous well expressed in the sediments around the town of Maastricht in southern Holland. The current boundary stratotype was established in 1911 by the Comité d'étude du Maastrichtian as the Tuffeau section, exposed in the ENCI quarry at St. Pietersburg on the Maastricht outskirts. Unfortunately, only the upper Maastrichtian is exposed in this quarry and its upper boundary has traditionally been regarded as incomplete (though a 1996 restudy of the quarry concluded that a complete K-T boundary succession was present in certain man-made cave sections within the quarry). In terms of boundary

stratotypes the Campanian-Maastrichtian boundary was established by the International Commission on Stratigraphy (ICS) in 2001 at the 115.2 m level in Grande Carrière Quarry, Tercis-les-Bains, Landes Province, in southwestern France. A total of 12 criteria (all of equal weight) were defined as useful in recognizing the Campanian-Maastrichtian boundary which falls just above the first appearance of the ammonite *Pachydiscus neubergicus* in this section.

The overlying Danian was established by Desor in 1847 for the stratigraphic successions present at Stvens Klint and Faxse in Denmark. Desor originally regarded the Danian as a Cretaceous stage because it is characterized in these two localities by chalk lithofacies. Later, it was shown that these sections were equivalent temporally to the Montian stage of Belgium that had long been regarded by continental European stratigraphers as the lowermost stage of the Tertiary. After a short debate concerning whether to place the new Danian-Montian stage in the Cretaceous or the Tertiary, the latter was accepted, largely on the basis of similarities between this fauna and that of the Midway Formation of the US Gulf Coast, That had also long been regarded as being basal Tertiary. These correlations notwithstanding, controversy continues regarding the correct placement of the Danian, largely on the basis that a number of characteristically 'Cretaceous' taxa (including bryozoans, brachiopods, echinoids, gastropods, bivalves and , perhaps, planktonic foraminifera) that don't become extinct until the end of the Danian where chalk deposition also effectively ceases worldwide. Hansen (1970) regarded the Danian as the time interval between the (Maastrichtian) 'White Chalk' exposed at Stvens Klint and the basal Selandian conglomerate exposed at Hvallose in Jutland.

The Danian boundary stratotype was established by the GCCP in 1996 at base of the boundary clay in the El Haria section, near the town of El Kef, Tunisia. Like the Campanian-Maastrichtian boundary. Multiple criteria are used to recognize the Maastrichtian-Danian boundary (which is also the Cretaceous-Tertiary, Cretaceous-Paleogene, and Mesozoic-Cenozoic boundary), including an iridium (Ir) anomaly and a major extinction horizon for foraminifera and calcareous nannoplankton. The boundary stratotype for the base of the Selandian epoch (= top of the Danian) has not been established to date.

Like almost all chronostratigraphic boundaries, the Maastrichtian-Danian interval is difficult to correlate because (1) most so-called boundary successions are profoundly incomplete, often juxtaposing sediments of markedly different ages (e.g., Campanian beneath Eocene) and (2) biozones (see **Figure 1**) contained within the interval are demonstrably diachronous and often facies limited. For example, the traditional uppermost Maastrichtian planktonic foraminiferal

zone—the *Abathomphalus mayroensis* Taxon Range Zone—is based on a open ocean, deep-dwelling species that is not present in shallower marine environments, including those represented by the El Kef boundary stratotype. The result has been unjustified assumption and subsequent confusion regarding what constitutes a complete record of the uppermost Maastrichtian – lowermost Danian sequences of events, especially between different ecological realms and locations remote from one another.

### The nature of the Maastrichtian-Danian turnover patterns

#### Historical concept

Despite the problems associated with attempts to achieve a high-resolution, temporal correlation of end-Cretaceous and early Danian sediments, it is abundantly clear that something extraordinary happened to the Earth's biosphere in the Late Cretaceous. In many lineages characteristic elements of the Late Cretaceous marine and terrestrial biotas are simply not present in the Early Paleocene fossil record. The standard list of Late Cretaceous victims includes coccoliths and planktonic foraminifera (both of which survive into the Danian but with an almost complete species-level taxonomic turnover), rudistid and inoceramid bivalves (both of which were common constituents of the Late Cretaceous chalk seas and both of which became entirely extinct), ammonite cephalopods (the traditional index fossil group of Cretaceous biostratigraphy all of whose representatives became entirely extinct), marine reptiles (e.g., ichthyosaurs, plesiosaurs, mosasaurs; all entirely extinct), flying reptiles (= pterosaurs, extinct), and all non-avian dinosaurs (extinct).<sup>1</sup> On one hand, this might not seem a very long list, especially given the fact that these groups comprise a relatively small collection of suborders, superfamilies, families, and genera in a much larger Late Cretaceous biota. Nevertheless, several victim groups were among the set of dominant marine and terrestrial players on the Late Cretaceous ecological stage whose demise effected many other groups in both direct and indirect ways. Also, since many evolutionary advantages flow from ecological incumbency, the removal of these groups from the ecological scene (by whatever means) opened up opportunities for evolutionary-ecological transformation and diver-

<sup>1</sup> Modern birds are nested phylogenetically within the dinosaur clade and so are considered dinosaurs in terms of their ancestry. Recent discoveries of feathered Cretaceous dinosaurs in China confirms this phylogenetic link and puts the 'obvious morphological distinctions' between extinct non-avian dinosaurs and modern birds—which are often cited by those who would try to preserve phylogenetically unwarranted taxonomic distinctions between these two groups—in a somewhat different light.

sification among Late Cretaceous survivor lineages that simply would not have been possible otherwise.<sup>2</sup>

In order to understand the character of this extinction event, the obvious questions to ask are as follows. (1) When did these extinctions occur? (2) Did they effect only these traditional victim groups? (3) Did any groups diversify or prove unusually extinction resistant over this interval? (4) Were these Late Cretaceous extinctions associated with any physical event(s) that could have been responsible for the extinctions? Before answers to these questions can be attempted, however, some further aspects of the Late Cretaceous – Early Tertiary fossil record must be understood.

#### *Sources of bias in the fossil record*

While all information we possess about fossils is traceable ultimately to observations made on actual specimens, many factors conspire to constrain the scope and depth of this knowledge for different fossil groups. For example, the contrast between the Late Cretaceous planktonic foraminiferal and dinosaur records could hardly be more striking even though both have played roughly equivalent roles in understanding end-Cretaceous extinction patterns and processes. Planktonic foraminifera are very common constituents of Maastrichtian and Danian marine sediments deposited over a broad range of marine depth habitats. Species can be recovered from these sediments worldwide, sampled in great temporal detail (owing, not least, to the small size of foraminiferal shells), and placed within an a very highly resolved biostratigraphy-taxonomy, albeit the latter of whose phylogenetic dimensions are not especially well known. Dinosaurs on the other hand, are comparatively rare constituents of Maastrichtian terrestrial sediments and occur in only a narrow range of terrestrial habitats. Uppermost Maastrichtian dinosaurs are known to occur in only one area of the world (western US) and cannot be sampled in great temporal detail, because of the spotty occurrence of complete or near-complete skeletons. Dinosaur biostratigraphy and taxonomy are not as well known as planktonic foraminiferal taxonomy (e.g., it is difficult to assess the shifting patterns of erosion-prone terrestrial sections for chronos-

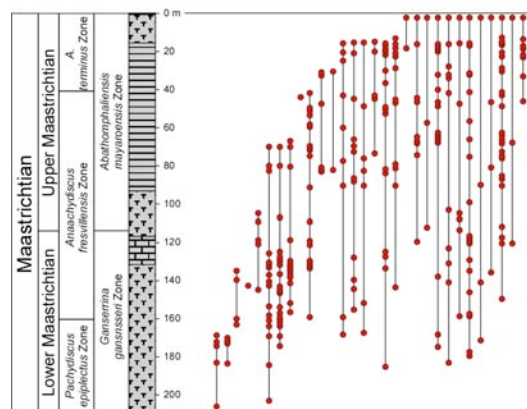


Figure 2. Maastrichtian ammonite biostratigraphy at Zumaya, Spain. Note that the majority of species (and, by implication, the genera and families they represent) disappear from this section during the course of the Maastrichtian, not at the Maastrichtian-Danian boundary. In fact, the last appearance datum of no ammonite species has been found to coincide with the Maastrichtian-Danian boundary in this section. Moreover, of the 12 species whose last appearance is within 1.5 m of the boundary, about have exceedingly rare or patchy biostratigraphic distributions, which suggests patchy, uneven, extinction-susceptible population structures. In this section, the 'mass extinction' of ammonites amounts to the near coincident disappearance of 6-7 previously abundant species, a phenomenon that would hardly be noticed in other parts of the Cretaceous ammonite record. Note also that, because of the patchy occurrence pattern characteristic of all ammonite species in this section, the idea that some ammonite species may have survived into the lowermost Danian interval cannot be rejected statistically. Redrawn from Marshall and Ward (1996).

trigraphic relations to stratotype successions, new dinosaur species turn up each year). Nevertheless, owing to the complex nature of vertebrate skeletons, more is known about dinosaur phylogeny than planktonic foraminiferal phylogeny. The Late Maastrichtian-Danian fossil records of other groups can be thought of as ranging through a spectrum of temporal, geographic, taxonomic, and phylogenetic resolutions the boundaries of which are set by dinosaurs and planktonic foraminifera.

Not only are there intrinsic difference between the quality of the fossil records of different groups there are also several fundamental sources of uncertainty about the details of all fossil records that constrain interpretations based on palaeontological observations. First, lack of a detailed, global chronostratigraphy for Maastrichtian-Danian sediments means that the vast majority of fossils can only be located as occurring—or not occurring—within these relative coarse temporal intervals. Thus, while it is possible to say that the extinction of plagiptychid bivalves and azhadarchid pterosaurs both occurred in the Maastrichtian, it is not possible to place these ex-

<sup>2</sup> This dependency on the unpredictable elimination of competition between lineages is referred to as contingency in the evolutionary literature and it is widely reported that, were it not for the contingent elimination of non-avian dinosaurs in the Late Cretaceous, the explosive radiation of mammals—in which our own lineage, primates, took part—would not have taken place. While this is true in a general sense, it is not the case that we owe our existence solely to the end-Cretaceous extinction since many other antecedent as well as subsequent contingencies also played important roles in mammal-primate evolution.

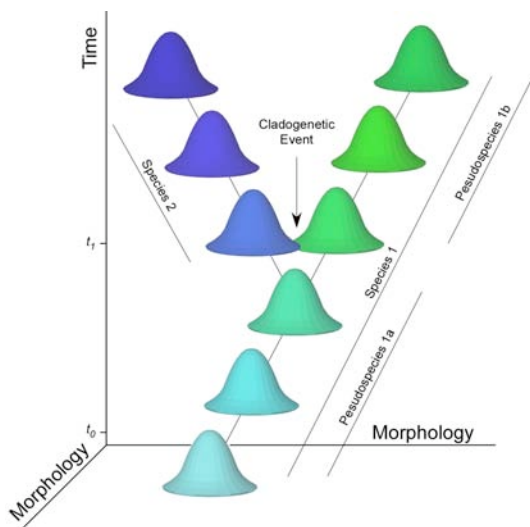


Figure 3. An example of the distinction between true extinction and pseudoextinction. Morphological change often occurs during the course of a lineage's evolutionary history. Morphological changes that result in a daughter species diverging from its ancestor are said to have arisen via cladogenesis (= lineage splitting). In the diagram cladogenesis has taken place approximately half-way up the time axis and resulted in the production of Species 2 from Species 1. Cladogenetically produced species are true species with a definite beginning (the cladogenetic event), history, and end (the extinction event). However, after a lineage has undergone so much within-lineage (= anagenetic) morphological change that no individuals at time  $t_1$  exhibit the same morphological states as individuals in ancestral populations (time  $t_0$ ), biostratigraphers often find it useful to differentiate between the  $t_0$  and  $t_1$  populations by giving a different species name to the latter. This convention, in effect, results in the 'extinction' of the  $t_0$  species, not because of the death last individual belonging to the lineage, but merely as the result of a nomenclatural change. Such nomenclatural extinctions are termed pseudoextinctions. Without a detailed knowledge of the phylogenetic and nomenclatural history of a lineage, it is often impossible to distinguish true extinction from pseudoextinction.

tinctions accurately within the span of the Maastrichtian, or to say whether they occurred simultaneously with respect to one another, without going back and restudying the original material. In particular, it is not appropriate to assume that simply because an extinction event is listed as Maastrichtian all species comprising the group in question ranged through the entire Maastrichtian and then simultaneously became extinct at a horizon coincident with the Maastrichtian-Danian boundary.

It is standard practice for biostratigraphic range charts to represent the chronostratigraphic ranges of fossil groups as solid lines joining individual occurrence horizons that denote intervals of time along a temporal axis (Figure 2). Because we experience time as a continuum it is tempting to regard these axes as representing

time as a continuous variable. In fact, these charts represent time as a discontinuous variable with the vertical range line always being drawn through the entire interval irrespective of whether the actual time of extinction is known. This graphing convention often gives the (erroneous) impression that all extinction events occur at stage/age boundaries and that there is some pronounced tendency for extinctions to occur together in time.

Similarly, use of higher taxonomic categorizations (e.g., families, genera) as proxies for species in extinction studies often leads to unappreciated distortions of the fossil record by inexperienced interpreters. The taxonomic categories of family and genus are used most often in extinction studies because these are regarded as more stable and comparable than species-level data across the broad scope of life's diversity. Because these are composite categories, however, the presence of a family at one point in time may represent a rather large number of species whereas at another point in time (especially if the latter is close to the group's extinction event) the actual number of species represented may be much smaller (Figure 2).

Pseudoextinction is another problem. In an evolving lineage two types of morphological transformations can occur. The first (anagenesis) results in the progressive transformation of the entire species from one morphological condition or state into another. The other (cladogenesis) results when a single species is split into two or more daughter species one of which may continue to exhibit the morphological condition of the ancestral population(s). Whereas the extinction of a lineage by the physical death of the last individual within the population must be regarded as a true extinction event, the physical death of the last individual within an extant population that simply happens to exhibit an ancient or atavistic morphological condition is not the same sort of event. This latter situation is termed pseudoextinction (Figure 3). Although the phenomenon of pseudoextinction need not be distinguished from true extinction in most routine biostratigraphic studies (after all, the pseudoextinction event does take place at a particular time), the differences between pseudoextinction and true extinction are profound in the context of extinction studies. Mammal systematist/palaeobiologist David Archibald has estimated that as many as 25 percent of the extinctions recorded in three different early Puercan (= lowermost Danian) mammal lineages were pseudoextinctions.

Raw observations can also be deceiving in terms of the simple observation of fossil groups' last occurrence distributions. Since the last observed occurrence of each species is only an estimate of its true extinction coordinate in time

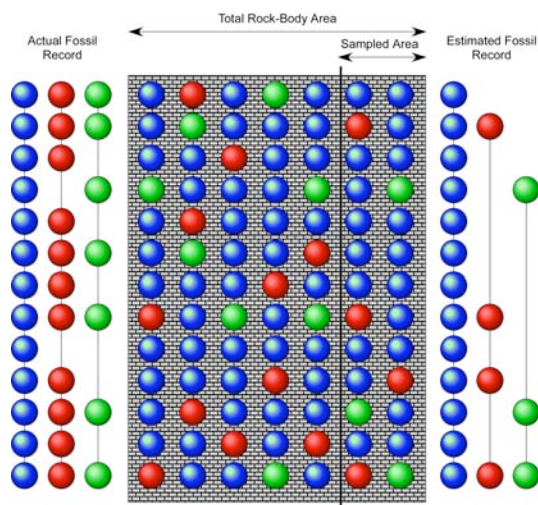


Figure 4. A hypothetical example of the Signor-Lipps Effect. The total fossil record of any species is provided by the sum total of all occurrences of the fossil within a body of rock. However, because a relatively small portion of that total rock body is ever available for sampling, the known fossil record represents a subset of the total fossil record. Because of this distinction between the total and known fossil records, and because of additional biases that might arise as a result of changes in the relative abundance of fossil species over time, changes in facies within single stratigraphic successions, and sampling patterns, estimates of the pattern of last appearance datums (e.g., coincident vs. progressive) are usually biased toward the recovery of progressive patterns. In this example, note that despite the fact that all three species range through the entire section, ranges based on the subset of occurrences in the two right-hand columns yield a sequential extinction pattern. This phenomenon has been used to argue that progressive extinction patterns imply an abrupt extinction mechanism. Such arguments are invalid—as was pointed out by Signor and Lipps 1982—because the progressive bias applies to genuinely progressive as well as genuinely abrupt true extinction patterns. The best one can do is not to reply on the apparent pattern of biostratigraphic last-appearance datums as reliable estimates of true extinction rates.

and space<sup>3</sup> the vagaries of preservation and sampling will conspire to distort the observed extinction record for each species (and, by extrapolation, for each genus, family, etc.) to a greater or lesser extent (**Figure 4**). This phenomenon is termed the Signor-Lipps Effect by the nominal authors in 1982, though Alan Shaw offered an essentially identical description of the same phenomenon as early as 1964. There is no way to correct for the Signor-Lipps Effect. Using the distribution of gaps between known occurrences within a species' or higher taxon's stratigraphic range, and making use of several simpli-

<sup>3</sup> See Biozones article in this volume for additional discussion.

fying assumptions, it is possible to estimate a confidence interval above which it is appropriate to regard the species or group as being truly extinct. Nevertheless, there is no method whereby an investigator may retrospectively pinpoint a taxon's 'true' extinction level. For groups of taxa various scenario-based extinction geometries can be evaluated using extensions of the confidence-interval method, but this approach will always identify a spectrum of geometries, ranging from randomized patterns to a strictly simultaneous geometry, as being equiprobable.

Finally, simple taxonomic uncertainty conspires to complicate data reported in the palaeontological literature. Certain species or higher groups that appear to become extinct at particular stratigraphic levels appear again, later in time at the same locality or in a different region altogether. Sometimes the morphological condition of the specimens at the second appearance is similar to that of pre-disappearance specimens and sometimes it is not. If the second appearance is regarded as a continuation of the pre-disappearance taxonomic entity it is referred to as a Lazarus taxon and should not be regarded as having undergone anything other than a local extinction at the lower horizon. However, if the second appearance specimens differ in some characteristic way from the characteristic pre-disappearance forms such that their placement within the previously existing lineage is questionable, the second appearance may be regarded as a suspect or 'Elvis' taxon in which case the status of the group's extinction is uncertain.

Taking all of these potential biasing factors into consideration, the following sections outline our current understanding of Maastrichtian-Danian biotic turnover patterns for six different ecologically subdivided biotas. In all cases the data presented are based on the family-level compilations provided by *The Fossil Record 2* (Benton, 1993) as the most up-to-date single source of stratigraphic information across the broad spectrum of fossil groups. Though not as detailed taxonomically as J. J. Sepkoski's *Compendium of Fossil Marine Animals* (2002) the former has the advantage of encompassing terrestrial as well as marine taxa and being compiled, reviewed, and adjudicated by specialists in each group.

#### *Marine Microfossils*

Marine microfossils, including protistan autotrophs and heterotrophs, have traditionally been thought to be one of the broad taxonomic groups most effected by the end-Cretaceous extinction. Review of the family-level fossil record largely bears this out. Among the major marine microfossil groups (**Figure 5**), only diatoms fail to exhibit a Maastrichtian extinction-intensity peak. For coccoliths, benthic foraminifera, and radiolaria this peak is more-or-less isolated (suggesting operation of a causal process or processes that

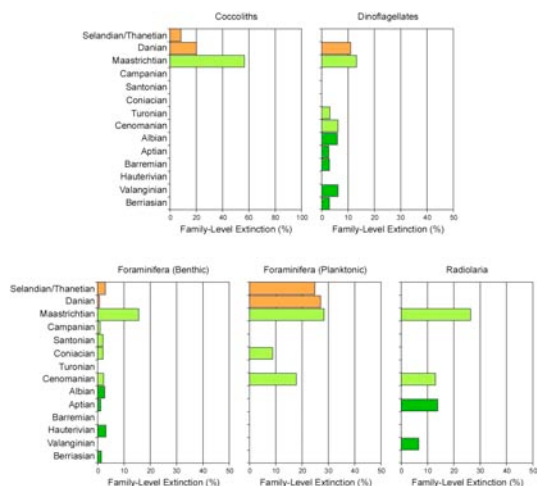


Figure 6. Cretaceous-Paleocene, stage-level extinction patterns for marine microfossil families. Note change in scale in the coccolith diagram. Data tabulated from Benton (1993).

was confined to the Maastrichtian. For dinoflagellates and planktonic foraminifera though, the Maastrichtian peak appears to be part of a larger pattern that encompasses both the Maastrichtian and Paleocene intervals. Overall Maastrichtian extinction intensities across all six marine microfossil groups are less than 20 percent suggesting an overall species loss similar to that of the total Maastrichtian estimate (see above).

Interpretation of this Maastrichtian-Danian microfossil record is complicated by several factors. A considerable controversy continues regarding the correct interpretation of 'Cretaceous' planktonic foraminiferal species that are routinely found in lowermost Danian sediments. Some specialists regard Cretaceous isotopic values obtained from the analysis of particular species' skeletons, along with the widespread chaotic disruption of bedding patterns in lowermost Danian sediments, as indicative of widespread shelf failure at the Maastrichtian-Danian boundary with consequent reworking of Cretaceous species into Danian sediments. This shelf failure was presumably caused by the physical shock of bolide impact along with subsequent earthquakes. Others regard the recovery of Danian isotopic results from other 'Cretaceous' species, the pristine preservation of many millions of 'Cretaceous' microfossil skeletons in Danian sediments (fully comparable with those of undoubted Danian species and distinct from obviously reworked Cretaceous species), and the fact that Danian occurrences of 'Cretaceous' species exhibit a clear biogeographic signal of greater penetration into the Danian in higher latitudes (where the effect of boundary disturbances is known to be reduced) as evidence for the survivorship of some species

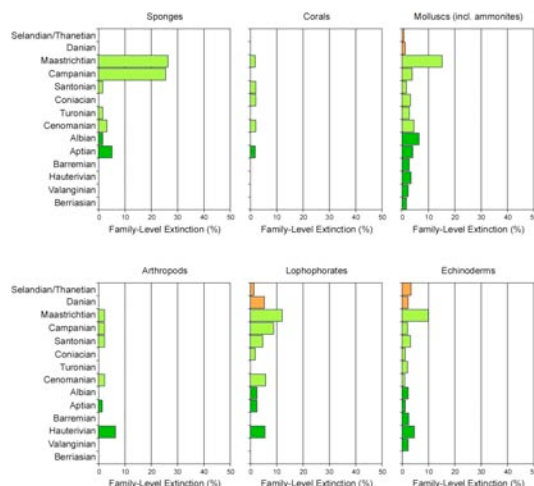


Figure 5. Cretaceous-Paleocene, stage-level extinction patterns for marine invertebrate families. Data tabulated from Benton (1993).

into Danian times.<sup>4</sup> Two families are involved in this controversy, Globotruncanidae and Rugoglobigerinidae.

Relatively low Maastrichtian extinction intensities for dinoflagellates and diatoms have been accounted for by noting that the biology of these groups include resting cyst stages and that these may have enhanced their overall survivorship potential. Species-level data for both groups from the K-T section on Seymour Island, Antarctica do not support this interpretation. Seymour Island cyst-forming dinoflagellates and diatoms exhibit progressive turnover patterns across the K-T boundary suggesting that extinction-inducing environmental changes were not confined to any single horizon. There is an increase in diatom resting spores in the Upper Maastrichtian interval of this high-latitude section, but this occurs throughout the succession and is not confined to any single stratigraphic horizon. Moreover, since no modern diatom resting spore has been successfully revived after more than two years' dormancy, this sets an inferred maximum duration of environmental disruption that could be tolerated before wholesale extinction of the indigenous diatom flora—for which there is no evidence—would occur.

#### Marine Invertebrates

Extinctions among marine invertebrate groups exhibit a different range of patterns (Figure 6) from those of marine microfossils. Here, family-level data suggests that poriferans were among

<sup>4</sup> There are also specialists who cite phylogenetic criteria as bearing on the survivorship question despite the fact that these arguments can be rejected on both logical and analytic grounds.

the most strongly effected groups whereas corals exhibit scarcely any effect at all. Between these extremes molluscs, brachiopods, bryozoans, and echinoderms exhibit broadly progressive extinction patterns that rise throughout the Late Cretaceous to a Maastrichtian peak and then fall off into the Paleocene, while marine arthropods exhibit a coral-like indifference to whatever factors were driving these long-term changes within other groups.

Given its iconic status within the pantheon of end-Cretaceous victims, the mollusc record is particularly interesting. Throughout the Cretaceous mollusc extinction intensities are comparatively low. The traditional mollusc victim families of Inoceramidae, and the rudistid families Radiolitidae and Hipporitidae all record last appearances in the Maastrichtian, but these three losses alone represent over 20 percent of all marine bivalve family-level extinctions. Overall, Maastrichtian mollusc losses are subequally split between bivalves (14 families lost) gastropods (8 families lost, including acetoneiids) and cephalopods (12 families lost). Note that, contrary to the popular perception of ammonites as being iconic K-T victims, at the family level bivalves suffered more than ammonites during the Maastrichtian. It should also be noted that all of these groups suffered the bulk of their losses within the Maastrichtian and not at the K-T boundary itself.

Bryozoans are another group with an especially intriguing Cretaceous extinction record. Numbers of extinct bryozoan families appear to rise in a more-or-less uniform stage-level pattern to a Maastrichtian peak that represents just over 12 percent of the total Maastrichtian assemblage. While all three bryozoan orders are effected by this protracted extinction, the ecological hammer appears to have fallen more forcefully on cheilostomes than on ctenostome or cyclostome forms. Interestingly, none of these extinctions is thought to have effected long-term patterns of bryozoan diversification substantially. The relatively comparable level of Maastrichtian extinction intensity exhibited by the bryozoans' sister group, the brachiopods is a bit misleading in that the data presented in **Figure 6** have been expressed as percentages. In fact, overall Maastrichtian brachiopod family richness is less than a third that of bryozoans and the actual number of brachiopod families that become extinct during this stage is comparably reduced. Among echinoderms irregular echinoid families bore the brunt of the Maastrichtian extinction pulse.

Taken as a whole, it is difficult to avoid the impression that marine invertebrates were being subjected to much longer-term extinction pressures than their protistan counterparts with the Maastrichtian representing the apotheosis of trends that first become evident in the early part of the Late Cretaceous. Moreover, once the Maastrichtian catharsis was reached it has rela-

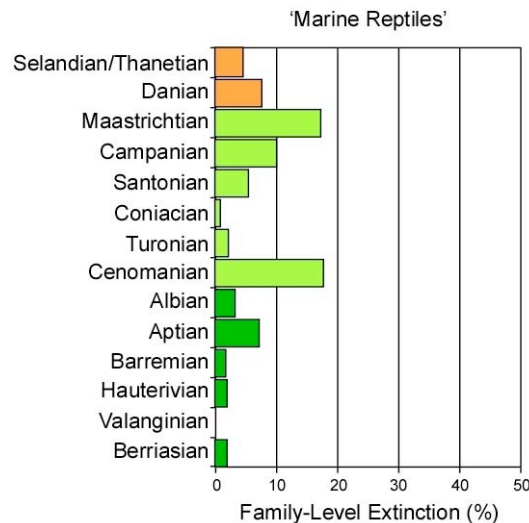


Figure 7. Cretaceous-Paleocene, stage-level extinction patterns for marine vertebrate families. Data tabulated from Benton (1993).

tively less overall effect on marine invertebrate family-level diversity than did the protistan reductions. As for the patterns of species-level extinction distributions, despite two decades of intensive study the fine-scale extinction pattern is known only for ammonites in two late Maastrichtian sections (Seymour Island, Antarctica and Zumaya, Spain). In both cases extinctions observed extinction horizons are not concentrated at the K-T boundary, but rather are spread throughout the entire interval (see **Figure 2**).

#### *Marine Vertebrates*

This group, largely comprising fish, ichthyosaurs, mosasaurs, sauropterygians, and marine turtles, has rarely received much attention in Maastrichtian extinction studies despite the iconic status of mosasaurs and plesiosaurs as stereotypical K-T victims. One sometimes also sees ichthyosaurs mentioned as participants in the end-Cretaceous extinction event, but this is erroneous. The last ichthyosaur became extinct in the Albian. Overall, (**Figure 7**), marine vertebrates exhibit a distinct and rather abrupt Cenomanian peak, followed by a protracted Late Cretaceous build up to a subordinate Maastrichtian peak, after which extinction intensities decline throughout the Paleocene. While it should be noted that the pattern shown in **Figure 7** is dominated by fish data, and that marine reptiles do show a much more distinct Maastrichtian extinction peak, it is also true that comparatively few Maastrichtian marine reptile families were present and that these were formed out of relatively few genera. Moreover, no marine reptile extinction horizon is known to coincide with the K-T boundary.

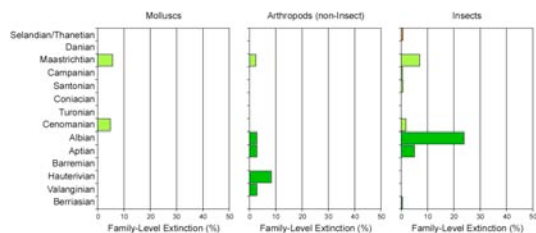


Figure 8. Cretaceous-Paleocene, stage-level extinction patterns for terrestrial-freshwater invertebrate families. Data tabulated from Benton (1993).

### Terrestrial Invertebrates

Relative to comparable marine taxa, freshwater and terrestrial invertebrates (gastropods, bivalves, chelicerates, crustaceans, ostracods, and insects) exhibit very modest levels and episodic patterns of extinction intensity throughout the Cretaceous with the Maastrichtian stage representing a decidedly subordinate intensity peak (Figure 8). Combined data from this ecological realm is inevitably biased by the very large number of insect families that, in all Cretaceous stages, are represented by values that are well over an order of magnitude larger than those for any other group. Despite this faunal size discrepancy though, Maastrichtian levels of percent extinction intensity for both freshwater and terrestrial mollusc and non-insect arthropod families are both less than those for insect families. The general character of Maastrichtian family-level extinctions for these former groups appears fully consistent with the qualitative notion of background, rather than mass, extinction. It should also be noted in passing that insects suffer their greatest Cretaceous extinction in the Albian rather than in the Maastrichtian.

### Terrestrial Vertebrates

The Maastrichtian terrestrial vertebrate extinction record (freshwater fish, amphibians, reptiles, dinosaurs, and mammals) is by far the most diverse of any ecological realm (Figure 9). Even more than their marine counterparts, terrestrial fish faunas provide no evidence for heightened Maastrichtian extinction intensities. Indeed Maastrichtian fish families exhibit the lowest family-level extinction intensity of any Cretaceous stage. This remarkably quiescent record is exceeded only by that of amphibians which fail to record any family-level extinctions in any Cretaceous stage. Cretaceous extinction level for non-dinosaurian reptiles are much higher, but neglect to exhibit a pronounced Maastrichtian peak despite the loss of five crocodylomorph families. This pattern is reversed, however, in the Dinosauria with its impressive 21 dinosaur families lost over the course of the Maastrichtian. Supporters of catastrophic dinosaur extinction scenarios hold that most, if not all, of these extinction

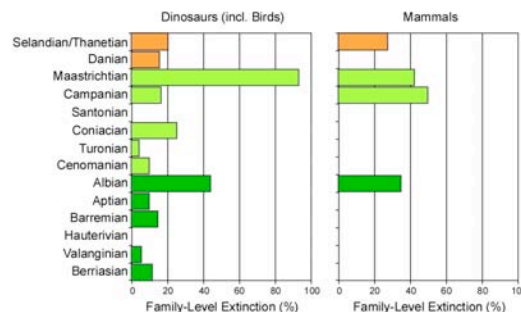
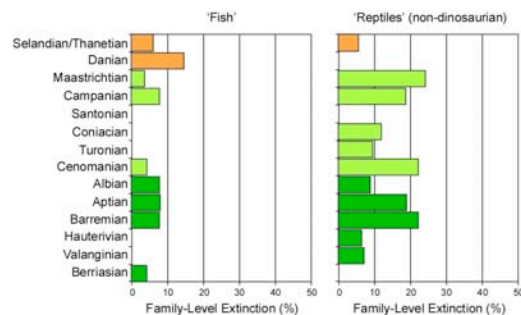


Figure 9. Cretaceous-Paleocene, stage-level extinction patterns for terrestrial-freshwater vertebrate families. Note change in scale in the dinosaur and mammal diagrams. Data tabulated from Benton (1993).

occurred at the K-T boundary despite the fact that no 'in place' dinosaur bone has been found within more than a metre of that horizon to date. Finally, as noted for Cretaceous family richness patterns, the Cretaceous mammalian extinction record bears an intriguing similarity to that of the Dinosauria, with coincident Albian and Maastrichtian peaks along with a unique Campanian peak which exceeds that of the Maastrichtian in terms of overall extinction intensity. While dinosaurs (including birds) and mammals represent the two most severely effected clades among all terrestrial groups, and two of the most severely effected across all ecological realms, it should nevertheless be kept in mind that, in terms of overall extinction intensity, dinosaurs and mammals represent only ten percent of all Maastrichtian land-based families and less than five percent of the overall Maastrichtian biota

### Plants

As has been noted elsewhere in the extinction literature, Cretaceous plants appear to have been relatively extinction resistant (Figure 10). There is a hint of a slight increase in Maastrichtian plant extinction intensities, but nothing that could be spoken of as being extraordinary relative to other Late Cretaceous stages. In addition, the pattern of extinctions suggested heightened extinction susceptibility beginning in the Campanian and continuing into the Danian. Over this time interval

the Maastrichtian extinctions that do occur are focused in gymnosperm lineages.

### Extinction Causes

There are three single-cause models, and one composite cause model that are currently used to account for the end-Cretaceous extinctions. The former are based on changes in global sea-level, increases in large-province volcanism, and bolide impact.

#### Sea-level

Three distinct, short-term, sea-level drops occurred during the Maastrichtian. These were superimposed on a long-term declining trend from the all-Cretaceous sea-level highstand at or near the Cenomanian-Turonian boundary. The oldest of these is an ~ 100 m drop across the Campanian-Maastrichtian boundary, followed by a slightly larger and more acute drop across the early-late Maastrichtian, followed by a significantly larger (~ 200 m drop) and still more abrupt drop that took place at or just before the end of the Maastrichtian. These sea-level drops are reflected in  $\delta^{18}\text{O}$  isotopic values that suggest a long-term cooling of global climates throughout the Turonian-Maastrichtian interval (presumably due to decreased albedo and reduced atmospheric  $\text{CO}_2$ ) coupled with extreme sea-surface temperature instabilities in the Maastrichtian. Aside from further reducing the already reduced area of submerged continental shelf available for colonization and foraging by marine taxa, these sea-level drops would be expected to have resulted in intensified of global climate gradients (due to reduced equator-to-pole heat transfer efficiency), increased seasonality, and the development of local centres of bottom water anoxia. Sea-level has long been a suspected cause of many 'mass extinction' events in the geological past and. A total of seven major sea-level lowstands have occurred over the past 250 m.y. and of these three exhibit a stage-level association with peaks in the extinction-intensity curve.

#### Large Igneous Province (LIP) Volcanism

The Maastrichtian witnessed a particularly large flood-basalt volcanic event when the (then) island continent of India moved over the Reunion mantle plume or 'hotspot' that is currently located in the southern Indian Ocean. Radioisotopic dates indicate that these Deccan volcanics were erupted in a series of quasi-discrete events that range in age from  $65.7 \pm 1.3$  Ma to  $65.4 \pm 1.3$  Ma. These dates suggest that over  $1 \times 10^6 \text{ km}^3$  of extrusive volcanics were emplaced over an ~ 300,000 – 500,000 year interval that straddled the Maastrichtian-Danian boundary (65.5 Ma). The primary climatic effect of these eruptions would have been a brief global cooling (due to

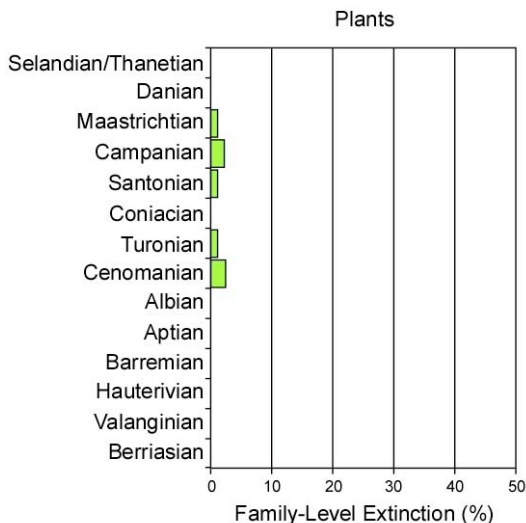


Figure 10. Cretaceous-Paleocene, stage-level extinction patterns for terrestrial plant families. Data tabulated from Benton (1993).

increased albedo brought about by injection of  $\text{SO}_2$  into the stratosphere) longer-term global warming (due to release of volcanogenic  $\text{CO}_2$ , possibly along with the melting of frozen methane hydrates on the continental shelves), and acid rain (due to the  $\text{SO}_2$ ). Secondary effects would include enhanced marine anoxia (due to global warming and sluggish marine circulation), disruption of weather patterns (due to the thermal anomaly created by the cooling lava), enhanced local-regional earthquake activity, and increase rates of subareal weathering. The emplacement of large igneous-volcanic bodies such as the Deccan Traps has long been a suspected cause of many 'mass extinction' events in the geological past and stage-level and associations between them and peaks in the extinction-intensity curve on six occasions in the past 250 m.y.

#### Bolide Impact

Few people interested in science can be unaware of the dramatic discovery that an ~ 10 km (diam.) comet or asteroid collided with the Earth at the precise time of the Maastrichtian-Danian boundary. Indeed, the iridium (Ir) anomaly in marine and terrestrial sediments that marks this event has been accepted as the primary defining feature of this boundary in temporally complete K-T successions worldwide. Subsequent subsurface geological investigations, first in cores from boreholes drilled near the town of Chixculub on Mexico's Yucatan Peninsula, and later from regional Bouguer gravity surveys, revealed the presence of a 250 km wide, circular, multi-ringed basin that corresponds to predictions of the crater size such an impact would be expected to leave. Radioisotopic dates of melted basement rock from the original Chixculub cores confirmed the age of this

crater as  $65.5 \pm 0.1$  Ma. In 1996 this date was accepted as the official age of the Maastrichtian-Danian (= K-T) boundary.

The physical and climatic effects of a Chicxulub-size impact would be expected to be similar to those of an LIP volcanic event. Unlike a volcanic event, a thermal blast would precede the arrival of a massive shock wave at localities thousands of miles away from the impact site itself. At the same time, a variety of materials would be injected into the stratosphere resulting in a sharp-but-short global cooling phase, followed by a longer-term global warming. Swarms of major earthquakes would also have been produced locally as the Earth's crust adjusted to the deformation. Some have predicted global darkness brought about by this stratospheric dust injection to have plunged the earth into a months to years-long night, but recent reviews of this proposed effect have reduced the duration of impact-related global darkening considerably. Acid rain would be produced, both as a result of the bolide's passage through the atmosphere and its ejection of a large volume of vaporized evaporitic material from the impact site, though, once again, the severity of this acid-rain phase has been downgraded recently from initial estimates. The initiation of global wildfires as a result of melted ejecta was another part of the original bolide impact scenario that, once again, has been downgraded as a result of subsequent research findings. The remaining, accepted, primary and secondary phenomena (see above) are all remarkably similar to the predicted effects of an LIP volcanic event, with the bolide impact effects able to be distinguished from these only in terms of (1) different trace element signatures in impact vs. volcanogenic glass spherules, (2) the production of different mineralogic artefacts (e.g., multiple sets of shock lamellae in the crystal lattices of mineral grains), and (3) the shorter period of time over which the primary and secondary effects would have operated. With respect to the latter, it should be noted that, although the intensity of the post-impact environmental effects would be greater than those generated as a result of LIP volcanic eruptions, these effects would also be expected to have attenuated at a much more rapid rate over time since—unlike LIP eruption event scenarios—disruptive event renewal would not have been possible. In effect, the important ecological distinction that can be drawn between bolide impact and volcanic disruptions is that of a single, massive, disruptive shock to global ecosystems after which normal conditions are re-established versus a continuous series of less intense shocks spread over a much longer time interval. Bolide impacts had long been discounted as a major extinction cause in the past but interest in this mechanism has undergone a dramatic turn-around since 1980. Still, of the six major bolide impact events (crater diam.  $\geq 50$  km)

that are known to have occurred over the last 250 m.y., only three exhibit stage-level associations with peaks in the extinction-intensity curve.

#### Multiple Causes

Although it has not been defined precisely—especially in terms of positive or negative feedbacks between different disruption sources—a commonly stated body of opinion suggests that the most reasonable stance is to admit that all of the previous mechanisms, as well as others, took place in the Maastrichtian and may have contributed to precipitating the end-Cretaceous extinctions, each in their own way. The interesting feature of this model is not the existence of causal mechanisms but their apparently coincident timing. This model gains credibility not from the detail with which its adherents can presently construct scenarios of predicted environmental effects, but from (1) the variety of extinction patterns present among the various groups effected by the overall extinction event (see above), (2) the lack of a consistent and/or simple ecological signal among organisms that inhabit different ecological realms, (3) the fact that all local peaks in extinction-intensity, regardless of size, are associated with the time series of at least one of these component mechanisms, and (4) the fact that, over the last 250 million years, all three large extinction events occur during a time of confluence between two or more of these component mechanisms.

Opinion surveys among research palaeontologists with regard to the most likely cause of the end Cretaceous extinctions were conducted in 1984 and 1996. On both occasions 'geologists' (= researchers with expertise outside palaeontology) were overwhelmingly in favour of the single-cause, bolide impact explanation for end-Cretaceous extinctions—especially the dinosaur extinctions—whereas palaeontologists (including experts in dinosaur and non-dinosaur groups) were overwhelmingly in favour of the multiple cause model. If this survey were to be repeated this author is quite sure the results would be similar.

#### See Also

**Arthropods, Atmosphere evolution, Biozones, Brachiopods, Bryozoans, Climate change, Coccoliths, Corals, Diatoms, Dinoflagellates, Echinoderms, Extinctions, 'Fish', Foraminifera, Molluscs, Plate tectonics, Principles of Stratigraphy, Radiolaria, Sea-level change, Sequence stratigraphy, Tetrapods, Time scale, Volcanism.**

#### Further Reading

Archibald, J.D., 1996. Dinosaur extinction and the end of an era: what the fossils say. *Critical*

- moments in paleobiology and Earth history. Columbia University Press, New York, 237 pp.
- Benton, M.J., 1993. The fossil record 2. Chapman & Hall, London, 845 pp.
- Galvin, C., 1998. The great dinosaur extinction controversy and the K-T research program in the late 20<sup>th</sup> Century. *Earth Sciences History*, 17: 41–55.
- Glasby, G.P. and Kunzendorf, H., 1996. Multiple factors in the origin of the Cretaceous-Tertiary boundary: the role of environmental stress and Deccan Trap volcanism. *Geologische Rundschau*, 85: 191–210.
- Hallam, A. and Wignall, P.B., 1997. Mass Extinctions and their Aftermath. Oxford Science Publications, Oxford, 328 pp.
- Hoffman, A. and Nitecki, M.A., 1985. Reception of the asteroid hypothesis of terminal Cretaceous extinctions. *Geology*, 13: 884–887.
- MacLeod, N. et al., 1997. The Cretaceous-Tertiary biotic transition. *The Journal of the Geological Society of London*, 154: 265–292.
- Marshall, C. R. and Ward, P. D. 1996. Sudden and gradual molluscan extinctions in the latest Cretaceous of western European Tethys. *Science* 274: 1360–1363.
- Ryder, G., Fastovsky, D. and Gartner, S., 1996. The Cretaceous-Tertiary event and other catastrophes in earth history. *The Geological Society of America Special Paper 307*, Boulder, 569 pp.
- Sarjeant, W.A.S., 1999. Dinosaur extinction: sudden or slow, cataclysmic or climatic? *Geoscience Canada*, 23(3): 161–164.
- Sepkoski, J.J., Jr., 2002. A compendium of fossil marine animals. In: D. Jablonski and M. Foote (Editors), *Bulletins of American Palaeontology* 363. Palaeontological Research Institution, Ithaca, New York, pp. 563.
- Sharpton, V.L. and Ward, P.D., 1990. Global catastrophes in earth history: an interdisciplinary conference on impacts, volcanism, and mass mortality. *Geological Society of America, Special Paper 247*, Boulder, 631 pp.
- Shaw, A., 1964. *Time in stratigraphy*. McGraw-Hill, New York, 365 pp.
- Signor, P.W., III and Lipps, J.H., 1982. Sampling bias, gradual extinction patterns and catastrophes in the fossil record. In: L.T. Silver and P.H. Schultz (Editors), *Geological implications of impacts of large asteroids and comets on the Earth*. Geological Society of America Special Paper 190, Boulder, pp. 291–296.
- Silver, L.T. and Schultz, P.H., 1982. *Geological implications of impacts of large asteroids on the Earth*. Geological Society of America, Special Paper 190, Boulder, 500 pp.
- Williams, M.E., 1994. Catastrophic versus non-catastrophic extinction of the dinosaurs: Testing, falsifiability, and the burden of proof. *Journal of Paleontology*, 68: 183–190.

Suggested reference:

**MacLeod, N.** in press. End-Cretaceous extinctions. In **R. C. Selley, L. R. M. Cocks and I. R. Plimer** (eds.), *Encyclopedia of Geology*. Academic Press, London.