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## The Cretaceous–Tertiary biotic transition

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**Abstract:** Mass extinctions are recognized through the study of fossil groups across event horizons, and from analyses of long-term trends in taxonomic richness and diversity. Both approaches have inherent flaws, and data that once seemed reliable can be readily superseded by the discovery of new fossils and/or the application of new analytical techniques. Herein the current state of the Cretaceous–Tertiary (K–T) biostratigraphical record is reviewed for most major fossil clades, including: calcareous nannoplankton, dinoflagellates, diatoms, radiolaria, foraminifera, ostracodes, scleractinian corals, bryozoans, brachiopods, molluscs, echinoderms, fish, amphibians, reptiles and terrestrial plants (macrofossils and palynomorphs). These reviews take account of possible biasing factors in the fossil record in order to extract the most comprehensive picture of the K–T biotic crisis available. Results suggest that many faunal and floral groups (ostracodes, bryozoa, ammonite cephalopods, bivalves, archosaurs) were in decline throughout the latest Maastrichtian while others (diatoms, radiolaria, benthic foraminifera, brachiopods, gastropods, fish, amphibians, lepidosaurs, terrestrial plants) passed through the K–T event horizon with only minor taxonomic richness and/or diversity changes. A few microfossil groups (calcareous nannoplankton, dinoflagellates, planktonic foraminifera) did experience a turnover of varying magnitudes in the latest Maastrichtian–earliest Danian. However, many of these turnovers, along with changes in ecological dominance patterns among benthic foraminifera, began in the latest Maastrichtian. Improved taxonomic estimates of the overall pattern and magnitude of the K–T extinction event must await the development of more reliable systematic and phylogenetic data for all Upper Cretaceous clades.

**Keywords:** K–T boundary, mass extinctions, taxonomy, phylogeny.

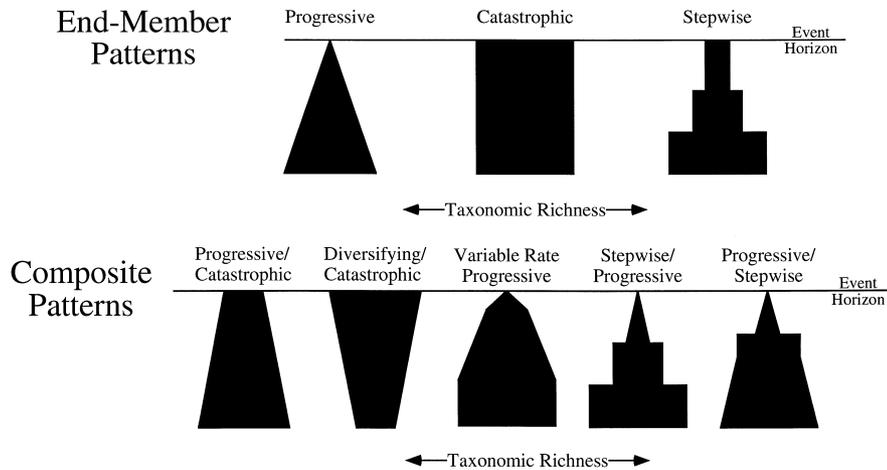
Turnover patterns among dinosaurs, ammonites, calcareous nannofossils and planktonic foraminifera during the end Cretaceous extinction event are causes célèbres for advocates of various mass extinction scenarios (Fig. 1). Rarely, however, has there been a concerted attempt to survey these as well as other animal and plant groups to determine whether the extinction/survival pattern of one group is matched by that of another. This paper provides a new look at the broader palaeontological record on either side of the Cretaceous–Tertiary (K–T) boundary.

Magnitudes of extinction and origination are usually measured by plotting the ranges of species, genera and families against time (Raup & Sepkoski 1984). The validity of such analyses depends on the sample size, completeness of the fossil record, and the nature of the taxa themselves (that is, whether they are real evolutionary entities or taxonomic artefacts). If the record were complete the only problem would be to recognize species and species lineages. The K–T fossil record is not complete, however, and although many analytical techniques can be employed to estimate the taxonomic completeness of particular groups (see Schoch 1986), the extent to which the record is incomplete is often not known. Some of the

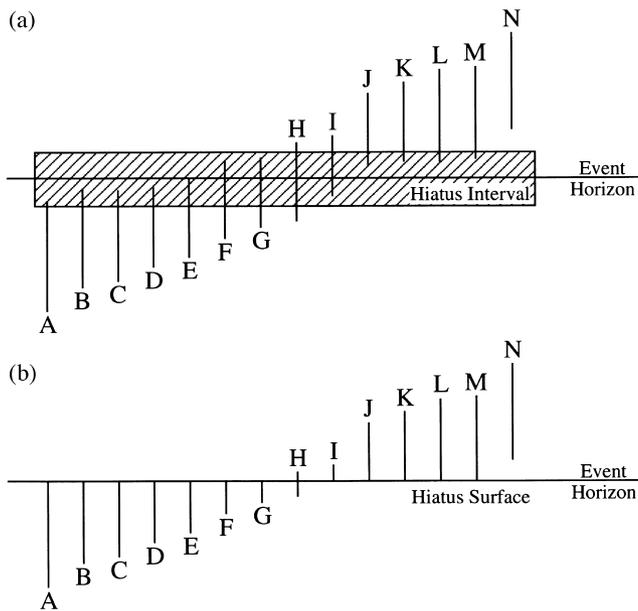
more obvious phenomena that may lead to incorrect identification of extinction/origination events are listed below (see also Smith 1994).

### Deposition hiatuses

Hiatuses are ubiquitous in the stratigraphical record at all temporal scales and in all depositional settings (Hedberg 1976; Ager 1973, 1993). Hiatuses can occur without any lithological expression (e.g. in condensed sequences, by variable sediment accumulation rate patterns, or by coarse sampling schemes, see MacLeod & Keller 1991; MacLeod 1995*a, b*). A temporary cessation of deposition in any one area will give the impression of multiple contemporaneous extinctions followed by multiple contemporaneous originations (Birkelund & Hakansson 1982), because true ranges will be truncated at both ends (Fig. 2). This is particularly pertinent for the K–T boundary controversy since many of the classic sequences contain missing intervals (MacLeod & Keller 1991; Kennedy 1993; MacLeod 1995*a, b*).



**Fig. 1.** Theoretical patterns of mass extinction in the fossil record. Three end-member patterns indicate different causal mechanisms (e.g. progressive means relatively long term, moderate intensity environmental change; catastrophic is a single, short-term, high intensity environmental change; stepwise is multiple short-term moderate-high intensity episodes of environmental change). However, these three models are not mutually exclusive. A combination of end-member models may more accurately describe K-T extinction patterns in the stratigraphical record (see Figs 3, 10) and, in turn, may imply the operation of multiple causal mechanisms.



**Fig. 2.** Potential bias of biostratigraphical data towards a catastrophic faunal turnover pattern via the presence of an unrecognized hiatus. (a) Hypothetical distribution of biostratigraphical ranges for taxa A-N across an event horizon; y-axis=time. (b) Distribution of the same datums as they would appear in the stratigraphical record; y-axis=stratigraphic position. If the event horizon lies within an interval of non-deposition or post-event erosion, the stratigraphical distribution of relatively short-ranging taxa may be disrupted so as to appear to terminate (and originate) abruptly. Compare this diagram to fig. 1 of Bramlette (1965). All of the sections used by Bramlette (1965) to infer an abrupt K-T turnover pattern for marine plankton are now known to contain boundary hiatuses of up to tens of thousands of years in duration (see MacLeod & Keller 1991, and references therein).

### Lagerstätten

The presence of unusually good preservation with many identifiable species will enhance the species diversity for brief time intervals, giving the impression of sudden origins at the beginning of the Lagerstätten interval, followed by severe extinctions at its end.

### Reworking of fossils

Fossils and/or clasts containing fossils that are reworked from older into younger sediments, and burrows filled with younger sediments, will give a false impression of an extended range by a 'delayed' time of extinction or 'early' time of origination. Examples of both have been reported from K-T successions. Non-biotic vertical mixing (Berger & Heath 1968) can have the same effect, though mixing models indicate that it would be confined to a few centimeters and recognizable by a smooth and exponentially declining decay curve above the true last appearance datum.

### Circular arguments for dating

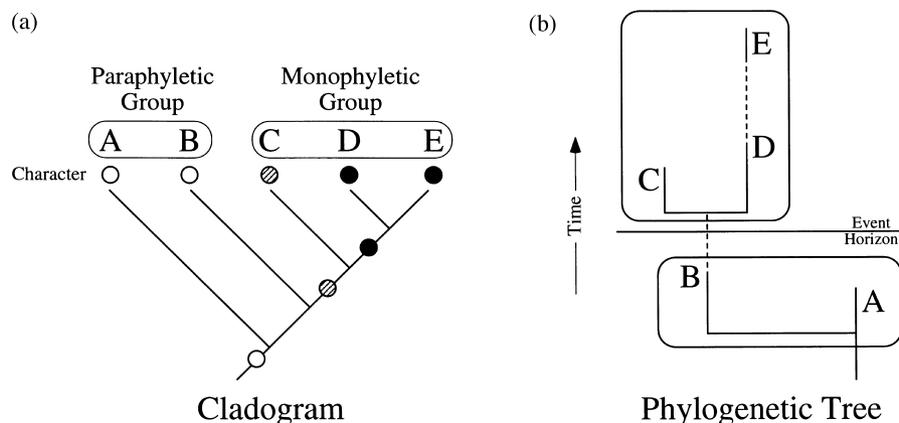
If rocks are dated using particular index fossils then the validity of the age assignment for the rock unit cannot be used to date unambiguously origination or extinction events for those fossils. For example, if dinosaurs or ammonites are regarded as being confined to Mesozoic strata, then any dinosaur-bearing or ammonite-bearing unit will necessarily be assigned a Mesozoic age regardless of its true (e.g. possible Tertiary) chronological age.

### Emigration-immigration and facies change

The movement of animals into or out of an area will give a signal of only local significance. Such movements may be brought about by facies changes reflecting changing local conditions. In theory this might be detected by finding the fossil in younger deposits elsewhere, but this depends on a high degree of temporal completeness.

### Poor sampling

If the fossil record of any particular species or group is poor and patchy, or if a good fossil record is coarsely sampled, we can have little confidence that observed occurrences truly reflect past events. Furthermore, data reproducibility experiments, carried out by distributing similar rock samples containing planktonic foraminifera to a variety of scientists, have shown large degrees of variation in reported faunal composition (see Keller *et al.* 1995; MacLeod 1996a), suggesting that either the distributions of microfossils may be more spatially heterogeneous than previously suspected, or that reports of



**Fig. 3.** Distinctions between monophyletic and paraphyletic taxonomic groupings in the study of mass extinction as seen on a cladogram (a) and in an equivalent phylogenetic tree (b). A monophyletic group is a set of taxa that uniquely share a homologous, derived character (Smith 1994). Taxa C-E all share a unique character (the grey symbol) or its derived homologue (the black symbol). A subsidiary monophyletic group composed of taxa D and E can also be recognized. A monophyletic group includes the ancestral taxon of a lineage and all its descendants. A paraphyletic group contains an ancestral taxon and some, but not all of its descendants. Paraphyletic groups are usually defined by a combination of present and absent (=negative evidence) characteristics. Monophyletic taxa are part of the evolutionary process and possess a unique history that transcends taxonomic convention. Paraphyletic taxa are artificial in the sense that their defining attributes are matters of systematic convention and not an intrinsic part of evolutionary history. Stratigraphical ranges, taxonomic richness values, and extinction rate estimates for higher taxonomic groups should be constructed on the basis of monophyletic sets of taxa in order to avoid bias due to an imperfectly observed fossil record and/or inappropriate taxonomic practice.

faunal compositions may be strongly biased by different processing methods, species concepts, or other factors.

### Idiosyncratic taxonomy

Species named solely because they occur at a certain level (biostratigraphical species) or in a certain area (biogeographical species) will distort true species ranges. There are instances where the same morphotaxon is given different names simply because individuals lived on either side of a major stratigraphical boundary. One example, among sharks, is the common practice of changing the generic name *Cretolamna* to *Otodus* according to which side of the K-T boundary the specimen occurred.

### Phylogenetic mistakes

The use of genera and families as units of analysis can distort the fossil record since unnatural groups may be treated as though they had the same evolutionary significance as natural (monophyletic) groups (Fig. 3). This has been demonstrated most clearly for fishes and echinoderms by Patterson & Smith (1987, 1989) and Smith & Patterson (1988). These authors were concerned with the taxonomic quality of the data used by Raup & Sepkoski (1984) which had been claimed to support extinction periodicity. Patterson & Smith (1987, 1989) showed that 58% of the fish and echinoderm families which had been claimed to show extinction periodicity were either polyphyletic (the members of the family did not share an immediate common ancestor), paraphyletic (the group shared a unique common ancestor but not all members were included), or monospecific. These non-monophyletic groups are phylogenetic mistakes and cannot be used as evidence of extinction (see Discussion). Moreover, Patterson & Smith (1987, 1989) showed more pseudoextinctions in their genus-level analysis.

The following are brief reports of turnover patterns in a variety of microfossil, invertebrate macrofossil and vertebrate

macrofossil groups across the K-T boundary, in which the possible biasing mechanisms described above have been given due consideration. These summaries represent the state of the K-T fossil record for the groups discussed. Any hypothesis or scenario seeking to explain or otherwise account for the K-T mass extinction should provide mechanisms consistent with these patterns of long and short-term extinction and survivorship.

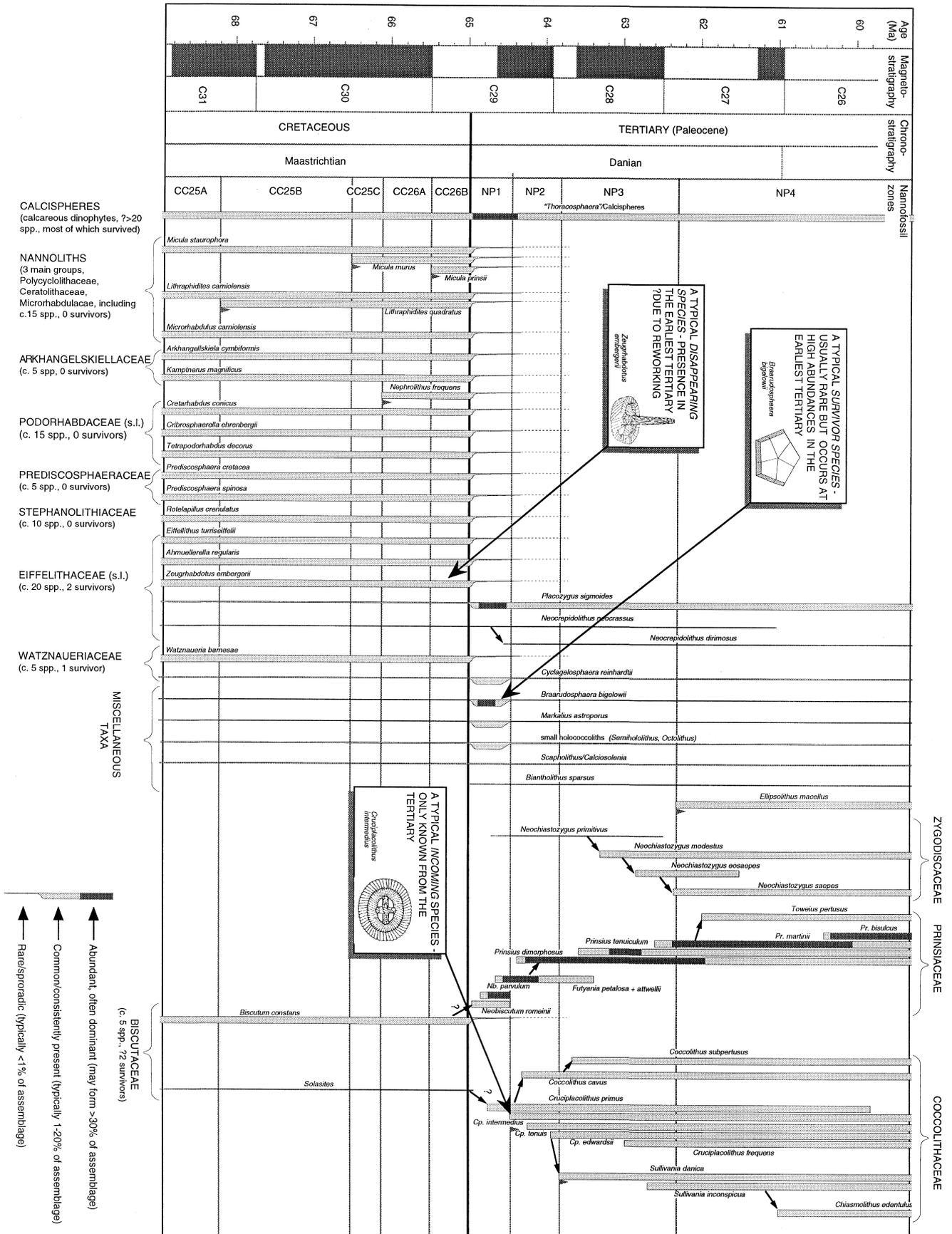
### Microbiota

#### *Calcareous nannoplankton*

The floral turnover across the K-T boundary is the most dramatic feature in the fossil record of calcareous nannoplankton (comprising coccoliths, nannoliths and calcispheres). These groups have been studied in detail from virtually all known marine boundary successions. Moreover, the record of nannofloral change across the boundary is well-established at the species level (Fig. 4).

Syntheses are provided by Thierstein (1981), Gartner (1996) and Pospichal (in press). Percival & Fischer (1977) divided the Maastrichtian and Danian nannofossil flora into vanishing species, persistent species and incoming species. Precise numbers of species in these categories depends on subjective species concepts, but using mid-range concepts, and excluding calcispheres, we recognize 80 vanishing Maastrichtian species, 10 K-T survivors, and about 30 incoming Danian species.

The vanishing species are those that occur in the topmost Maastrichtian but do not occur consistently in Danian strata and do not give rise to obvious Tertiary descendants. Members of this group may form >90% of Maastrichtian assemblages in most deep-sea cores from this interval and include numerous long-ranging species. There does not appear to be any foreshadowing of the K-T event by nannofossil extinctions in the Maastrichtian. Species-level Maastrichtian nannofossil extinctions do occur, but there is no evidence of an increase in



the extinction rate towards the K-T boundary (Pospichal 1994), nor is there any strong evidence of anomalous assemblages immediately prior to the boundary (Pospichal 1994; Ehrendorfer 1993; Gartner 1996).

Representatives of the vanishing flora (the relative number of which depends upon one's interpretation, see below) occur in the lowermost Danian and may dominate particular assemblages. In most sections these vanishing species show a rapid decline in abundance over a lowermost Danian interval of a few tens of centimetres to a few metres, typically corresponding to the first 20 000–80 000 years of the Danian (Fig. 4; Pospichal 1995). During their decline the relative abundances of each species within the assemblage of vanishing species remains essentially constant and, despite extensive efforts, consistent last appearance datums within the Danian have not been identified for any of these taxa.

Various explanations for these Danian occurrences of Maastrichtian nannofossils have been offered. Survivorship of these taxa into the Paleocene is an obvious and simple explanation. The main problems with this scenario are (1) if the vanishing group as a whole survived the apparently anomalous conditions of the earliest Danian ocean, why did they then fail to recover when more normal conditions were resumed (by Zone NP2; Gartner 1996), (2) why did members of this large group of species not have widely varying, biogeographically related distributions in the (presumably) highly variable early Danian ocean (as the surviving and incoming species did), and (3) why do they not exhibit clear last appearance data?

These questions have led many nannofossil palaeontologists to entertain the alternative scenario of a global catastrophic event, which rapidly (perhaps over 1–10 years) killed off most of the nanoflora, leaving only a few survivor species. This alternative scenario requires an explanation for the presence of Cretaceous specimens above the boundary. Possibilities include bioturbation, reworking, and mixing of remobilized material. Such mechanisms are entirely consistent with knowledge of and interpretations of other parts of the nannofossil record. However, definitive evidence may never be found to prove whether or not the Cretaceous specimens in the lowermost Danian are *in situ*.

Persistent (or survivor) species are Upper Cretaceous species regarded as occurring *in situ* in the Danian, because they exhibit high relative abundances, consistent occurrences in Danian strata, and/or represent the inferred ancestors of Danian species. These species dominate nannofossil assemblages between the decline of the Cretaceous floras and evolution of incoming Danian species. Most of these taxa do not

belong to the major coccolith or nannolith families but to evolutionarily conservative taxa of uncertain affinities (miscellaneous taxa of Fig. 4). These groups are usually rare (indeed only sporadically present), but become much more abundant in the lowest Danian. By contrast only a very few of the more common Cretaceous taxa persist. Calcspheres are exceptionally abundant in the survivor assemblages. Kienel (1994) suggested that a major turnover occurs within this group, but in the lower Danian rather than at the K-T boundary.

The first incoming species occur shortly above the boundary in expanded sections (e.g. El Kef, Tunisia) and then give rise to easily traceable lineages (Fig. 4). The origins of these new Paleocene lineages are not easy to determine. This is partly due to a lack of careful phylogenetic research in this interval, but also reflects the facts that the lowest Danian species are all very small and that the new lineages have structures that differ very significantly from those of any obvious Mesozoic precursors.

### *Dinoflagellates*

The K-T dinoflagellate record is difficult to interpret with confidence because only a small proportion of modern dinoflagellate species, and by inference K-T species, produce fossilizable organic-walled cysts. While ancient cyst-forming species have provided palynologists with a fossil record that can be used for correlation and palaeoenvironmental analysis, the K-T dinoflagellate fossil record most likely remains an underestimate of the total number dinoflagellate species that actually existed during K-T time. Consequently, it may be highly misleading to infer turnover patterns among ancient floras on the basis of data from cyst-forming species alone.

Details of the K-T dinoflagellate record are best known from sections at El Kef, Tunisia (Brinkhuis & Zachariasse 1988) and Seymour Island, Antarctica (Elliot *et al.* 1994; Askin & Jacobson 1996). In both successions, first and last appearances of dinoflagellate cysts are not confined to single levels or restricted intervals near the boundary, but occur throughout the uppermost Cretaceous and lowermost Tertiary in a broadly progressive pattern. The turnover rate does increase in the uppermost Maastrichtian (close to the K-T boundary), but this interval precedes the emplacement of impact debris in all studied sections and is probably better correlated with the latest Maastrichtian eustatic sea-level rise (see Haq 1991). A pronounced decline in marine palynomorph species in this uppermost Maastrichtian interval occurs on Seymour Island (Askin & Jacobson 1996).

### *Diatoms*

Diatoms are microscopical unicellular algae whose valves are made of opaline silica. Because of the instability of this form of silica, diatoms are highly susceptible to dissolution, recrystallization, and/or other diagenetic processes. The presence of diatoms diminishes down the geological column, and in pre-Eocene sediments they are known from only a handful of localities worldwide (see Harwood & Gersonde 1990).

Living diatoms are found in a wide variety of freshwater and marine settings, but there are no known occurrences of diatoms in Mesozoic freshwater facies. Until recently, the lack of diatomaceous K-T successions led to wildly varying estimates of diatom survival across the K-T boundary. These estimates ranged from 13% to 100% survivorship, and were based

**Fig. 4.** Calcareous nannofossil record across the K-T boundary. The diagram includes most common low-latitude species. High latitude assemblages show similar patterns, but with some different species. Numerous rare species, particularly disappearing Cretaceous species, are not shown. Species are grouped into families. For each Cretaceous family, estimates are given of the number of species in the topmost Maastrichtian interval and the number of these taxa that definitely survive into the Danian (e.g. 10 spp., 0 survivors). The pattern of decline in abundance of questionably reworked disappearing species in the Danian varies between sections. Gradualistic evolutionary transitions within some lineages are indicated by placing the species very close together. Arrows indicate other, less certain, evolutionary transitions. Magnetostratigraphy and biostratigraphy from Berggren *et al.* (1995). Nannofossil data from Heck & Prins (1987), Pospichal (1995, in press), Perch-Nielsen (1979), Romein (1979), Varol (1989) and personal observations.

primarily on presence/absence of Upper Cretaceous species in Paleocene floras (Wornardt 1972; Strelnikova 1975; Jouse 1978; Fenner 1985). However, there was general agreement that the characteristic Upper Cretaceous genus *Gladiopsis* became extinct at or just below the K–T boundary. Harwood (1988) described a diatom flora from the K–T succession on Seymour Island, Antarctica. This high-latitude locality contains the only diatomaceous K–T boundary succession presently known. From that succession, Harwood (1988) reported 84% of Upper Cretaceous diatom species surviving into Tertiary strata.

High diatom survivorship rates across the K–T boundary event horizon were predicted by Milne & McKay (1982) and Kitchell *et al.* (1986) who suggested that the ability of some diatom species to form dormant resting spores during times of environmental stress (especially during low nutrient/light conditions) enabled these species to survive a short-term catastrophic event. Diatom resting stages are readily recognizable in the fossil record (Hargraves 1986; Kitchell *et al.* 1986), and Harwood (1988) noted a great increase in their relative abundance at and above the K–T boundary on Seymour Island. However, such increases in resting spore frequencies are known from other stratigraphical levels. Accordingly, the hypothesis that an increase in diatom resting spores in the Seymour Island section might have resulted from local (i.e. non-impact related) environmental factors cannot be ruled out.

On a broader scale, a survey of Santonian to lower Eocene diatom assemblages, undertaken by one of the authors (P.C.), indicates that out of 447 valid Upper Cretaceous species, only 203 species (46%) survive to the Upper Palaeocene and Eocene. Since only a single diatomaceous K–T boundary succession is known, this figure cannot be taken as indicative of the magnitude or pattern of diatom extinctions across the K–T boundary. However, it does suggest that a substantial, though by no means catastrophic, turnover among diatom species took place within the Late Cretaceous–early Palaeogene.

A preliminary analysis of these Santonian–lower Eocene data also shows strong discrepancies in survivorship rates among planktonic and benthic diatom taxa. Planktonic genera exhibit substantially higher survivorship rates (50–90%) relative to benthic genera (10–40% survivorship). Since the ability to form resting stages is more common among modern planktonic (but not benthic) diatom species (Hargraves & French 1983), this might explain the high survivorship rates reported by Harwood (1988) for the predominantly planktonic Seymour Island floras (see also Kitchell *et al.* 1986). However, modern marine diatom resting stages have not been known to remain viable for more than two years (Hargraves & French 1983). This suggests that if resting stages were the mechanism used by the Seymour Island diatoms to survive the K–T event, that event must have had a very short duration. Regardless, a short-event scenario is inconsistent with the high relative frequency of diatom resting stages throughout the lowermost Danian on Seymour Island (Harwood 1988).

### *Radiolaria*

Radiolaria have a geological record dating from at least Ordovician times. The mineral skeletons or tests of polycystine radiolarians are secreted by the organism following uptake of monosilic acid from seawater and its transformation into amorphous silica (Opal-A). After death, the skeletal test can be fossilized in a series of mineral phases from Opal-A through

Opal-CT (cristoballite/trypidite) to quartz, depending on diagenetic history (mainly time, temperature and pressure conditions). Due to the high susceptibility to dissolution of the initial and transitional silica phases in both marine and connate waters, the fossil record of radiolaria is extremely patchy, both stratigraphically and geographically.

Very few studies of radiolarian faunal transitions across the K–T boundary, or of highest Maastrichtian and lowest Paleocene radiolarians, have been published. These include: Frizel & Middour (1951), Borisenko (1958, 1960), Foreman (1968), Dumitrica (1973), Kozlova (1983), Nishimura (1986, 1992), Goltman (1988), Ling (1991), Hollis & Hanson (1991), Hollis (1993, 1996) and Strong *et al.* (1995). Of all these publications, only two authors claim to have studied radiolarian assemblages from either questionably complete (Foreman 1968) or complete (Hollis 1993; Hollis in Strong *et al.* 1995) K–T successions.

Foreman (1968) concentrated on the analysis of upper Maastrichtian Nassellaria from four localities in the Moreno Formation in California. She considered five identifiable species to have survived from the late Maastrichtian to the early Paleocene: *Amphipyndax stocki*, *Cornutella californica*, *Dictyomitra cf. multicosata*, *?Stauroidictya fresnoensis* and *Stichomitra alamedaensis*. These species were recovered throughout a core section of c. 6 m in association with other undescribed forms of definite Cretaceous character, together with a predominantly ?Palaeocene radiolarian assemblage. Foreman (1968) did not address the problems of possible reworking or sedimentary gaps. Biostratigraphical control was also based on a marked change in dinoflagellates and spores at the same level as the radiolarians in this series of samples as recorded by Drugg (1967).

Hollis (1991, 1993) investigated five onshore sections from New Zealand, and re-examined faunas from the flanks of Lord Howe Rise previously examined by Dumitrica (1973) from coeval strata at DSDP Site 208. The New Zealand rocks are siliceous limestones, mudstones and cherts whereas lithologies from DSDP Site 208 are primarily chalks and cherts. An iridium-rich boundary clay layer is reported in three of the onshore New Zealand sections. Biostratigraphical age control is provided by foraminifera, dinoflagellates and calcareous nannofossils, and Hollis (pers. comm. 1996) discounts the possibility of reworking on the grounds of assemblage composition and preservational state of individuals together with sedimentological evidence. Hollis (1993) found no evidence for mass extinctions of radiolarians at the K–T boundary. Forty-two of the 45 taxa identified by Hollis (1991) from Cretaceous rocks had reliable Palaeocene occurrences. Reference to ranges of Cretaceous–Tertiary taxa in Hollis (1991, 1993) suggests that a faunal turnover in radiolarians occurred in the mid Palaeocene (at least in southern high latitudes), in contrast to the earlier major floral turnovers experienced by calcareous nannoplankton at the K–T boundary.

Although the K–T boundary in these sections does not mark a faunal discontinuity, it was a time of changing composition among siliceous plankton. In particular the frequency of radiolarian-rich samples, radiolarian/diatom ratios, nassellarian/spumellarian ratios and Si/Ca ratios all increase across the K–T boundary (Hollis 1991, 1993). These compositional data suggest that marine productivity increased in the southern high latitudes and contradict predictions of the Strangelove Ocean model (Hsü & MacKenzie 1985). Additional support for high phytoplankton productivities in the southern high latitudes across the K–T boundary comes from

the isotopic work of Stott & Kennett (1990), and show that they may have been related to climatic cooling (Stott & Kennett 1990; Hollis 1996).

### *Planktonic foraminifera*

The idea that foraminifera suffered a pronounced extinction across the K-T boundary dates back to the 1930s (e.g. Glaessner 1937). Abrupt turnover in planktonic foraminiferal faunas at the K-T boundary began to be mentioned in the late 1950s (e.g. Troelson 1957; Reiss 1957). In introducing Schindewolf's (1962) concept of neocatastrophism ('Neokatastrophismus'), Newell (1962) identified the K-T boundary as one locus of mass extinction in Earth history and identified planktonic foraminifera as one of the principal victims of this event.

The abrupt turnover of the planktonic foraminifera across the K-T boundary in many sections was cited by Bramlette (1965) as evidence that this event took place on a much shorter time scale than the Permo-Triassic mass extinction. Bramlette (1965) acknowledged that a stratigraphical hiatus was present in most K-T boundary sections, thus imparting the appearance of an instantaneous biotic turnover to those records, but speculated that the K-T boundary hiatus 'may involve many thousands of years but probably [represented] much less than a million . . .' (Bramlette 1965, p. 1697). Interestingly, much of the early literature on the K-T planktonic foraminiferal mass extinction also contains anecdotal accounts of Cretaceous species in Danian strata (e.g. Troelson 1957).

The 1980 proposal of the asteroid impact scenario (Alvarez *et al.* 1980) resulted in renewed interest in the planktonic foraminiferal record across the K-T boundary. Detailed sampling of several classic K-T boundary localities (e.g. Gubbio, Italy; El Kef, Tunisia; Brazos River, Texas), and the discovery of new K-T boundary successions (e.g. Agost and Caravaca in Spain), has forced a re-evaluation of the K-T planktonic foraminiferal record. In particular, Keller (1988*b*, 1989, 1993; Canudo *et al.* 1991; Keller & Benjamini 1991) reported many species previously thought to be confined to the Upper Cretaceous, associated with undoubtedly Tertiary faunas above the K-T boundary impact debris layer.

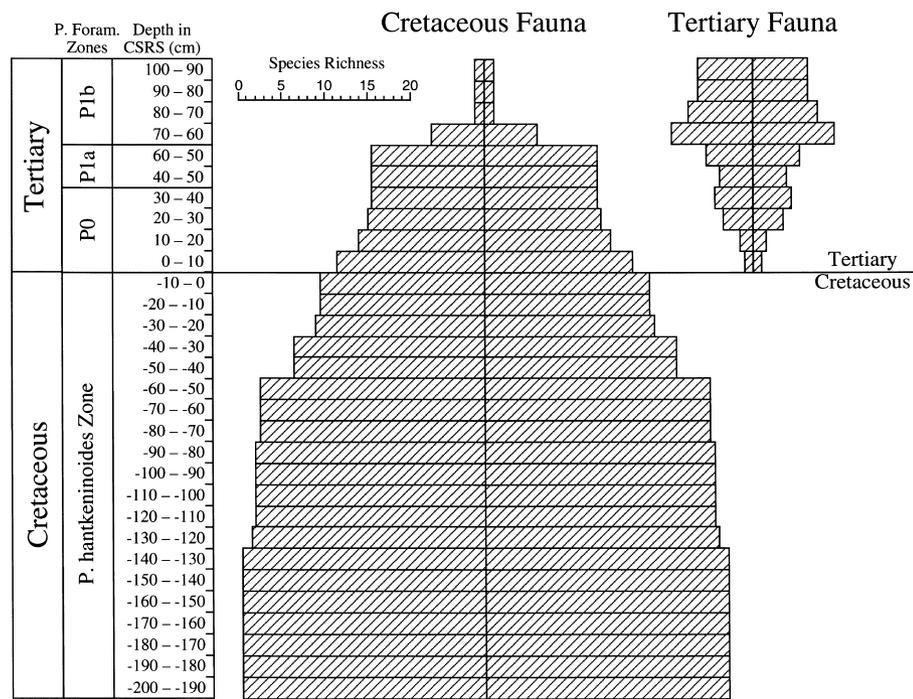
Subsequent work by independent investigators (e.g. Liu & Olsson 1992) and a heretofore unprecedented biostratigraphical blind test of the El Kef stratotype succession (see Keller *et al.* 1995; MacLeod 1996*a, c*; Ginsburg *et al.* in press) have confirmed Keller's observations. It appears that planktonic foraminiferal extinctions occurred prior to, at, and well after the K-T boundary event on a global scale. Olsson & Liu (1993) and Liu & Olsson (1992) have argued that the presence of Cretaceous morphotypes in Danian rocks is the result of reworking. To assess this interpretation, Keller's data have been extensively tested for both survivorship, reworking (Barrera & Keller 1990; Schmitz *et al.* 1992; MacLeod & Keller 1994; MacLeod 1995*a, b, c*, 1996*a, b, d*) and the Signor-Lipps effect (MacLeod 1996*a, b, d*; see Discussion). Results of these tests have revealed patterns of isotopic, geographical, morphological and stratigraphical variation that are inconsistent with reworking or a significant Signor-Lipps effect within these data, but consistent with Keller's original interpretation of widespread planktonic foraminiferal survivorship into the early Danian.

MacLeod & Keller (1991) combined planktonic foraminiferal and calcareous nannoplankton data from thirteen bio-

stratigraphically complete marine K-T boundary successions to determine which of these sections and cores contained boundary hiatuses, and if possible, to estimate the location and duration of these hiatuses. Results showed that previous data used to support models of catastrophic faunal and floral turnover across the K-T boundary, and the physical evidence used to associate a bolide impact with that turnover, have often come from boundary successions that contained unrecognized hiatuses (e.g. Gubbio, Italy; Stevns Klint, Denmark). Other sections (e.g. Brazos River, Texas; Nye Kløv, Denmark), exhibiting a more progressive turnover pattern, were shown to be chronostratigraphically complete across the boundary. Comparative stratigraphical analysis of these sections and cores (MacLeod & Keller 1991; MacLeod 1995*a, b*, 1996*a, b, d*) indicates that the temporal and environmental distribution of marine boundary hiatuses are consistent with predictions of sequence stratigraphical models for the rapid eustatic sea-level rise that is known to have taken place during the Cretaceous-Tertiary transition (Haq *et al.* 1987; Haq 1991). A summary of global biostratigraphical data from MacLeod & Keller (1991) and MacLeod (1995*a, b*, 1996*a*) reveals a broadly progressive pattern of planktonic foraminiferal extinction and origination through the latest Maastrichtian and earliest Danian (Fig. 5).

From a biogeographical point of view (MacLeod & Keller 1994), these data suggest that the K-T planktonic foraminiferal turnover took place in a series of waves that removed taxonomically and geographically unified components of the Late Cretaceous fauna (Fig. 6). The first of these waves began in the latest Maastrichtian (*Plummerita hantkeninoides* Zone) and primarily affected large, highly ornamented, intermediate and deep-dwelling globotruncanoid species in the low and middle latitudes. Survivors of this extinction pulse appear to have crossed the K-T boundary horizon without suffering significant additional loss in species richness. Local species extinctions do occur at the K-T boundary for many Cretaceous species; however, when appropriate, high-resolution, global correlations are made, and the composite record of K-T planktonic foraminiferal turnover assembled (MacLeod & Keller 1991; MacLeod 1996*a*), no Cretaceous species can be assigned unambiguously to an extinction horizon coincident with the K-T boundary.

The planktonic foraminiferal K-T survivor fauna persisted some 40 000–100 000 years into the Tertiary after which it suffered a second wave of extinctions that removed Cretaceous survivors in the low and middle latitudes. Throughout these first two extinction waves high-latitude planktonic foraminiferal faunas appear to have suffered relatively little extinction. However, all but a few of these high latitude Cretaceous survivor populations disappear from the stratigraphical record in overlying Danian biozones. The incoming fauna of Tertiary planktonic foraminiferal species occupied a very small portion of overall Tertiary species diversity in the earliest Danian, but expanded to replace Cretaceous survivor species as these became extinct in the low and middle latitudes in the early Danian and later in the high latitudes. This temporally expanded and geographically structured interval of planktonic foraminiferal extinctions seems strongly suggestive of a long period of environmental instability across the K-T boundary, perhaps driven by relatively long-term eustatic sea-level/climatic fluctuations, with some contribution from relatively short-term volcanic and impact-related event(s) at or near the boundary horizon itself, coupled with post-boundary competition from radiating Danian lineages.



**Fig. 5.** Spindle diagrams of observed changes in Cretaceous and Tertiary planktonic foraminiferal species richness across the K-T boundary (based on a synthesis of biostratigraphical data from El Kef, Tunisia; Agost, Spain; and Brazos Core, Texas; see MacLeod 1996a). Positions in the sequence represent binned (10 cm) intervals along the K-T Composite Standard Reference Section (K-T CSRS) for these three successions. Note that in terms of the observed data, the Cretaceous planktonic foraminiferal fauna loses approximately one-third of its Maastrichtian species richness in the uppermost Maastrichtian *P. hantkeninoides* Zone, and that the decline in species richness beginning in this interval carries through the K-T boundary horizon without any significant deflection. The most dramatic reductions in Cretaceous species richness in these sections occur at the top of Tertiary Zone P1a almost 300 k.y. after the K-T boundary. Analysis of the original biostratigraphical data (MacLeod 1996a) suggests that, in these three sections, the pre-boundary decline in planktonic foraminiferal species richness and the post-boundary occurrence of Cretaceous morphotypes cannot be accounted for by the Signor-Lipps effect and reworking respectively.

### Agglutinated benthic foraminifera

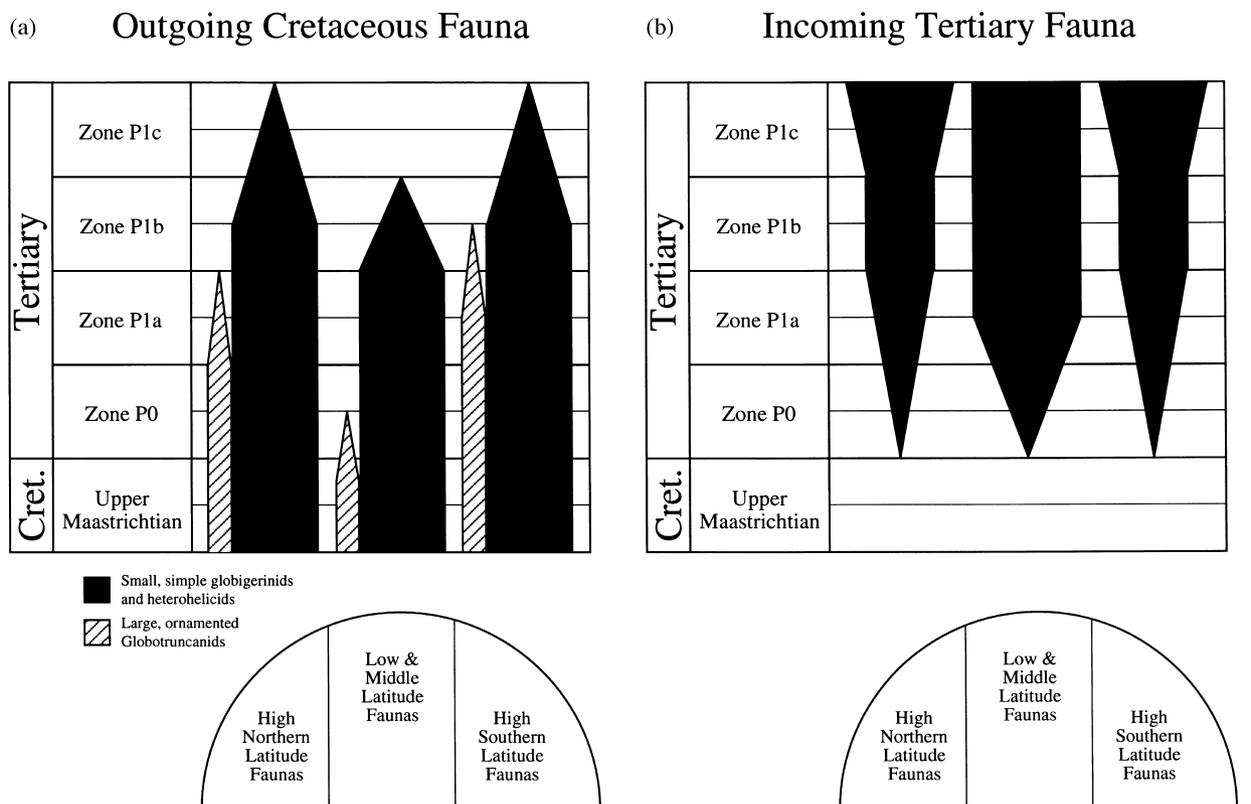
The record of agglutinated benthic foraminifera exhibits few species extinctions in the Late Cretaceous, though deep-water agglutinated benthic foraminiferal assemblages do appear to exhibit a local shift to dominance by opportunistic species during the first few hundred-thousand years of the Palaeocene. In acid residues from the Gubbio sections (Central Italy), a significant decrease in agglutinated foraminiferal abundance and diversity, and a shift in community structure, are observed across the K-T boundary. Upper Maastrichtian assemblages are also dominated by epifaunal suspension and detritus feeders whereas the lower Danian boundary clay is dominated by infaunal species that were probably bacteriovores. These changes may have been a consequence of the significant decrease in the flux of organic matter to the sea floor associated with the K-T boundary event.

Tubular agglutinated species (e.g. *Rhizammina*) alone show an 80% reduction in numbers beginning 5 cm below the boundary (Fig. 8). The first genus to increase in numbers above the boundary is *Reophax* (Event 1 in Figs 7 and 8), a form known to colonize modern deep-sea environments following disturbances by strong currents (Kaminski 1985; Kaminski *et al.* 1988) and ash falls (Kuhnt & Hess 1994). It is possible that organic matter scavenged from the water column by settling fine-grained particles may have been able to sustain a bloom of small infaunal *Reophax*.

Following the event, successive maxima of two other infaunal taxa occur within Zone P1a; *Spiroplectammina* ex. gr. *dentata* and *S.* ex. gr. *spectabilis*, corresponding to events 2 and 3 in Figs 7 and 8). These assemblages may represent periods of

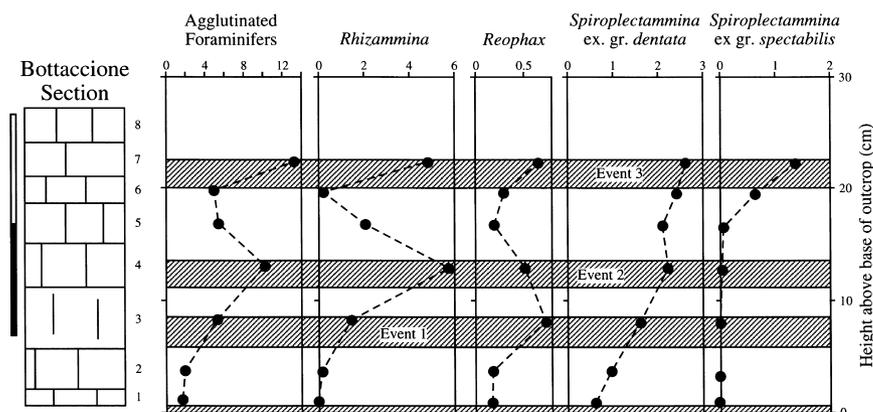
increased organic flux associated with erratic phytoplankton blooms within an early Palaeocene period of generally low productivity. Similar patterns of abundance increase have recently been observed at two other K-T boundary sections in Spain (Kuhnt & Kaminski 1993; Coccioni & Galeotti 1994). An increase in *Spiroplectammina* above the K-T boundary has also been reported from the flysch sediments of the Alpine Gossau in central Asia (Peyrt *et al.* in press). The *Spiroplectammina* biofacies, which appears to characterize the upper part of Zone P0 and the lower part of Zone P1a, seems an especially useful lowermost Danian marker horizon.

The timing and structure of the agglutinated benthic foraminiferal recovery undoubtedly depended on deposition of organic matter from the mixed layer. The succession of biofacies across the K-T boundary is consistent with a model of strongly reduced primary productivity in the earliest Palaeocene. In an early Palaeocene lower and middle latitude Strangelove Ocean, sufficient nutrients may have been available in the mixed layer to sustain large blooms once the phytoplankton flora re-established itself after the K-T boundary event. It is likely that export production from occasional phytoplankton blooms provided the nutrients needed to support agglutinated benthic foraminiferal assemblages. Once the flux of organic matter became more substantial, a high-productivity adapted community of r-selected infaunal forms began to thrive. The initial drop in agglutinated benthic foraminiferal abundance and diversity appears to have taken place in the late Maastrichtian (Fig. 8). Ultimate recovery of agglutinated benthic foraminiferal community structure during the early Palaeocene occurred in several stages lasting several hundred thousand years (Kuhnt & Kaminski 1993). This



**Fig. 6.** Schematic diagram of differential geographical responses of the global planktonic foraminiferal fauna to the K-T mass extinction event. There is no scale on the x-axis and the widths of the bars are not meant to imply that either Cretaceous or Tertiary planktonic foraminiferal species richnesses were the same in all biogeographical provinces. Figure based on results of MacLeod & Keller (1994).

**Fig. 7.** Abundance of important groups of deep-water agglutinated foraminifera across the K-T boundary in the Bottaccione section near Gubbio, Italy. The scale bar along the vertical axis is divided into 10 cm intervals. Numbers alongside the section represent bed numbers. Position of the K-T boundary is at the level of 0.0 on the right-hand scale. All abundance values are given as individuals  $>63 \mu\text{m}$  per gram of dissolved sediment.



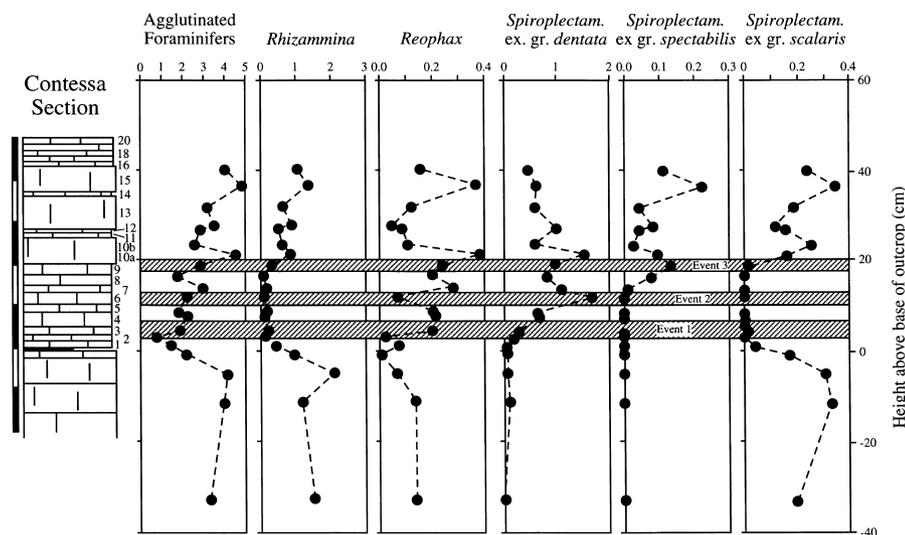
perturbation of a component of the benthic foraminiferal fauna may have been linked to the evolution and recovery of the phytoplankton that are the source of nutrients for detritus-feeding organisms.

#### *Calcareous benthic foraminifera*

Lipps & Hickman (1982) considered that shallow water benthic foraminifera underwent a mass extinction at the K-T boundary whilst deep-sea foraminifera were generally unaffected. Miller (1982), however, concluded that neither shallow nor deep-dwelling species exhibit a pattern of mass extinction. More recent investigations of Tethyan faunas (Keller 1988a;

Coccioni & Galeotti 1994) and faunas from the southern Atlantic (Widmark & Malmgren 1992) and high southern latitudes (Thomas 1990) agree with the latter interpretation, though Speijer & Van der Zwann (1996) have argued for an explicitly impact-related mass extinction.

Keller & Lindinger (1989), working in the relatively shallow water deposits of El Kef, Tunisia, described relatively warm temperatures followed by sudden global cooling that triggered reduced surface water productivity during the late Maastrichtian, and led to reduced calcareous benthic foraminiferal diversity. These authors considered this productivity low to continue (along with associated unstable environmental conditions) some 300 000 to 400 000 years into the Tertiary.



**Fig. 8.** Abundance of important groups of deep-water agglutinated foraminifera across the K–T boundary in the Contessa section near Gubbio, Italy. The scale bar along the vertical axis is divided into 10 cm intervals. Numbers alongside the section represent bed numbers. Position of the K–T boundary is at the level of 0.0 on the right-hand scale. All abundance values are given as individuals >125  $\mu\text{m}$  per gram of dissolved sediment.

Ortiz and Keller (pers. comm.) have also suggested that a short-term episode of global warming, sea-level rise, and expanded oxygen minimum zone conditions on the continental shelf, resulted in decreased abundances of species in many sections, along with a switch in ecological composition that favoured infaunal, low oxygen-tolerant species. Epifaunal and low oxygen intolerant species presumably migrated to refugia during this time because these Cretaceous species reappear in overlying Danian sediments. Speijer & Van der Zwan (1996), however, speculated that these changes in the El Kef assemblage were the result of climatic feedback mechanisms triggered by bolide impact. In an analogous study of the Caravaca K–T boundary section in southern Spain, Coccioni & Galeotti (1994) argued that the reduction in diversity coincided with a decrease in the rate of organic flux to the ocean floor via the Strangelove Ocean model.

Most likely, both oxygen minimum zone expansion and productivity decrease played a role in this benthic foraminiferal ecological event. It should be noted though, that while fluctuations in the oxygen minimum zone are commonly associated with sea-level changes and have been known to exert a long-term effect on benthic foraminiferal populations throughout the last 100 million years, there is no known mechanism for reducing the amount of organic carbon reaching the sea floor by eliminating a large part of the marine phytoplankton population and then keeping that population depressed for geologically significant time periods (75 000–80 000 years), the Strangelove Ocean model. Indeed, phytoplankton doubling times are on the order of hours to days and the direct effects of a bolide impact (e.g. darkness, acid rain) are estimated to last for only a few months to (at most) a few years (see D'Hondt 1995). While interpretations of the causes of the faunal dominance changes observed in upper Maastrichtian benthic foraminiferal assemblages will no doubt continue, the bulk of the evidence indicates that the latest Cretaceous was not a period of widespread calcareous benthic foraminiferal extinctions.

#### Larger benthic foraminifera

The so-called larger foraminifera are benthic taxa that develop complex and characteristic internal skeletons. Skeletally, they are the most elaborate foraminifera and their phylogenies are

usually well established. Modern larger benthic foraminifera occur world-wide, but in the tropical-subtropical belts only. It is in regions that had palaeoclimates similar to these that the larger foraminifera provide evidence of variations in species richness or faunal composition across the K–T boundary.

Because the larger foraminifera are benthic and confined to the shallow seas of the inner continental or island shelves, few managed to cross the widening Atlantic Ocean. Thus, the larger foraminiferal faunas of the Americas and Euro-Afro-Asia were different in both the Late Cretaceous and the Early Tertiary. Many suprageneric groups of larger foraminifera became extinct in the Late Cretaceous, and others appeared for the first time during the Palaeocene. However, few if any species made an evolutionary first appearance in the Danian or its equivalents. Many workers believe that the extinctions of Tethyan lineages occurred virtually simultaneously, though the chronostratigraphical control necessary to evaluate this hypothesis is lacking. No obvious environmental, sedimentological, geochemical or isotopic anomalies coincide with the extinction of any Maastrichtian larger foraminiferal taxon.

#### Ostracodes

There are few analyses of ostracode occurrence patterns across the K–T boundary that provide reliable data. Perhaps the most important single K–T ostracode record is that of the El Kef (Tunisia) boundary stratotype section. Donze *et al.* (1982) and Peyrouquet (1983) recorded presence/absence patterns of 50 upper Maastrichtian and lower Danian species from this succession. These data show an interruption in ostracode occurrence near the boundary horizon itself, but many Lazarus taxa are re-established subsequently. Peyrouquet considered this pattern to reflect expansion of the oxygen minimum zone at the time of the K–T boundary event. Evidence for oxygen based on the morphology of *Krithe* is considered questionable, especially insofar as Peyrouquet made no comment on the possibility that the rising carbonate compensation depth across the boundary interval may have influenced these faunas.

Marine, inner to middle shelf ostracodes from the Brazos River, Walkers Creek, and Littig Quarry, Texas have been described by Maddocks (1985). Although these sections may not be entirely complete across the boundary (e.g. the Brazos River sections contain an obviously disconformable coarse

clastic unit that has been interpreted by some as a 'tsunami deposit'), a progressive pattern of faunal replacement was recognized.

An ostracode fauna from sections along the Colville River, northern Alaska has been described by Marincovich *et al.* (1990) and Brouwers & De Deckker (1993). The Arctic Ocean was largely isolated in the Late Cretaceous–Early Tertiary, and this is reflected in the preponderance of endemic ostracode taxa in these sections. However, the older beds do contain *Cypridea*, a freshwater genus usually regarded as indicative of the Cretaceous. Nonetheless, a combination of facies changes reflecting the uppermost Maastrichtian marine transgression (see Haq 1991), along with the endemic nature of this fauna, make the Colville River ostracode record difficult to evaluate in terms of its bearing on the ostracode record across the K–T boundary.

In the Far East, Ye (1993) reported the presence of an assemblage of marine shelf ostracode species that implied the presence of a K–T boundary sequence, but provided no details as to the nature of the faunal transition. Pang & Whatley (1990) noted the need to define the Chinese K–T boundary in a paper that provides references to ostracode assemblages and relevant Chinese literature. Musacchio (1990) described *Neuquenocypris*, a non-marine genus thought to range from Aptian to Paleocene from the Neuquen basin. The associated ostracode fauna was qualitatively described as resembling that of the Maastrichtian, but with reduced diversity.

In the most comprehensive synoptic study of K–T ostracodes presently available, Whatley (1990) recorded 70 generic originations (representing 678 species originations) and 230 generic extinctions (representing 1372 species extinctions) during the Maastrichtian. Coles (1990) reviewed Cenozoic North Atlantic deep-water and adjacent shelf ostracode faunas, and found diversity was lower in the Palaeocene than at any other time in the Tertiary. These reviews lack the precise chronostratigraphical control needed to determine the timing, magnitude, and geographical scope of extinctions occurring within the boundary interval itself. Based on these studies, the entire Late Cretaceous interval appears to have been a time of major change for ostracode faunas. Much more work needs to be done to establish the precise character, ecology and timing of this turnover.

## Invertebrate macrofauna

### *Scleractinian corals*

About half the number of extant scleractinian corals genera are zooxanthellate (exhibit intracellular symbiosis with dinoflagellate algae zooxanthellae). These 'z-corals' are commonly colonial and restricted to warm, shallow, photic-zone tropical waters. The remaining azooxanthellate ('az-corals') are commonly solitary and collectively eurytopic. This z/az distinction cuts across formal scleractinian classifications. Thus, the algal symbiosis has been lost in some groups and evolved more than once. Colonial forms of both z- and az-corals contribute to a variety of tropical reefs and deeper or colder water carbonate buildups (Stanley & Cairns 1988). The functional, ecological and biogeographical importance of scleractinian symbiosis has meant that the z/az distinction pervades most coral studies explicitly or otherwise, including those pertaining to mass extinctions.

Unfortunately, there is still no universally applicable way of knowing whether extinct scleractinian taxa were zooxanthel-

late. Consequently, there is considerable ambiguity in the use of most terms related to this aspect of fossil coral biology in the systematic literature. For present purposes, however, these conceptual distinctions can be conveniently gathered into two groups. Group I includes Tethyan (in both strict and broad senses) tropical, reef-dwelling, reef-building, hermatypic, z-like corals. Group II includes boreal, temperate, non-reefal, deep- and cold-water, ahermatypic, az-like corals that are geographically widespread and, in certain instances, overlapping in distribution with Group I.

Rosen & Turnsek's (1989) analysis remains the most extensive global study of K–T extinctions in scleractinian genera and species based on actual taxonomic records. This study determined that about 60% of Late Cretaceous scleractinian genera, failed to survive into the Palaeocene. To place this figure in context, approximately the same number of scleractinian coral taxa failed to survive from the Early to Mid-Cretaceous, and 20–40% of Mid-Cretaceous genera failed to persist into the Late Cretaceous. All patterns appear statistically significant given current data. Partitioning of these data into Groups I and II shows the same relative extinction patterns for both groups through the Cretaceous. However, extinction intensities are generally greater for Group I than Group II, especially in the Upper Cretaceous. Of the total number of Maastrichtian taxa (about 160 species), 97–98% species and 83% genera are unknown in the Tertiary. These figures may also partly reflect stratigraphical 'chauvinotypy' (Rosen 1988, p. 447). Palaeobiogeographical analysis of Maastrichtian species yielded a Tethyan cluster dominated by Group I corals, but no similar differentiation emerged for the Palaeocene.

The widely held belief that post-Cretaceous Group I faunas were rare, if not absent, until the Eocene is inconsistent with the long-known Thanetian Ranikot fauna (Duncan 1880). Recent research (Bryan 1991; Moussavian & Vecsei 1995) suggests that the Group I hiatus may have lasted only until the late Danian. In addition, Late Cretaceous Group I corals are typically rather small (usually <0.5 m), rarely branching and occur in bedded deposits (e.g. Coates & Jackson 1987; Smith *et al.* 1995; Skelton *et al.* in press), often downslope relative to rudist facies (e.g. Matteucci *et al.* 1982; Skelton *et al.* in press). Group I corals of the Tertiary to Recent are much larger, branching forms dominate some assemblages, and buildups span a range of depths and energy conditions (e.g. Bryan 1991).

Although the stratigraphical resolution in the data described above is coarse, it suggests that K–T extinctions took place at a progressively increasing rate through the last stages of the Cretaceous. Recent work in the Oman Mountains has revealed a rich 'Gosau-type' (broadly Santonian) Group I fauna of Maastrichtian age (Smith *et al.* 1995) indicating that extinction rates prior to the Maastrichtian may have been lower, taxonomic richness may have remained higher, and extinctions may have been more concentrated in the later Maastrichtian than previously realized. The foregoing patterns also suggest that Group I corals were more susceptible to K–T extinction factors than Group II corals (see Rosen & Turnsek 1989). While this conclusion may seem at odds with the analyses of Sheehan (1985) and Raup & Boyajian (1988) who found that 'reefs [cf. Group I] are not so different', these authors were addressing relative intensity of extinctions through time. Present patterns (cf. point 2) accord with theirs, whilst additionally showing that in terms of the K–T extinctions, there were also significant differences between Groups I and II.

Explanations compatible with the apparently greater extinction susceptibility of Group I corals range from a collapse of algal symbiosis (due to volcanic or meteorite-impact dust, high nutrient levels, reduced global irradiance), large-scale tectonically and/or eustatically generated loss of shelf seas, increased terrigenous input in shallow marine Tethyan habitats, climatic cooling, climatic 'over-warming' (cf. coral bleaching), and the ever-popular, but surely mistaken (Skelton *et al.* in press), notion of competition from rudists (Kauffman & Johnson 1988). Algal symbiosis collapse may also explain how the characteristic might have evolved independently in different coral groups (see above). Perhaps zooxanthellae survived the K-T boundary in a non-symbiotic state, or in hosts other than corals. Alternatively, the algal symbionts of the Cretaceous may have belonged to one or more species that became extinct, with new symbiotic species arising in the Tertiary. Unfortunately, it is difficult to test such ideas as it is still difficult to estimate how many Group I corals of Late Cretaceous age were specifically zooxanthellate (see above), because there remains insufficient understanding of living zooxanthellae, and because zooxanthellae are not preserved as fossils. Nevertheless, use of coral data to support the widespread concepts of ecosystem collapse and post-extinction recovery (in this case of reef ecosystems) must be tempered by recognition of the considerable changes that took place in the respective ecosystems of which Group I corals were a part, on either side of the K-T boundary.

### *Bryozoans*

Species belonging to two orders of bryozoans (Cheilostomata and Cyclostomata) are present in Cretaceous and Palaeocene marine shelf sediments. However, poor knowledge of their systematics and stratigraphical distributions constrain interpretations of bryozoan extinction and survival across the K-T boundary.

Maastrichtian bryozoan faunas are known from several parts of the world, but Palaeocene faunas are much rarer. The only regions where bryozoans are found on both sides of the K-T boundary are Denmark and possibly the Majunga basin in Madagascar (Brood 1976). Bryozoans have not been recorded from such classic K-T boundary sections as Brazos River (Texas), Gubbio (Italy), El Kef (Tunisia), and Zumaya (Spain).

Bryozoans are the dominant macrofossil group in the Danish Maastrichtian and Danian. They occur in chalks, including the grey Maastrichtian chalk of Stevns Klint where their skeletons are carbon stained and rich in iridium (Hansen *et al.* 1987), and in bryozoan limestones that often accumulated as mounds on the sea-bed (Thomsen 1976). More than 500 species are present (Håkansson & Thomsen 1979), but nothing has yet been published on species ranges across the K-T boundary.

Håkansson & Thomsen (1979) have summarized unpublished data from the Nye Kløv section. These authors found species diversity to be high in the white chalk at the top of the Maastrichtian (where *c.* 70 cheilostome species were found), dropping to four species in the basal Danian marl, and recovering to a peak of more than 40 species in a bryozoan limestone approximately 6 m above the K-T boundary before declining again in the overlying Danian pelagic chalk. Of 115 cheilostome species, only 11 are found in both the Maastrichtian and Danian parts of the sequence at Nye Kløv. However, this very low survivorship ratio (9.6%) is a local

feature because a number of the Maastrichtian species reappear in the Danian elsewhere in the basin. The four species from the basal Danian marl at Nye Kløv form a specialized community of rooted and free-living colonies very different from the faunas above and below this unit (see also Håkansson *et al.* 1996).

Within Denmark there is a strong facies-related difference between Maastrichtian and Danian bryozoan faunas (Håkansson & Thomsen 1979). Whereas pelagic chalks contain high diversity faunas in the Maastrichtian, bryozoans are almost lacking in Danian chalks. Bryozoan limestones have similar diversities in the Maastrichtian and Danian, but cheilostomes dominate in biomass in the Maastrichtian and cyclostomes in the Danian. Selective extinction of pelagic chalk species and of cheilostomes is implied by these data. The low K-T extinction rate of cyclostomes is supported by data in Brood's (1972) monograph of Scandinavian cyclostome species which shows a much greater extinction across the Campanian-Maastrichtian boundary (23 of 51 species) than across the Maastrichtian-Danian boundary (2 of 56 species).

The relative fates of cheilostomes and cyclostomes can be compared on a coarser scale by looking at the compositions of Maastrichtian and Palaeocene bryozoan assemblages worldwide. Taylor & Larwood (1988, fig. 5.7) showed that the K-T event did little to disturb the long-term temporal trend in the proportion of these two groups, and a more complete database analysed by Lidgard *et al.* (1993) revealed no significant differences between within-assemblage percentages of Maastrichtian and Palaeocene cheilostomes.

Tentative global genus and family data are available at stage-level for the Cretaceous and Palaeocene. On the basis of his extensive taxonomic experience, Ehrhard Voigt recognized the extinction of 38 cheilostome genera and 32 cyclostome genera during the Maastrichtian (reported in Taylor & Larwood 1988). Viskova (1994) compiled data on Late Cretaceous and Palaeocene bryozoan genera, finding that the Maastrichtian contained high diversities of cyclostomes (178 genera) and of cheilostomes (172 genera), but that the generic diversity of both groups declined equally and by more than a half by the upper Palaeocene. Therefore, the selective extinction of cheilostomes mentioned above is not apparent in Viskova's analysis based on her global generic database. At a higher taxonomic level still, the diversity of cyclostome and cheilostome families shows no more than a slight fall across the K-T boundary (Taylor & Larwood 1988; fig. 6 of Lidgard *et al.* 1993). The database of Taylor (1993) shows the presence of 20 cyclostome families in the Maastrichtian of which 2 (10%) became extinct during or at the end of the stage, and 28 cheilostome families with 4 (14%) extinctions.

Gallagher (1991) regarded the greater abundance of bryozoans in Palaeocene compared to Maastrichtian strata of the Atlantic Coastal Plain (USA) as a function of the differential survival of the mostly non-planktotrophic bryozoans relative to planktotrophic molluscs. It would be interesting to see whether there is any evidence for selective extinction of planktotrophs within the bryozoans, but this may be difficult because of the very small numbers of planktotrophic species that existed in the Late Cretaceous.

Much more research needs to be done on the rich Maastrichtian and Danian bryozoan faunas of Denmark to establish or refute the existence of a significant and geologically instantaneous K-T extinction, and to seek evidence for selectivity related to biological traits, clade membership and habitat distribution. The few data that are available suggest

that cheilostomes were more strongly affected than cyclostomes, and pelagic chalk species more than bryozoan limestone species. Ecological recovery, at least in the Danish area, appears to have been rapid in geological terms, judging by the presence of abundant and diverse bryozoan faunas in the lower Danian type area. Whatever the short-term effects of any K-T mass extinction may have been, with no more than 13% of families becoming extinct there seems to have been little effect on the long-term pattern of bryozoan evolution, at least not when compared with the profound extinctions of the Permian-Triassic.

### *Brachiopods*

The work of Surlyk & Johansen (1984) and Johansen (1987) gives a clear and indisputable indication of a sudden diminution in brachiopod species at the K-T boundary in Denmark. Johansen's analysis (1987) of the brachiopod fauna in the lowest 0.5 m of the basal Danian Fish Clay at Nye Kløv dealt with a large collection of minute and immature specimens, most of which she concluded had been derived from the upper Maastrichtian chalk. Thirty-five species were named, of which six were said to be restricted to the Fish Clay, six were common in the Maastrichtian and not present in lower Danian strata, and the remainder were claimed to be new to the Danian. The weakness in this analysis lies in the identification of established taxa from a collection of immature specimens. Many brachiopod genera and species assume different morphological shapes during their ontogenetic development prior to emerging as mature specimens. This applies particularly to species of *Terebratulina*, *Gisilina* and *Rugia* that form a substantial part of the fauna examined by Johansen (1987).

Surlyk & Johansen (1984) believed the sudden extinction of brachiopod species at the K-T boundary to coincide with an equally sudden extinction of coccoliths and planktonic foraminifera, and suggested a common cause for all three events. However, restudy of the Nye Kløv planktonic foraminiferal fauna has shown that this succession is characterized by very few extinctions at or near the boundary horizon (Schmitz *et al.* 1992; Keller *et al.* 1993). Furthermore, it is not uncommon to find a paucity of brachiopod species within clay facies. An obvious analogy to the basal Danian Fish Clay is that of the Plenus Marls in Britain. This facies supports very few brachiopod species, but is followed by a chalky facies of early Turonian age that supports a diverse brachiopod fauna related both generically and specifically to lower and upper Cenomanian forms. These results and observations suggest that the interpretations of Surlyk & Johansen (1984) and Johansen (1987) may need to be revised.

Although global temperatures were rising at the end of the Cretaceous (Schmitz *et al.* 1992; Keller *et al.* 1993), a variety of data suggest that a short-term cooling pulse occurred just before the K-T boundary. This was followed by a warm interval where temperatures returned to pre-event ranges. Bearing in mind the geographic variation characteristic of Cretaceous brachiopod faunas and the time factor between the late Maastrichtian and early Danian, it is not surprising that slight morphological changes may have inspired new taxa. Examples of this taxonomic practice in Danish faunas have been recorded by Posselt (1894), Nielsen (1909, 1914) and others. Such taxonomic splitting has tended to obscure the direct relationship that certainly exists between faunas from other European localities of late Maastrichtian and Danian age (e.g. The Netherlands, Belgium, France, Poland, Russia).

Far more species than have been described by Danish authors escaped the K-T event and regained their diversity in the Danian, thus exemplifying the extraordinary ability of this group to adapt and survive.

### *Cephalopods*

The Ammonoidea almost became extinct on several occasions during their long evolutionary history (House 1993). Each time, a progressive decline in diversity ceased just short of extinction. In this sense, the only difference characterizing the K-T event is that the ammonoids finally failed to pull through. The terminal decline in ammonoid diversity began at least 30 million years before their final extinction. From a Cretaceous peak of 31 families in the Albian there was a progressive decrease to 14 families in the Campanian and only 12 in the Maastrichtian, although at the generic level this overall decline was interrupted by a marked increase in numbers during the Campanian (Wright 1986). The decline was also characterized by an increasing patchiness in the areal distribution of the faunas. No new families appeared during the last 20 million years of the Cretaceous. On the other hand, some of the longest-living ammonoid families existed almost to the end of the Maastrichtian.

The best documented late Maastrichtian ammonoids occur in Europe. Kennedy (1993) reviewed faunas from Denmark, Poland, Austria, the Cotentin Peninsula (France) and the Bay of Biscay. Some 14 or 15 ammonite species were present in these areas during latest Maastrichtian time. These faunas show considerable diversity, falling into 12 different genera that represent all four Cretaceous suborders: Phylloceratina, Lytoceratina, Ancyloceratina and Ammonitina. Several species are very long-ranging. However, the Stevns Klint (Denmark), Zumaya (Bay of Biscay) and Sopelana (Bay of Biscay) sections are all chronostratigraphically incomplete, lacking strata that represent at least 50 000–100 000 years in the earliest Danian and an undetermined interval in the Maastrichtian (MacLeod & Keller 1991; Ward & Kennedy 1993).

Near Bjala, in eastern Bulgaria, about 45 m of upper Maastrichtian strata are exposed beneath the Danian (Marin & Stoykova 1994). Here the faunas are very similar to those of other European sections, with 13 genera and 22 species representing all four suborders. There is a gradual decrease in diversity up this sequence and the last (indeterminate) specimens occur 40 cm below the K-T boundary. Further east, at Tetricaro in southern Georgia, the Maastrichtian has yielded 16 species belonging to 9 different genera (Adamia *et al.* 1993). Exact stratigraphical ranges of these Georgian species are not specified.

One of the most interesting upper Maastrichtian sequences outside Europe is that of Seymour Island, Antarctica. In a thick sequence, Macellari (1986) recorded nine species terminating in the top 100 m of his Unit 9. The top of this unit is now known to lie about 9.5 m below an Ir anomaly that is thought to mark the local K-T boundary. Subsequent investigations (Elliot *et al.* 1994) have extended the last appearance datum of some of these species upwards to a level only 2 m below the Ir anomaly. This Antarctic succession has not been collected as intensely as some of the European sections and it remains uncertain how gradual the extinctions were (Marshall 1995; see also Discussion below). However, these data do indicate that high latitude faunas may exhibit an

uppermost Maastrichtian extinction pattern that is similar to that recorded from lower latitudes.

Among the Coleoidea, the Belemnitida are by far the most abundant and familiar Mesozoic representatives. They too declined throughout much of the Late Cretaceous to become extinct near the end of the Maastrichtian (with the exception of *Bayanoteuthis* which Doyle *et al.* 1994 provisionally excluded from the Belemnitida). As they declined, they became restricted to high latitudes in the southern and northern hemispheres. Southern forms disappeared quite early in the Maastrichtian, and the last remaining family (the Belemnitellidae) became limited to northern Europe alone, surviving to near the end of the Maastrichtian.

The Nautiloidea appear to be a much simpler cephalopod group, much overshadowed by the ammonoids and belemnites through the Mesozoic. Yet, they continued largely unchanged across the K-T boundary. Kennedy (1993) pointed out that nautiloids may have had a different reproductive strategy, producing few, large eggs with a large yolk and embryo. In contrast, ammonites apparently produced numerous small eggs. This distinction may have played a role in survival of the nautiloid clade, especially if the end-Cretaceous event was associated with a reduction in phytoplankton abundance.

### *Gastropods and bivalves*

Inoceramid and rudist bivalves, together with nerineid and acteonellid gastropods, were important components of many Upper Cretaceous benthic faunas. Although the extinction of these groups has traditionally been associated with the K-T boundary (see Alvarez *et al.* 1980), it has been claimed that they became extinct by the middle Maastrichtian (Kauffman 1984; Johnson & Kauffman 1996). Inoceramid prisms are known to occur in the upper Maastrichtian (Ward *et al.* 1991), but these occurrences do not reach the K-T boundary. Polar extinction of inoceramids has been recognized by Crame (pers. comm.) before the Maastrichtian, but movement into shallower, Tethyan habitats is shown by this family. In Arabia, several inoceramid species are associated with rudists and acteonellids (Smith *et al.* 1995) in the upper Maastrichtian, but these are of early late Maastrichtian age and occur below an unconformity and deep water sediments with no macrobenthos preserved. Upper Maastrichtian inoceramids also occur in Madagascar (W. J. Kennedy pers. comm.) and in Cotentin, North France, but, apart from *Tenuipteria*, not at Maastricht. This rather strange pattern of late Maastrichtian occurrence might be consistent with global cooling and increased oceanic temperature stratification. The pattern of local rudist disappearance has been related to loss of habitat before the K-T boundary (Swinburne 1990).

Extinctions are apparent in the Pectinacea and Ostreacea. The pectinid family Neitheinae is represented by two species in the lower Maastrichtian of the Middle East, and at least one of these continues to be common in the upper Maastrichtian of Arabia and at Maastricht and Cotentin (North West Europe). No member of this subfamily has been found in post-Cretaceous rocks. A major group of ribbed Mesozoic oysters (the Palaeolophidae) and the majority of genera of the Exogyrinae do not seem to have survived beyond the late Maastrichtian (Malchus 1990).

The Trigoniidae are widespread in the Maastrichtian but usually limited to one species in any assemblage. They seem to have survived into the Tertiary only in Australasia.

A profound change also took place in the solenacean bivalves. In addition to Cretaceous representatives of the Solenidae and the Pharidae, elongate, near vertical burrowing shells belonging to the Quenstedtiidae and the Veneridae have not been reported from Tertiary rocks.

The gastropods as a whole (and the carnivorous forms in particular) were undergoing a considerable increase in diversity through the later Cretaceous and did not show any reversal of this pattern through the K-T boundary event at the taxonomic level of species within families (Taylor *et al.* 1980). Some gastropods, however, did not survive from the Mesozoic into the Tertiary.

The archaeogastropods certainly underwent considerable redistribution at the end of the Cretaceous but their classification is difficult. It is possible that some Late Cretaceous taxa among the Trochoidea, superficially resembling the Palaeozoic family Euomphalidae but with nacreo-prismatic aragonite shell structures, are related to the Pseudophoroidea. If so, this group includes long-term K-T boundary survivors. On the other hand, they may not belong to the Pseudophoroidea, in which case the group may not have survived into the Tertiary. It is also uncertain whether the essentially Mesozoic family Amberleyidae survived the K-T event, though it is possible that some Recent deep water trochids are their descendants.

The Nerineoidea may also be opisthobranchs. They have no authentic record in the Old World above the upper Campanian. (Note: records from the Maastrichtian of Baluchistan may be attributed to the Turritellidae or Campanilidae, see Noetling 1897.) Sohl (1987) discussed their rapid pre-end Cretaceous decline, but also mentioned abundant lenticular rock masses, largely formed of the shells of single nerineid species, in the Maastrichtian of Puerto Rico. Consequently, it appears that the Cretaceous nerineid extinction had a pronounced geographical as well as temporal element.

Among the opisthobranchs, the acteonellids persist in some numbers into the upper Maastrichtian, but have never been recorded from younger rocks. The family Pseudomelaniidae (=Trajanellidae not Pseudomelaniidae auct.) also does not survive into the Tertiary but in addition is very rare in the uppermost Cretaceous, and may not have survived up to the boundary.

Of approximately 100 gastropod families known to occur in the Late Cretaceous, only one, the Acteonellidae, is known to have become extinct during the late Maastrichtian. Five other families and some undefined groups of trochids reached the Maastrichtian, but are not known from the upper Maastrichtian. Eighty-one bivalve families are recognized in the later Cretaceous. Of these, 10 do not extend above the Maastrichtian, but only five of these (plus one subfamily) are known with certainty from the upper Maastrichtian. There is presently no evidence to indicate that the extinction of any of these molluscan families occurred at the K-T boundary, although approximately 3% did become extinct during the late Maastrichtian.

Jablonski & Raup (1995) have recently published an analysis of selectivity in the end-Cretaceous marine bivalve extinctions in which they claim a 70-80% reduction in diversity at the species level and a 50% reduction at the genus level coincident with the K-T boundary. However their analysis does not subdivide the latest Maastrichtian and, in their own words (p. 389), 'our results apply to extinction at the K-T boundary event only to the extent that genus-level bivalve extinctions were concentrated at the end of the Maastrichtian stage'. In the absence of detailed collections of bivalve faunas from

uppermost Maastrichtian strata, the statements made herein with respect to the magnitude and timing of the K-T bivalve and gastropod turnover are consistent with Jablonski & Raup's (1995) results.

### *Echinoderms*

Of the five echinoderm classes, holothurians have by far the poorest fossil record, being based almost exclusively on their isolated microscopic body-wall spiculation. The Late Cretaceous record of holothurian spicules is entirely derived from mid-latitude chalks and clays. Gilliland (1990, 1992) distinguished 22 distinct Late Cretaceous spicule morphotypes, all of which extend into the Tertiary. An additional 14 spicule morphologies found in extant holothurians are known from pre-Late Cretaceous deposits and must also presumably have survived the transition. All five orders of holothurians and all 13 of the families known to have existed by the Late Cretaceous passed into the Tertiary. Indeed, at this coarse level of analysis, Gilliland found that no distinctive spicule morphologies were lost at the K-T boundary.

Almost as little is known about the fate of Late Cretaceous asteroids and ophiuroids, because of the rarity of articulated specimens and the lack of attention given to isolated ossicles. Our entire knowledge comes from the work of Rasmussen (1950, 1972) and Gale (1986, 1987: asteroids only) who documented Maastrichtian and Palaeocene faunas of Denmark and northern Europe, working largely from isolated ossicles. Although changes at species level occurred, all five upper Maastrichtian asteroid genera and four ophiuroid genera continued into the Danian in Denmark. An analysis of asteroid and ophiuroid taxa across the K-T boundary in the type Maastrichtian area is in progress (Jagt, personal communication).

The K-T crinoid fauna is now reasonably well-known from north-western Europe, thanks to the work of Rasmussen (1961, 1972) and Jagt (1995). Rasmussen (1961) observed that 13 of the 15 Maastrichtian benthic genera were also known from Danian deposits, and that the major decline in crinoid diversity occurred after the Danian, when groups such as bourgueticrinids, holopodinids and isocrinids largely disappeared from shelf environments (except in high southern latitudes: Stillwell *et al.* 1994). Representatives of these groups survive today only in deep-sea environments. Jagt (1995) found a major drop in diversity of crinoids at the end of the Maastrichtian, with the diverse shallow-water comatulid-dominated fauna of the latest Maastrichtian being replaced by a lower diversity bourgueticrinid-dominated fauna in the Danian. However, since most of the comatulid genera are known to survive in other areas such as the Danian of Denmark, this drop in diversity must to a large extent represent a local sampling problem associated with a change of facies.

Two clades survived to the end of the Maastrichtian and then disappeared from the fossil record, the saccocoids and the microscopic roveacrinids (Jagt 1995). Roveacrinids are unique amongst crinoids in being obligate planktotrophs and saccocoids have also been interpreted as planktotrophs. Together with the comatulids, these constitute about 20% extinction at the generic level.

Of all echinoderm classes echinoids have by far the best fossil record, yet this group has been surprisingly neglected in K-T boundary analyses. In his pioneering study, Kier (1974) found a substantial drop in the numbers of echinoids described

from the Palaeocene compared with the upper Cretaceous. He identified only 108 Palaeocene species as opposed to 1137 Senonian species, based on the Lambert & Thiéry's (1909-1925) compilation. Roman (1984) subsequently estimated that this change represented more than a five-fold decrease in the numbers of species, though how much of this may simply be accounted for by sampling biases was not considered.

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, all genera 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. Stokes (1979) analysed changes in spatangoids and concluded that the K-T boundary event had little impact on this group. He found that there were more profound changes in generic composition at the Campanian-Maastrichtian and Palaeocene-Eocene boundaries than at the end of the Maastrichtian. A detailed cladistic analysis of the Maastrichtian and Paleocene species of *Cyclaster* and related taxa (Jeffery in press *a*) shows that this group of spatangoids was unaffected by the K-T boundary event.

Van der Ham *et al.* (1987) recently revised the echinoid fauna from the Maastrichtian and Danian of the Maastricht district. Their table summarizing stratigraphical distributions implies that, at a generic level, about 35% of late Maastrichtian taxa became extinct. Those disappearing are, in the main, representatives of Tethyan clades that appear in the uppermost units as a broad and shallow phytal platform began to develop in the region. Only one fossiliferous horizon with Danian fossils is known from this region (Van der Ham 1988) and this is in chalk facies. This 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 facies change. A similar major faunal and facies change has been noted across the K-T boundary at Kazakhstan (Jeffery in press *b*), with again extinction at a generic level of around 33%.

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 these data were used to construct patterns of survivorship and extinction by Shimanskii & Solovyev (1982) and Roman (1984). Roman found that the K-T boundary coincided with a major extinction in echinoids, with 83 out of 127 genera (70%) supposedly present for the last time in the Maastrichtian. However, a more recent phylogenetically based analysis of world-wide data has found extinction levels of no more than about 35% for clades at generic level (Jeffery & Smith in press), and has shown earlier estimates to have been grossly inflated because of incorrect stratigraphical ranges and inconsistent taxonomic assignment. Furthermore, they found a clear systematic bias in the taxa most heavily affected by extinction, with irregular echinoids more strongly affected than regular echinoids.

Three groups were particularly badly hit by extinction; stomopneustid regular echinoids and cassiduloid and holasteroid irregular echinoids. Highest extinction rates are found amongst shallow-water carbonate-platform faunas, but a few groups in other environments were also strongly affected. For example, the specialist deposit-feeding echinoid clade

composed of the holasteroid *Stegaster* and its relatives, found in upper continental slope and deep-water basin clastic facies of mid-latitudes, disappeared at the K–T boundary. Echinoderms were clearly affected by changes at the K–T boundary, but the dearth of phylogenetically standardized taxonomic studies, combined with sampling biases and facies changes that occurred at this time, greatly complicate any direct interpretation of the fossil record.

Of the five classes, holothurians show no evidence of extinction at a fairly coarse level (i.e. disappearance of characteristic spicule morphologies, roughly equal to taxa at the family level). Asteroids and ophiuroids are hardly affected at the generic level, but this is based almost entirely on the fossil record in mid-latitude chalks: nothing whatsoever is known about low-latitude, shallow carbonate platform faunas. The same is true for crinoids, except that the two planktotrophic clades, roveacrinids and saccocomids, extend into the top zone of the Maastrichtian and then become extinct. Echinoids overall have extinction levels of around 35% of clades at the generic level, but show a strong taxonomic and geographic bias (Jeffery & Smith in press). Taxa such as cassiduloids that had their greatest diversity in low-latitude shallow-water carbonate platform environments, were most severely reduced in diversity at the end of the Cretaceous, whereas mid-latitude deeper-water chalk-facies faunas were much less affected, displaying much higher levels of extinction at the end of the Danian than at the end of the Maastrichtian. This is reflected in a latitudinal bias seen in the extinction of echinoids with mid to high latitude faunas displaying lower extinction levels than low-latitude faunas. Furthermore, the marked reduction in diversity of crinoids at the end of the Danian mirrors the pattern seen in echinoids from mid-latitude chalks.

The emerging pattern points to habitat loss, specifically the drowning of carbonate platforms, as playing a major role in restructuring the echinoderm fauna at the end of the Cretaceous. Major transgressions have previously been shown to be strongly correlated with periods of significant change in the composition of Jurassic echinoid faunas (Thierry & Neraudeau 1994). However, clearly not all extinctions can be attributed to this cause. Extinctions of the planktotrophic crinoid clades as well as of the specialist deposit-feeding deeper-water holasterid echinoids in middle latitudes, show that a multiplicity of factors must have been involved in determining K–T echinoderm extinction and survivorship.

## Vertebrate Macrofauna

### *Fish*

The fossil record of jawed fishes, which stretches back some 430 million years, is rich and varied and provides fossils from a wide range of sediment types. Classification of many groups of fishes is also more refined than that of most other animal groups. This means that patterns of extinction/origination may be tied to phylogenies in order to provide some estimate of what is real extinction and what is artificial (see Discussion). On the other hand it must be acknowledged that the fossil fish record is very patchy and can be misleading to the extent that many of our observations may be locality dependent.

Information on family-level extinction in fishes can be obtained from Gardiner (1993), Capetta *et al.* (1993) and Patterson (1993). The modern fish world is dominated by cartilaginous fishes (846 species in 45 families) and teleost actinopterygians (ray-finned fishes) (23 637 species in 426

families). Other fish groups are represented by a handful of agnathans (lampreys), non-teleostean actinopterygians (bichirs, sturgeons, garpike and bowfin), and sarcopterygians (coelacanth and lungfishes) (135 species, counts from Nelson 1994). Only cartilaginous fishes and teleosts contribute significantly to extinction patterns of fishes at the K–T boundary.

For the cartilaginous fishes (sharks, rays and chimaeras), 35 families pass through the K–T boundary, seven became extinct within the Maastrichtian, and one originated in the Danian. The seven fatalities (Polyacrodontidae, Hybodontidae, Anacoracidae, Sclerorhynchidae, Rhomodontidae, Hypsobatidae and Parapalaeobatidae) all appear to be monophyletic and therefore are cases of real extinctions. Expressed another way, the K–T boundary was survived by 80% of cartilaginous fish families. The survival rate between the Campanian–Maastrichtian is 95% and that between the Danian–Thanetian is 94%. Therefore there is a reduced survival rate at the K–T boundary, but it may be questioned whether this reduction is significantly acute to implicate a catastrophic mechanism.

Capetta (1987) has compiled the most comprehensive data base for elasmobranchs (sharks and rays) by documenting generic occurrences throughout the Cretaceous and the Tertiary. His counts show a significant disappearance of genera within the Maastrichtian: 23/53 (or 43.4%) became extinct and this compares with 26.3% disappearance within the Campanian and 8.1% in the Danian. However, while the extinction rate is high, so is the origination rate: in the Maastrichtian 22.6% are first occurrences (comparative figures for the Campanian and Danian are 21.4% and 18.9% respectively). It therefore appears that the Maastrichtian was a time of high generic turnover and not only a period of high extinction. One fact that needs to be checked is how many of the Maastrichtian genera which disappeared are monophyletic and represent real extinctions and how many are paraphyletic, representing parts of species lineages which crossed the K–T boundary and are therefore not evidence of extinction (Smith & Patterson 1988).

For teleost fishes the K–T record consists of 43 families which pass through the K–T boundary, four became extinct within the Maastrichtian and nine originated within the Danian. The four extinctions were probably real events because they involved monophyletic families with a total of eight genera and 13 species: Saurodontidae, Ichthyotringidae, Cimolichthyidae and Dercetidae (taken here to include *Stratodus*). Therefore, about 10% of teleost fish families became extinct and 90% survived. Comparing this with stages either side of the K–T boundary, there is an 81% survival from the Campanian to the Maastrichtian, and an 85% survival from the Danian to the Thanetian. At this crude level of analysis there is no reason to believe that a K–T elasmobranch mass extinction took place.

The teleost record shows clearly the effects of Lagerstätten as mentioned by Patterson (1993) and Patterson & Smith (1989). There are at least two peaks of teleost diversity; one in the Campanian and another in the Eocene. The first is due to a diverse fauna at Sedenhorst, Westphalia. The second is due to the occurrence of the famous fish-bearing deposits of Monte Bolca, Italy and the London Clay of the Anglo-Paris Basin. This is set against the relative paucity of Palaeocene and upper Eocene fish localities.

### *Amphibians*

There is no evidence for amphibian extinctions at the K–T boundary and tangible evidence of lineages passing through

the event unaffected. The latest known temnospondyl amphibian is an unnamed chigutisaurid from the Aptian-Albian of Victoria, Australia (Warren *et al.* 1991). Its only significance to this discussion lies in the fact that there are no good Australian continental vertebrate assemblages from the Cenomanian to the Eocene. Thus, temnospondyls may have died out before, at, or after the K-T event.

The albanerpetontids are an enigmatic and specialized small amphibian family of two genera, initially assumed to be salamanders, but now considered to represent a distinct lineage (McGowan & Evans 1995). The family is known from the Maastrichtian to the upper Palaeocene of North America, from the Middle Jurassic to the Miocene of Europe, and from the Cretaceous of Asia (Milner 1993). There is no evidence of family or generic-level extinctions at or near the K-T boundary, the genus *Albanerpeton* bracketing the K-T boundary in both North America and Europe. All evidence suggests that this family survived unscathed in these two regions at least.

About 160 species of living caecilians (Gymnophiona) have been described from South America, Africa, the Seychelles, India and Southeast Asia. The first record is from the Lower Jurassic of Arizona. The only other fossils are vertebrae of modern type from the Upper Cretaceous of Sudan, and the Palaeocene of South America. There is therefore no direct fossil evidence of extinction or survival at the K-T boundary. Some immunologically based cladistic analyses (Case & Wake 1977) show congruence between dichotomies producing modern families and the pattern of Gondwana rifting in the areas where they occur. Mitochondrial DNA sequence data support the interpretation that much of modern diversity was established in the Mesozoic by vicariance during the break-up of Gondwana (Hedges *et al.* 1993). There is no evidence for a Palaeocene diversification such as might have followed a K-T mass extinction, with the survivors rediversifying.

About 350 species of living salamanders (Caudata) have been described from the northern continents, but with plethodontids extending into Central and South America and salamandrids into North Africa. There are ten families with living representatives and two extinct families, plus a scatter of disparate primitive genera with no family assignment from the Middle Jurassic to the Middle Cretaceous. Of these 12 families, five bracket the K-T boundary as fossils: Sirenidae (Campanian to Recent), Batrachosauroididae (Tithonian to Pliocene), Scapherpetontidae (Albian to Eocene), Amphiumidae (Maastrichtian to Recent) (Milner 1993) and Salamandridae (Maastrichtian to Recent) (Astibia *et al.* 1990). Four families have only post-K-T boundary records, but phylogenetic inference from cladogram structure (e.g. see fig. 5 of Larson & Dimmick 1993) imply that they either were present before the K-T event: Proteidae (Palaeocene to Recent) and Plethodontidae (Miocene to Recent); or that a stem-lineage shared with one other family was present: Cryptobranchidae (with Hynobiidae, Palaeocene to Recent) and Ambystomatidae (with Dicamptodontidae, Oligocene to Recent) (Milner 1993). Three families have no pre-Pliocene fossil records, but phylogenetic inferences from cladogram structure imply that they either were present before the K-T event (Rhyacotritonidae), or that a stem-lineage shared with one other family was present (Hynobiidae and Dicamptodontidae). There is no evidence among these groups for family-level extinctions.

The only high-resolution study of salamanders bracketing the K-T event is that of Archibald & Bryant (1990) on seven genera from Montana. These authors found that four genera passed from the Lancian (=Maastrichtian) to the Torrejonian

(=upper Danian) of Montana apparently unchanged (the sirenid *Habrosaurus dilatus*, the scapherpetontids *Lisserpeton bairdi* and *Scapherpeton tectum* and the batrachosauroidid *Opisthotriton kayi*), while one genus passed from the Lancian to the Puercan (=lower Danian) unchanged (the batrachosauroidid *Prodesmodon copei*). The remaining two genera did not cross the K-T boundary in Montana. However one, the scapherpetontid *Piceoerpeton* sp., was very rare in the Lancian, and is known elsewhere in North America to range into the Eocene. The other, the amphiumid *Proamphiuma cretacea*, makes its last appearance in the Judithian (=Campanian) of Montana. As a genus, *Proamphiuma* may have become extinct at or before the K-T boundary, but there is no morphological evidence to preclude it being the lineal ancestor of the Palaeocene–Recent amphiumid genus *Amphiuma*, in which case this would be a pseudoextinction. Thus, of seven Lancian genera of salamanders, six survived the K-T event unchanged and one either became extinct or underwent morphological transformation.

Over 3500 species of frogs (Anura) have been described from all continents except Greenland and Antarctica. There are 21 families with living representatives and two extinct families, plus a few disparate primitive forms from the early Mesozoic. The frog fossil record is geographically very uneven: fair for North America, Europe and South America, but very poor from other continents. Of these 23 families, seven bracket the K-T boundary as fossils: Leiopelmatidae (Tithonian to Recent); Discoglossidae (Bathonian to Recent); Pipidae (Hauterivian to Recent); Palaeobatrachidae (Valanginian to Pliocene); Rhynophrynidae (Tithonian (Henrici pers. comm.) to Recent); Pelobatidae (Tithonian to Recent); and Leptodactylidae (Santonian to Recent) (Milner 1993). Seven families have a post-K-T fossil record only: Pelodytidae, Myobatrachidae, Bufonidae, Hylidae, Ranidae, Rhacophoridae and Microhylidae; and eight have no record at all: Hyperoliidae, Heleophrynidae, Sooglossidae, Brachycephalidae, Rhinodermatidae, Pseudidae, Centrolenidae and Dendrobatidae (Milner 1993). Only one family might represent a Cretaceous extinction, namely the Gobiidae known from the Albian to Santonian of Mongolia and vicinity (Roček & Nessov 1993). However the latest gobiid record occurs well below of the K-T boundary and this family may only represent one genus upgraded to family status non-cladistically.

As with the salamanders, the only high-resolution study of frogs bracketing the K-T event is that of Archibald & Bryant (1990) on three genera from Montana. These authors found that the discoglossid *Scotiophryne pustulosa* passed from the Lancian to the Puercan of Montana apparently unchanged. The pelobatid genus *Eopelobates* sp. passed from the Lancian to the Torrejonian of Montana apparently unchanged, but this genus is currently something of a dump-genus, probably polyphyletic and hence of uncertain value. The third genus is the palaeobatrachid *Palaeobatrachus* sp. which makes its last appearance in Montana at the K-T boundary at the Bug Creek locality, but is known from the Torrejonian elsewhere. As with *Eopelobates* sp., the species unity of the various fragments is not established.

The inescapable conclusion from these data is that there is no evidence for family-level extinctions of amphibians at or near the K-T boundary, and, in terms of genera, no unambiguous evidence for complete extinction of any Lancian amphibian lineage in North America. The only possible exception (*Proamphiuma*) is equally explicable as a pseudo-extinction.

## Lepidosauria

All three living reptile groups, the Crocodylia, the Chelonia, and the Lepidosauria, are survivors from the Cretaceous. Only one, Lepidosauria, represents animals that are predominantly terrestrial.

Living lepidosaurs are divided between the Rhynchocephalia and Squamata. The Rhynchocephalia were a successful and geographically widespread group in the early Mesozoic, but were already in decline by the mid-Cretaceous. They are represented today by a single genus, the New Zealand *Sphenodon*. The Squamata (lizards, snakes and amphisbaenians) radiated in the Jurassic, continued successfully into the Cretaceous, and are the largest and most diverse group of living reptiles, with more than 6000 extant species.

Allowing for the metataxon status of Iguanidae and Agamidae (see Discussion for an explanation of metataxa), all living families of lizards either had known representatives in the Late Cretaceous or their presence may be assumed by extrapolation from the phylogenetic tree (e.g. by the existence of sister taxa). All living families therefore represent definite or inferred survivors from the Cretaceous. Of the groups occurring in the upper Maastrichtian, only two are unknown from the lower Tertiary—the mosasaurs and the polyglyphanodont teiids.

Mosasaurs were large (up to 15 m) marine predators of the Late Cretaceous (Turonian–Maastrichtian). In North America, they are known to have survived into the late Maastrichtian (Lower Hornerstown Formation, New Jersey; Moreno Formation, California; Gordon Bell pers. comm. 1995, contra Sullivan 1987), with representatives of both mosasaurine and pliolatycarpine lineages. Their decline during the late Maastrichtian would not be surprising. Mosasaurs were amongst the top predators of the Cretaceous marine ecosystem and anything that perturbed that ecosystem would have affected them.

A smaller Late Cretaceous group (North America, China, Mongolia; Estes 1983), the polyglyphanodont teiids, also failed to survive the K–T event, but these durophagous lizards were probably already in decline. They reached their peak diversity in the Campanian, and continued into the early Maastrichtian in North America (North Horn Formation, Utah; Estes 1983; Sullivan 1987). Only *Haptosphenus*, tentatively assigned to the polyglyphanodonts (Estes 1983), has been recorded from the upper Maastrichtian Hell Creek Formation of Montana.

For most of the latest Cretaceous, snake records are restricted to a number of primitive families (aniiliids, boids, madtsoiids and nigerophiids), all of which crossed the K–T boundary. Higher snakes (colubroids, Werner & Rage 1994) have recently been recorded from the middle Cretaceous (Albian–Cenomanian) of the Sudan, but apparently went through a major radiation in the Tertiary. Like snakes, the burrowing amphisbaenians are predominantly a Tertiary group although they are now known from the Campanian of China and Mongolia (Wu *et al.* 1993) and clearly crossed the K–T boundary.

Only one study (Archibald & Bryant 1990) has followed a complete lepidosaur assemblage through the K–T boundary interval (Lancian–Puercan) in one restricted area (northeastern Montana). Of 11 squamate species present in the Lancian study area, four (three lizards, one snake) survived into the Tertiary, although two more have been recorded from Tertiary localities outside the study area and two were already rare in the late Cretaceous. The only common Lancian lizards to be

lost completely were three teiid species. Bearing in mind the Late Cretaceous decline of the polyglyphanodonts, this may tell us more about teiid history than about the fate of squamates in general at the K–T boundary.

No known family of terrestrial squamates became extinct at the K–T boundary and, with the exception of teiids and the marine mosasaurs, the limited evidence available suggests that squamates suffered no major decline at this time. If there was a Late Cretaceous biotic crisis, squamates survived it, possibly because of their generally small size, variable metabolism, and ability to retire to favourable microhabitats. This said, the late Maastrichtian and early Palaeocene squamate record is still very limited. Squamates are preserved (and then recovered) only under a limited number of conditions, and the picture may change radically as the squamate fossil record improves.

## Archosauria

The clade Archosauria includes crocodylians, pterosaurs, dinosaurs and birds. Birds are now almost universally accepted as the sister group of maniraptorans, small advanced carnivorous dinosaurs from which they are descended.

Ten crocodile families are represented in the Maastrichtian. The last records of the Goniopholidae, Peirosauridae, Dolichochoampsidae and Paralligatoridae are in the Maastrichtian (Benton 1993). The Baurusuchidae may span the K–T boundary, based on a specimen of *Cynodontosuchus* from the El Molino Formation, Vila-Vila, Bolivia. The deposits in the Vila-Vila area have been correlated with the mammal-rich Tiupampa Beds, originally supposedly Maastrichtian in age, but dated in several more recent papers as early Paleocene (Gasparini *et al.* 1991).

Five families have both Maastrichtian and Tertiary representatives. The Thoracosauridae ranged from the Maastrichtian to the late Paleocene, and Trematochampsidae from the Maastrichtian to the mid Eocene. The last records of the Dyrosauridae are in the upper Eocene in Asia; one genus, *Hyposaurus*, spans the K–T boundary, occurring in the Upper Cretaceous in North and South America and the Palaeocene to Eocene in north and west Africa. The two remaining families, Alligatoridae and Crocodylidae, include living representatives; two alligatorines and the crocodylid (or possibly stem crocodylid) *Leidyosuchus sternbergi*, have been recorded from both the Lancian and Puercan in Montana (Archibald & Bryant 1990) and so crossed the K–T boundary at the species level. All the families discussed here are terrestrial–freshwater, except for the Dyrosauridae which are freshwater–marine. The group as a whole shows a 50% family survival rate across the K–T boundary. The only discernible trend apparent from this pattern is that no large crocodiles, such as the giant North American crocodylid *Deinosuchus*, survived.

The Azhdarchidae, which originated in the Berriasian, is the only pterosaur family recorded from the Maastrichtian. The azhdarchids include the last representatives of the pterodactyloid pterosaurs which attained their highest diversity in the mid-Cretaceous with ten families recorded (Wellnhofer 1991). All except the azhdarchids became extinct prior to the Maastrichtian. Two genera are known from upper Maastrichtian deposits; *Quetzalcoatlus* from the Javelina Formation in Texas and *Arambourgiania* from marine deposits in Jordan (Benton 1993). No Tertiary pterosaur remains are known and their extinction pattern was apparently a gradual decline through the Late Cretaceous.

**Table 1.** *Dinosaur distribution in the Maastrichtian*

Taxon	Maastrichtian geographic occurrence	Stratigraphic occurrence		Last recorded genus	
		Maastrichtian	Upper Maastrichtian	Europe*	North America†
<b>Saurichia</b>					
<b>Theropoda</b>					
Tyrannosauridae	NA	Present	Present		<i>Tyrannosaurus</i>
Ornithomimidae	As, NA	Present	Present		? <i>Ornithomimus</i>
Elmsauridae	As, NA	Present	Present		<i>Chirostenotes</i>
Oviraptoridae	As, NA	Present	—		
Dromaeosauridae	As, NA	Present	Present		cf. <i>Dromaeosaurus</i>
Troodontidae	As, NA	Present	Present		Troodon indet. (= <i>Paronychodon</i> )
Abelisauridae	SA	Present	—		
Deionochelidae	As	Present	—		
Noosauridae	SA	Present	—		
Therizinosauridae	As	Present	—		
Aublysodontidae	NA	Present	Present		
<b>Sauropoda</b>					
Camarasauridae	As	Present	—		
Diplocidae	As	Present	—		
Titanosauridae	As, Eu, In, NA, SA	Present	Present	<i>Magyosaurus</i>	
<b>Ornithischia</b>					
Nodosauridae	Eu, NA	Present	Present	<i>Struthiosaurus</i>	
Ankylosauridae	As, NA	Present	Present		<i>Ankylosaurus</i>
Hypsilophodontidae	Eu, NA	Present	Present		<i>Thescelosaurus</i>
Iguanodontia <i>incertae sedis</i>		Present	Present	<i>Rhabdodon</i>	
Hadrosauridae	As, Eu, NA	Present	Present	<i>Telmatosaurus</i>	<i>Edmontosaurus</i>
Pachycephalosauridae	As, NA	Present	Present		<i>Stygimoloch</i>
Protoceratopsidae	As, NA	Present	Present		<i>Pachycephalosaur</i>
Ceratopsidae	NA	Present	Present		<i>Triceratops</i>

\*Sîmpetru Formation, Hateg basin, Romania.

†Bug Creek interval, northeast Montana (may be earliest Palaeocene in age, see text).

NA, North America; As, Asia; SA, South America; Eu, Europe; In, India.

More has probably been written about the extinction of dinosaurs than of any other group of organisms. Families recorded from the Maastrichtian are listed in Table 1. In addition, there are indeterminate theropod footprints from Morocco (Weishampel 1990) and an euornithopod from Antarctica (Hooker *et al.* 1991); Maastrichtian dinosaurs are thus known from all continents except Australia. Late Maastrichtian records (Table 1) show little decline at family level except in Asia and South America, though this probably reflects the absence of relevant strata in those areas rather than positive evidence for a fall in diversity.

The western interior of North America is the only area where a continuous terrestrial sequence encompasses the K-T boundary, permitting documentation of changes in faunal diversity. Consequently, it has been the focus of several detailed studies. In the upper Campanian (Judithian), the dinosaur fauna is diverse, with 45 taxa determined to generic level in 13 families (Weishampel 1990) from the Judith River Formation of Alberta. In the upper Maastrichtian (Lancian) Hell Creek Formation in Montana, the corresponding figures are 24 genera in 12 families (Weishampel 1990). This decline in dinosaur diversity mirrors that shown by Sloan *et al.* (1986) based on older data, recording a decline from 30 genera in the Judithian (=middle Campanian) down to seven at the K-T boundary.

Archibald & Bryant's (1990) high resolution study of the non-marine fauna across the K-T boundary section in northeast Montana showed variable extinction rates for different vertebrate groups. Analysis of their raw data to allow for

factors such as palaeobiogeographical variation, disappearances that represent speciation events and rarity of taxa, produced an estimated 64% species survival rate (conversely, a 36% extinction rate) for the non-marine vertebrate fauna. The survival rate for non-avian dinosaurs was 0%. Twelve dinosaur genera (13 species) from the Bug Creek interval, overlying the Lancian at the top of the Hell Creek Formation, are the last recorded in the sequence (Table 1).

There is no consensus over the age of the Bug Creek interval. Its fauna contains taxa otherwise unknown after the Lancian (particularly dinosaurs) and others unknown before the Puercan (especially mammal taxa). Archibald & Bryant (1990) included the Bug Creek interval in the Puercan on the basis of the mammal faunas, thus dating it as earliest Palaeocene. Accepting this age, the presence of dinosaur remains in the Bug Creek interval can be explained in one of two ways; either they survived into the Paleocene, or they were reworked from the Hell Creek Formation. Archibald & Bryant (1990), in common with other studies, adopted the latter explanation on preservational and taphonomic grounds since there are no articulated dinosaur remains in the Bug Creek channel sediments. They interpreted their results in terms of geologically rapid change, but not a sudden catastrophic mass extinction at the K-T boundary.

A detailed field study of dinosaur diversity by Sheehan *et al.* (1991) claimed that no statistically meaningful decline was apparent through the Hell Creek Formation. These findings were claimed to support a sudden extinction event at the K-T boundary. Williams (1994) observed that the nature of the

analysis of Sheehan *et al.* (1991) might not detect a gradual decline at the top of the Hell Creek sequence. There remains, despite concentrated collecting, a barren zone of about 3 m below the K–T boundary, in which dinosaur bones and teeth are increasingly scarce. The highest unreworked bone comes from about 60 cm below the boundary clay—well below the iridium layer. Evidence from the Bug Creek channels and the highest few metres of the Hell Creek Formation is consistent with a decline in the dinosaur population, perhaps a steep and accelerating decline but not a sudden catastrophe (Williams 1994). Further, Hulbert & Archibald (1995) analysed the quantitative methodology used by Sheehan *et al.* (1991) to argue for a rapid end-Cretaceous dinosaur extinction event, and concluded that there was no statistical support for either a sudden or gradual decline in the number of dinosaur taxa at the close of the Cretaceous.

Diversity changes and extinction patterns in the western interior of the USA provide a test case for the demise of the dinosaurs. There are no means of determining if this was a local or global phenomenon due to lack of K–T terrestrial sequences elsewhere. An upper Maastrichtian non-marine fauna, including dinosaurs (Table 1), is known from the Sînpetru Formation (once regarded as Danian) in Romania (Grigorescu *et al.* 1994), but is overlain by middle to upper Miocene marine strata. Dinosaurs are certainly present in the uppermost Cretaceous of Asia; the highest occurrence known is a nest site from magnetochron 29R in south central China (Hansen 1990). This establishes a latest Maastrichtian age for the strata involved, but evidence of diversity and rate of decline is lacking. Dinosaur egg shell and protungulate mammal material from the Vilquechico Formation of Peru was dated as Paleocene by comparison with North American mammals (Kérourio & Sigé 1984), but more recent charophyte data and K–Ar dating of overlying volcanic tuffs suggest an early Maastrichtian age (Mourier *et al.* 1988).

In summary, non-avian dinosaurs apparently became extinct in the late Maastrichtian following a decline in diversity over several million years, and possibly an accelerated decline in the latest Maastrichtian, at least in North America. The last unreworked remains occur well below the iridium layer which marks the K–T boundary in North America, and the small amount of data from other continents indicate that no dinosaurs survived into the Palaeocene. However, there is no evidence for the timing and nature of non-avian dinosaur extinction in the rest of the world.

Recent discoveries have revolutionized the understanding of bird evolution in the Mesozoic and early Tertiary, although much of their fossil history is still missing. Two major groups of birds were coeval in the Late Cretaceous. The Enantiornithes were the dominant land bird group, and they coexisted with a separate lineage, the Ornithurae (including the Hesperornithiformes) and the Neornithes from which modern birds derive (Chiappe 1995). Enantiornithes did not survive beyond the Maastrichtian. Neither did several groups of ornithurines, but there is no positive evidence that these extinctions occurred at the K–T boundary. The toothed hesperornithiforms, in particular, have no unequivocal post-Campanian record. According to Feduccia (1995), birds appear to have suffered a bottleneck across the K–T boundary, a massive extinction from which only transitional shorebird morphotypes survived as the basis for a Tertiary bird radiation. However, fragments of several genera of Late Cretaceous birds can be assigned to four orders of living birds: Anseriformes, Gaviiformes, Procellariiformes and Charadriiformes.

The phylogenetic relations between these groups suggest that most, if not all modern bird orders must have differentiated before the end of the Cretaceous (Chiappe 1995, see also references therein), and therefore passed through the K–T boundary. These results are supported by modern bird 12s rDNA sequence studies (Cooper 1994).

Archosaurs fared badly within the Maastrichtian with the total extinction of pterosaurs, non-avian dinosaurs, and the enantiornithine birds, together with several ornithurine groups. The crocodiles are the only amphibious archosaur group and the only one in which a significant number of families passed through the boundary.

### Terrestrial plants

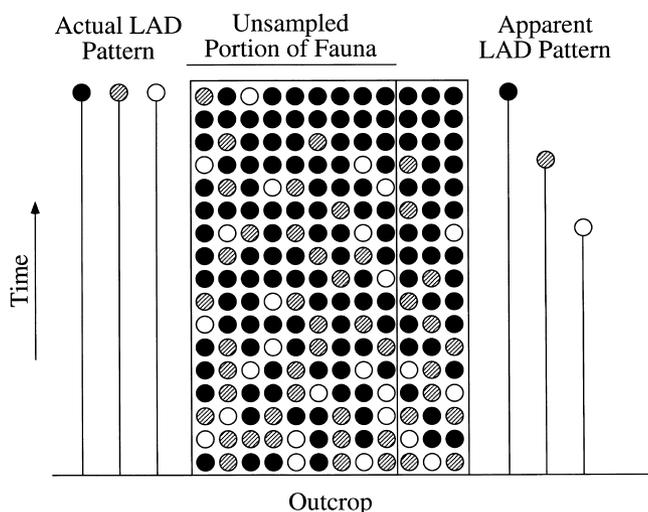
The record of megaflores and microfloras across the K–T boundary is best known from the western USA with additional microfloral data from Antarctica. Johnson & Hickey (1990) based their analysis of megaflores on 25 000 specimens from more than 200 localities in Montana, Wyoming, North Dakota and South Dakota. This summary shows that megaflores changes were taking place well before, at, and after the regional K–T boundary, as identified by Ir anomalies. Johnson & Hickey (1990) divided this turnover pattern into four different climatic zones that suggest progressive warming of the region.

In contrast to the megaflores record, the terrestrial microfloral record in the USA is typified by the abrupt disappearance of most Upper Cretaceous palynomorphs coincidental with the Ir anomaly, the existence of a very short-term fern abundance peak (the so-called 'fern spike') just above the Ir anomaly, and the progressive appearance of fully Danian palynomorph taxa (Nichols & Fleming 1990). (Note: plant megafossils are regarded as more accurate indicators of taxonomy, phylogenetic relationship, and species richness, whereas terrestrial palynomorphs are regarded as more accurate chronostratigraphical indicators of the presence of generalized higher taxonomic groups.) These palynomorph turnover patterns suggest that certain angiosperm taxa endemic to North America may have been severely effected by the K–T event, and that gymnosperms, ferns, other pteridophytes, and mosses were affected to a much lesser degree. In Canada, however, Sweet *et al.* (1990) have shown that palynomorph turnover patterns were more progressive, with disappearances occurring before, at, and after the K–T boundary. Moreover, these authors reported no fern spike in their sections, but rather angiosperm dominance extending from the Upper Cretaceous through the lowermost Danian. Sweet *et al.* (1990) concluded that morphologically complex palynomorphs were differentially susceptible to the K–T event, but offered no speculations as to what these patterns might reflect from functional or adaptive points of view.

In the high southern latitudes of New Zealand and Antarctica, the K–T megaflores and palynomorph record is very different from that of western North America, with no significant turnovers being recorded from the Seymour Island sections (Johnson & Greenwood 1993; Askin & Jacobson 1996).

### Discussion

New palaeoclimatological data from the entire Upper Cretaceous (e.g. Huber *et al.* 1995), and the upper Maastrichtian in



**Fig. 9.** Diagrammatic explanation of the Signor-Lipps effect. The apparent distribution of fossil last appearance datums (LADs) will always underestimate the true LAD distribution because the relative abundance of fossils varies within a section or core while the sample size usually remains constant or varies independently. Underlying factors responsible for intraspecific abundance fluctuations include a wide variety of biological, ecological, and diagenetic processes. As a result, it may be impossible to infer the correct pattern of either local or global last appearances from the observed biostratigraphical record. Note that recognition of the Signor-Lipps effect confers no ability to distinguish between alternative faunal turnover patterns.

particular (e.g. Keller *et al.* 1993; Barrera 1994; Barrera & Keller 1990, 1994), have shown that the latest Cretaceous was a time of sustained global temperature and marine productivity changes, of the type known to be correlated with major extinction events in other parts of the geological column. These data suggest that extinction mechanisms may have operated throughout the entire Upper Cretaceous rather than being concentrated within a very narrow time interval at its very end. The data reviewed above indicate that, aside from a few microfossil groups (e.g. calcareous nannoplankton, dinoflagellates, planktonic foraminifera), most clades experienced either long-term decline throughout the Upper Cretaceous (e.g. ostracodes, scleractinian corals, bryozoa, ammonite cephalopods, bivalves, echinoid echinoderms, archosaurs) or were relatively unaffected in terms of extinction levels by the K-T boundary event (e.g. diatoms, radiolaria, benthic foraminifera, brachiopods, gastropods, holothurian, asteroid, ophiuroid, and crinoid echinoderms, fish, amphibians, lepidosaurs, terrestrial plants). A few groups (e.g. benthic foraminifera) also exhibit changes in faunal composition across the highest Maastrichtian-lowest Danian interval.

It is uncertain whether increased levels of faunal and floral turnover in the uppermost Maastrichtian are sampling artefacts (e.g. a Signor-Lipps effect), or a response to environmental changes (e.g. sea-level fluctuations, increased rates of volcanism) that are known to have occurred during the latest Maastrichtian. The Signor-Lipps effect (Signor & Lipps 1982) arises from a number of causes, including interactions between sample size and relative abundance, differential susceptibility to diagenesis, and/or facies or palaeoecologically controlled distributions. These factors can result in the last observed appearance of a fossil taxon in a particular section or core not accurately reflecting its local or global last appearance datum

(Fig. 9). Thus, Signor & Lipps (1982, p. 291) concluded that gradual extinction patterns prior to a mass extinction do not necessarily eliminate catastrophic extinction hypotheses. However, uncertainty is implicit in the Signor-Lipps effect. This was recognized by Signor & Lipps (1982, p. 295) who cautioned 'Our arguments should not be interpreted as support for the impact hypothesis or any other theory invoking a catastrophe as the extinction mechanism. The evidence at hand for most environments is as compatible with a gradual extinction event as with a catastrophic one'.

Signor & Lipps' (1982) conclusion has been verified by Marshall (1995) who used stratigraphical confidence intervals to examine whether the observed progressive extinction patterns of Maastrichtian ammonites from Seymour Island were compatible with a catastrophic scenario. Marshall (1995, p. 731) concluded that while the 'pattern of [ammonite] disappearances is consistent with a sudden mass extinction at the Cretaceous-Tertiary boundary . . . computer simulation of the Seymour Island ammonite fossil record indicates a wide range of other extinction scenarios, including gradual extinctions ranging over as much as 20 m that are [also] consistent with the ammonite fossil record'. Marshall (1995) went on to observe that without saturation collecting it may be impossible to separate catastrophic from progressive extinction patterns based on the fossil record alone. Marshall's (1995) conclusions differ strongly from Ward's (1995a, b) claim that his study provided unambiguous evidence for catastrophic K-T faunal turnover among high-latitude invertebrate faunas.

While Marshall (1995) applied stratigraphical confidence limits to his study of potential Signor-Lipps effect bias, MacLeod (1996a, b) employed an array of different strategies to test for significant Signor-Lipps effect bias in planktonic foraminiferal data from El Kef (Tunisia), Agost (Spain), Brazos River (Texas), Nye Kløv (Denmark) and ODP Site 738 (Kerguelen Plateau). These investigations also attempted to identify the source of the bias (e.g. sample size, faunal composition, and palaeoecological factors). Although patterns of variation consistent with a Signor-Lipps effect were found in each succession, the magnitude of the effect was shown to be insufficient to account for the magnitude of the pre-boundary faunal turnover in three of the five sections/cores. It is also worth noting that the uppermost Maastrichtian changes in ecological dominance patterns observed in benthic foraminifera and bivalves suggest the presence of a period of latest Maastrichtian global environmental change. This result is consistent with the recognition of a stratigraphical interval, within which the K-T boundary is embedded, that is characterized by increased extinction intensity.

Attribution of seemingly anomalous occurrences of Cretaceous species in lower Danian strata to reworking and/or remobilization of sediments has also been used to justify catastrophic interpretations of what appear to be progressive faunal turnover patterns. Certainly reworking and remobilization of fossils do occur. However, in most cases it is exceedingly difficult to determine whether a particular specimen has been reworked and, if so, over what stratigraphical interval. The data presented above suggest that when K-T boundary successions are examined in detail, many characteristic Cretaceous species are found in lowermost Danian strata, often several metres above the boundary level. In some instances such species even comprise the bulk of the fauna (see Fig. 5; Pospichal 1995). Moreover, the simulations of Berger & Heath (1968) indicate that non-biotic vertical mixing of sediments in marine pelagic sediments can rarely account for specimen displacements of

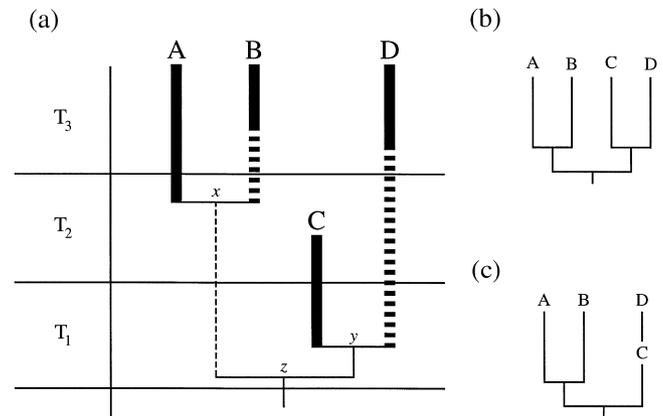
more than a few centimetres. Unless palaeontologists are to regard every unexpected occurrence of a species as a priori evidence for reworking throughout the stratigraphical column, the hypothesis of reworking must be verified by independent criteria. MacLeod (1994) reviewed the criteria that may be used to infer reworking in fossil faunas. MacLeod & Keller (1994) and MacLeod (1995a, b, c, 1996a, d) applied these tests to the K–T planktonic foraminiferal record.

Although the K–T records of most fossil groups have yet to be examined in detail for sampling problems and tested for reworking, by far the most serious factor complicating our interpretation of K–T extinction patterns is the current lack of adequate phylogenies at the species and higher taxonomic levels. Fortey (1983), remarking on the sudden extinction of many trilobite families at the end of the Cambrian and the sudden origination of many families in the Ordovician, pointed out that this phenomenon may be a taxonomic artefact. Many of the Cambrian families contain members more closely related to Ordovician trilobites than to other members of their own family. In other words, many Cambrian families are paraphyletic (see Fig. 3). These families did not become extinct because they were never real in the first place.

Use of phylogenetic relationships in extinction studies has been exemplified by Norell (1992), Archibald (1993) and Smith (1994). Consider the theoretical example illustrated in Figure 10, concerning four taxa (A–D) with observed stratigraphical ranges as given in solid heavy lines. The phylogenetic tree is shown to the right. This tree is constructed by identifying morphological characters uniquely shared by A and B, C and D, and A, B, C and D. The distribution of morphological characters implies that A and B shared a unique ancestor 'x', C and D shared a common ancestor 'y', while A, B, C, D shared a common ancestor 'z'. Inclusion of stratigraphical data imposes some time limits on the occurrence of these ancestors as well as the longevity of different lineages.

This phylogenetic tree implies that sister-groups must be of equal age. Thus, in Fig. 10, taxon B must have existed at least as long as taxon A; similarly, D must have existed as long as C; and A+B must have existed as long as C+D. Consequently the age of taxa B and D must, of necessity, be extended back as *range extensions* to match that of A and C respectively. Additionally there must have been an undetected lineage of species which occupied the time interval between A+B and C+D; this is referred to as a *ghost lineage* (Norell 1992). Of course, we have no idea of how many additional taxa may have occupied the time interval occupied by either the range extension or the ghost lineage, and much of palaeontological research is directed towards exorcising the ghost.

In this example it is assumed that taxa A–D are each monophyletic and can be recognized as such because each shows a unique character that serves as its morphological fingerprint. However, in palaeontological studies this is not always the case. Often there are taxa (species or genera) to which we give names without recognizing a unique attribute (e.g. stratigraphically or geographically recognized species). If one of these kinds of taxa should precede another taxon without overlapping in time, there remains the possibility that it is not monophyletic (it may be paraphyletic or a direct ancestor). For instance if taxon C had no recognizable fingerprint it may have been ancestral to or part of D (Fig. 10c). These kinds of palaeontological taxa have been called *metaphena* by Smith (1994) and *metataxa* by Archibald (1993). When counting extinctions these need to be left out of



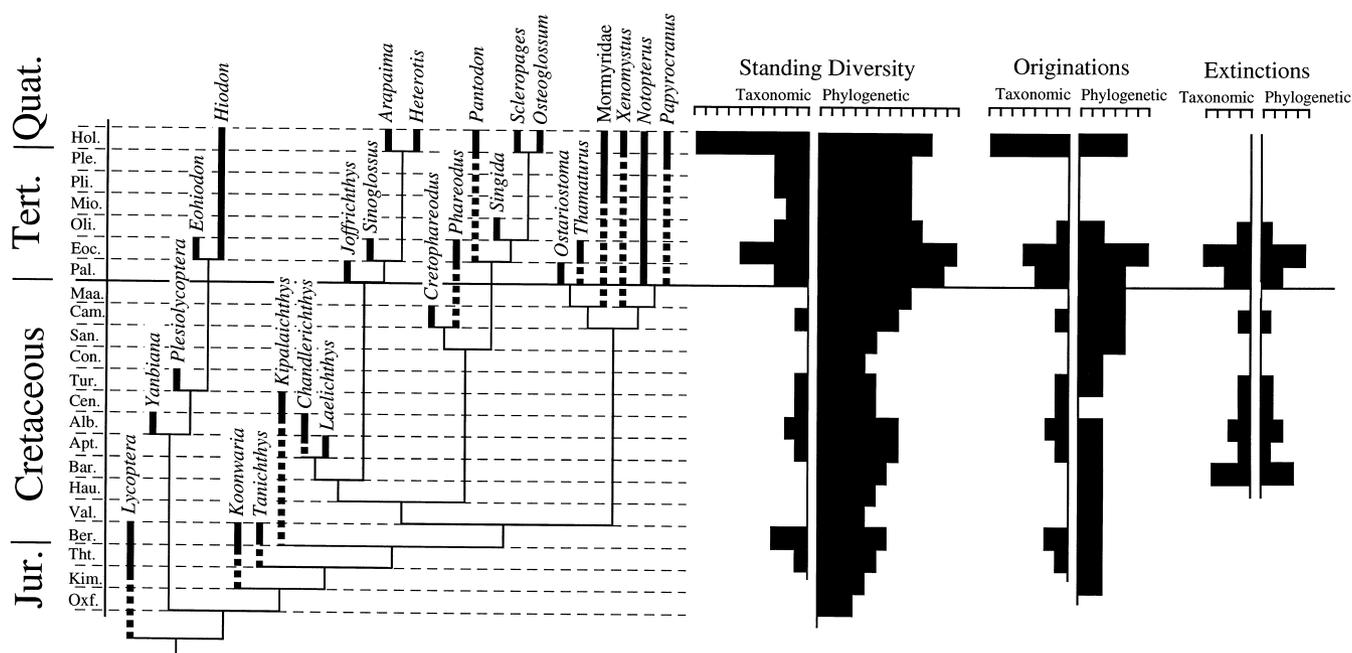
**Fig. 10.** Theoretical example illustrating the phenomena of range extensions (thick dashed lines) and ghost lineages (narrow dashed lines). Phylogeny at top right assumes all taxa are monophyletic. Phylogeny at bottom right assumes that taxon C is a metataxon and may be ancestral to D.

consideration because the reality of their extinction cannot be justified.

Phylogenetic considerations can give only a minimum idea of diversity. But the consideration of phylogeny can suggest patterns of extinction and origination which differ from those based on a taxonomic approach only. Smith (1994, fig. 7.1) worked through theoretical examples showing that phylogenetic considerations can lead to alternative estimations of diversity, times of origination, and times of extinction. For example, fishes of the Superorder Osteoglossomorpha, the most primitive group of living teleosts, have a fossil record extending down to the Upper Jurassic. All modern species are freshwater although there are marine fossil representatives. Relationships amongst osteoglossomorphs are quite well understood at both the family and generic level. The most recent generic phylogeny is that of Li (1994) and this is plotted in Fig. 11 against time. Like most fish records, species and genera are often only recognized from one time interval (and often one locality). Taking standing diversity through time, the taxonomic approach counts only fossil occurrences (allowing for Lazarus taxa, e.g. the fish genus *Hiodon* is not known from all intervening stages between the Eocene and the Recent). This leads to a pattern shown in the left side of the first column to the right where there is a burst of diversity in the Eocene. (Note: the Eocene burst in diversity for this group is not due to the Lagerstätten deposits mentioned above.)

The phylogenetically inferred pattern of standing diversity, extinctions, and originations is the more faithful record of the evolutionary history of the group. Consideration of the phylogeny includes the counting of ghost lineages and range extensions, and leads to the pattern in the right-hand side of the first column which shows not only a peak of diversity in the Eocene but a smaller one in the mid-Cretaceous. Even more interestingly, whereas the taxonomic summary seems to suggest an exponential increase in standing diversity in the Palaeocene (after a long, stable period of low diversity throughout the Cretaceous), the phylogenetically corrected data exhibit a sustained radiation in this group starting in the Santonian and continuing through the Eocene with no substantive change across the K–T boundary.

With respect to originations and extinctions, the taxonomic approach yields the patterns in the left-hand side of the second



**Fig. 11.** Generic-level phylogeny of teleosts of the Superorder Osteoglossomorpha (after Li 1994) plotted against time. To the right are paired columns reflecting standing diversity, originations and extinctions. In each pair the left-hand columns counts occurrences in the fossil record ignoring any phylogenetic framework while the right-hand columns take the phylogeny into consideration.

and third columns respectively. These patterns match one another closely because many genera are restricted to a single stage. Clearly this is a reflection of a sampling problem which, for originations, vanishes if a phylogenetic approach is adopted by counting the number of inferred branching events leading to the origin of new clades against each time stage (right-hand of second column). Until summaries such as these have been prepared for a large number of Cretaceous-Tertiary clades the real magnitude and pattern of the K-T extinction event will remain obscure.

### Conclusions

The record of biotic transitions at and around the K-T boundary is based on a mix of observations, ranging from detailed and authoritative biostratigraphical data synthesized from global sections and cores that represent a large suite of depositional environments (e.g. planktonic foraminifera), to taxonomic studies of higher categories based upon limited data from a relatively small number of geographical and ecological settings (e.g. lepidosaurs). Despite this variation, certain conclusions can be drawn from the current database.

First, global events at the K-T boundary occurred within a longer period of sustained biotic change. This longer episode affected different groups at different times, but most often manifested itself as a progressive reduction in biotic diversity throughout the Maastrichtian.

Second, a much shorter term global biotic event appears to have taken place close to the K-T boundary. This event is most prominent among a few groups of marine microfossils (e.g. calcareous nannoplankton, planktonic foraminifera), which seem to have remained relatively unaffected by the long-term Maastrichtian decline. Perhaps one of the questions we should be asking is why marine plankton were resistant to the longer-term Maastrichtian biotic crisis. The extent to which

this short-term, near-boundary event was influenced (or precipitated) by a bolide impact is uncertain. In most microfossil lineages, with the possible exception of calcareous nannoplankton, decline in species numbers begins prior to the occurrence of impact debris in various K-T boundary successions. The uppermost Maastrichtian decline in some of these groups may be a sampling artefact (e.g. Signor-Lipps effect) or it may reflect a biotic response to terrestrially forced global events (e.g. general climatic cooling due to intense volcanic activity, eustatic sea-level change). Given the patchy occurrence and low relative abundance of most microfossil species it will take sampling programmes of unprecedented intensity (even by K-T standards), coupled with sophisticated forms of data analysis, to resolve this question. It is interesting to note, however, that there does seem to be a marked geographical heterogeneity to the observed extinction pattern within this short-term K-T event, with high-latitude faunas and floras exhibiting reduced rates of extinction intensity. Such patterns are difficult to explain as sampling artefacts.

Third, the intensive scrutiny of lowermost Danian strata has resulted in the discovery of many more examples of the occurrence of Cretaceous morphotypes than were previously thought to exist (e.g. calcareous nannoplankton, planktonic foraminifera, dinoflagellates). Debates as to whether these taxa represent true survivors or reworked components of Cretaceous faunas are ongoing. In several instances geographical, morphological and isotopic tests of these seemingly anomalous Cretaceous faunas in Danian beds have supported the survivorship, rather than reworking, interpretation.

Fourth, biotic diversity needed a substantial time interval to recover from the K-T event. Except for the lowermost Danian interval, in which very reduced low and middle latitude faunas predominate, rates of new species accumulation were unprecedentedly high in many (but not all) groups, no doubt reflecting sustained radiation into vacant ecospace. Nevertheless,

new data (Jablonski 1995) suggest that North American marine bivalve faunas lagged significantly behind those of Europe and Asia in terms of their recovery rate. It remains to be seen whether this pattern is also present in other groups.

Fifth, the most tractable and significant area in which improvements can be made in the current K–T database is via the determination of accurate species- and genus-level phylogenies. So long as detailed phylogenetic relationships between the Cretaceous and Danian taxa remain unknown or subject to arbitrary taxonomic convention, the magnitude, pattern, and ecological–geographical character of both long- and short-term K–T biotic events will resist accurate determination.

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## References

- ADAMIA, S., SALAKADZE, N., NAZAROV, M., GONGADZE, G., GAVTADZE, T., KILASONIA, E. & ASANIDZE, B. 1993. Geological events at the Cretaceous–Palaeogene boundary in Georgia (Caucasus). *Geologica Balcanica*, **23**, 35–43.
- AGER, D.V. 1973. *The Nature of the Stratigraphical Record*. John Wiley & Sons, New York.
- 1993. *The New Catastrophism: The Importance of the Rare Event in Geological History*. Cambridge University Press, Cambridge.
- ALVAREZ, L.W., ALVAREZ, W., ASARO, F. & MICHEL, H. 1980. Extraterrestrial cause for the Cretaceous–Tertiary extinction. *Science*, **208**, 1095–1108.
- ARCHIBALD, J.D. 1993. The importance of phylogenetic analysis for the assessment of species turnover: a case history of Paleocene mammals in North America. *Paleobiology*, **19**, 1–27.
- ARCHIBALD, J.D. & BRYANT, L.J. 1990. Differential Cretaceous–Tertiary extinction of nonmarine vertebrates; evidence from northeastern Montana. In: SHARPTON, V.L. & WARD, P.D. (eds) *Global catastrophes in Earth history: an interdisciplinary conference on impacts, volcanism, and mass mortality*. Geological Society of America, Special Papers, **247**, 549–562.
- ASGAARD, U. 1979. The irregular echinoids and the boundary in Denmark. In: BIRKELUND, T. & BROMLEY, R.G. (eds) *Cretaceous/Tertiary boundary events symposium. I. The Maastrichtian and Danian of Denmark*. University of Copenhagen, 74–77.
- ASKIN, R.A. & JACOBSON, S.R. 1996. Palynological change across the Cretaceous–Tertiary boundary on Seymour Island, Antarctica: environmental and depositional factors. In: MACLEOD, N. & KELLER, G. (eds) *The Cretaceous–Tertiary mass extinction: biotic and environmental events*. W. W. Norton & Co., New York, 7–26.
- ASTIBIA, H., BUFFETAUT, E., BUSCALIONI, A.D., CAPPETTA, J., CORRAL, C., ESTES, R., GARCIA-GARMILLA, F., JAEGER, J.J., JIMENEZ-FUENTES, E., LE LOEUFF, J., MAZIN, J.M., ORUE-EXTEBARRIA, X., PEREDA-SUBERBIOLA, J., POWELL, J.E., RAGE, J.C., RODRIGUEZ-LAZARO, J., SANZ, J.L. & TONG, H. 1990. The fossil vertebrates from Laño (Basque Country, Spain); new evidence on the composition and affinities of the Late Cretaceous continental faunas. *Terra Nova*, **2**, 460–466.
- BARRERA, E. 1994. Global environmental changes preceding the Cretaceous–Tertiary boundary: Early-late Maastrichtian transition. *Geology*, **22**, 877–880.
- & KELLER, G. 1990. Foraminiferal stable isotope evidence for gradual decrease of marine productivity and Cretaceous species survivorship in the earliest Danian. *Paleoceanography*, **5**, 867–870.
- & — 1994. Productivity across the Cretaceous–Tertiary boundary in high latitudes. *Geological Society of America Bulletin*, **106**, 1254–1266.
- BENTON, M.J. 1993. Reptilia. In: BENTON, M.J. (ed.) *The fossil record 2*. Chapman & Hall, London, 681–715.
- BERGER, W. & HEATH, G.R. 1968. Vertical mixing in pelagic sediments. *Journal of Marine Research*, **26**, 134–143.
- BERGGREN, W.A., KENT, D.V., SWISHER, C.C., III & AUBRY, M.-P. 1995. A revised Cenozoic geochronology and chronostratigraphy. In: BERGGREN, W.A., KENT, D.V., AUBRY, M.-P. & HARDENBOL, J. (eds) *Geochronology, time scales, and global stratigraphic correlation*. SEPM (Society for Sedimentary Geology) Special Publications, **54**, 129–212.
- BIRKELUND, T. & HAKANSSON, E. 1982. The terminal Cretaceous in Boreal shelf seas: a multicausal event. In: SILVER, L.T. & SCHULTZ, P.H. (eds) *Geological implications of impact of large asteroids and comets on the Earth*. Geological Society of America Special Papers, **190**, 373–384.
- BORISENKO, N.N. 1958. Paleocene Radiolaria of western Kubanj. *Trudy Vsesoyuznyi Neftegazovyi Nauchno-Issledovalelskii Institut (VNII), Krasnodarskii Filial*, **17**, 81–100.
- 1960. New radiolarians from the Paleocene deposits of the Kubanj. *Trudy Vsesoyuznyi Neftegazovyi Nauchno-Issledovalelskii Institut (VNII), Krasnodarskii Filial*, **4**, 199–207.
- BRAMLETTE, M.N. 1965. Massive extinctions in biota at the end of Mesozoic time. *Science*, **148**, 1696–1699.
- BRINKHUIS, H. & ZACHARIASSE, W.J. 1988. Dinoflagellate cysts, sea level changes and planktonic foraminifers across the Cretaceous–Tertiary boundary at El Haria, northwest Tunisia. *Marine Micropaleontology*, **13**, 153–191.
- BROOD, K. 1972. *Cyclotomatous Bryozoa from the Upper Cretaceous and Danian in Scandinavia*. Stockholm Contributions in Geology, **26**.
- 1976. *Cyclotomatous Bryozoa from the Paleocene and Maastrichtian of Majunga basin, Madagascar*. *Geobios*, **9**, 393–423.
- BROUWERS, E.M. & DE DECKKER, P. 1993. Late Maastrichtian and Danian ostracode faunas from northern Alaska: reconstructions of environment and paleogeography. *Palaios*, **8**, 140–154.
- BRYAN, J.R. 1991. A Paleocene coral-algal-sponge reef from southwestern Alabama and the ecology of Early Tertiary reefs. *Lethaia*, **24**, 423–438.
- CANUDO, I.J., KELLER, G. & MOLINA, E. 1991. Cretaceous/Tertiary boundary extinction pattern and faunal turnover at Agost and Caravaca, S. E. Spain. *Marine Micropaleontology*, **17**, 319–341.
- CAPETTA, H. 1987. Extinctions et renouvellements fauniques chez les sélachiens postjurassiques. *Mémoires de la société géologique de France, new series*, **150**, 113–131.
- , DUFFIN, C. & ZIDEK, J. 1993. Chondrichthyes. In: BENTON, M.J. (ed.) *The fossil record 2*. Chapman & Hall, London, 593–609.
- CASE, S.M. & WAKE, M.H. 1977. Immunological comparisons of caecilian albumins (Amphibia: Gymnophiona). *Herpetologica*, **33**, 94–98.
- CHIAPPE, L.M. 1995. The first 85 million years of avian evolution. *Nature*, **378**, 349–355.
- COATES, A.G. & JACKSON, J.B.C. 1987. Clonal growth, algal symbiosis, and reef formation by corals. *Paleobiology*, **13**, 363–378.
- COCCIONI, R. & GALEOTTI, S. 1994. K–T boundary extinction: geologically instantaneous or gradual event? Evidence from deep-sea benthic foraminifera. *Geology*, **22**, 779–782.
- COLES, G. 1990. A comparison of the evolution, diversity, and composition of the Cainozoic Ostracoda in the deep water North Atlantic and shallow water environments of North America and Europe. In: WHATLEY, R.C. & MAYBURY, C.A. (eds) *Ostracoda and Global Events*. Chapman & Hall, London, 71–86.
- COOPER, A. 1994. Calibration of mitochondrial 12s rDNA sequences indicate many modern avian orders survived the K–T boundary impact. *Geological Society of America, Abstracts with Programs*, **26**, A-395.
- D'HONDT, S. 1995. Carbon isotopic recovery from mass extinctions: no Strangelove oceans on geologic timescales. *Geological Society of America Abstracts with Programs*, **27**, A-164.
- DOYLE, P., DONOVAN, D.T. & NIXON, M. 1994. Phylogeny and systematics of the Coleoidea. *University of Kansas Paleontological Contributions*, **5**, 1–15.
- DONZE, P., COLIN, J.P., DAMOTTE, R., OERTLI, H.J., PEYPOUQUET, J.-P. & SAID, R. 1982. Les ostracodes du Campanien terminal à l'Éocène inférieur de la coupe du Kef, Tunisie Nord-orientale. *Bulletin des Centres de Recherches Exploration-Production Elf-Aquitaine*, **6**, 307–335.
- DRUGG, W.S. 1967. Palynology of the Upper Moreno Formation (late Cretaceous–Paleocene) Escarpado Canyon, California. *Palaentographica, Abteilung B*, **118**, 1–71.
- DUMITRICA, P. 1973. Paleocene Radiolaria, DSDP Leg 21. In: BURNS, R.E. ET AL. (eds) *Initial Reports of the Deep Sea Drilling Project*, **21** U.S. Government Printing Office, Washington, D. C., 787–817.
- DUNCAN, P.M. 1880. Sind fossil corals and Alcyonaria. *Memoirs of the Geological Survey of India. Palaeontologica Indica* (Series 7 & 14), **1**, 1–110.

- EHRENDORFER, T.W. 1993. *Late Cretaceous (Maastrichtian) calcareous nannoplankton biogeography with emphasis on events immediately preceding the Cretaceous/Palaeocene boundary*. Woods Hole Oceanographic Institution, 93-15.
- ELLIOT, D.H., ASKIN, R.A., KYTE, F.T. & ZINSMEISTER, W.J. 1994. Iridium and dinocysts at the Cretaceous-Tertiary boundary on Seymour Island, Antarctica: implications for the K-T event. *Geology*, **22**, 347-355.
- ESTES, R. 1983. *Sauria terrestria, Amphibiaenia*. *Handbuch der paläoherpetologie*. Gustav Fischer Verlag, Stuttgart.
- FEDUCCIA, A. 1995. Explosive evolution in Tertiary birds and mammals. *Science*, **267**, 637-638.
- FENNER, J. 1985. Late Cretaceous and Palaeogene diatom biostratigraphy. In: BOLLI, H.M., SAUNDERS, J.S. & PERCH-NIELSEN, K. (eds) *Plankton stratigraphy*. Cambridge University Press, Cambridge, 713-762.
- FOREMAN, H.P. 1968. Upper Maastrichtian Radiolaria of California. *Special Papers in Paleontology*, **3**, 1-82.
- FORTEY, R.A. 1983. Cambrian-Ordovician trilobites from the boundary beds in western Newfoundland and their phylogenetic significance. *Special Papers in Paleontology*, **30**, 179-211.
- FRIZZEL, D.L. & MIDDOUR, E.S. 1951. Paleocene Radiolaria from southeastern Missouri. *University of Missouri School of Mines and Metallurgy, Technical Series*, **77**, 1-41.
- GALE, A.S. 1986. Goniasteridae (Asteroidea, Echinodermata) from the late Cretaceous of north-west Europe. 1. Introduction. The genera *Metopaster* and *Recurvaster*. *Mesozoic Research*, **1**, 1-69.
- 1987. Goniasteridae (Asteroidea, Echinodermata) from the late Cretaceous of north-west Europe. 2. The genera *Calliderma*, *Crateraster*, *Nymphaster* and *Chomataster*. *Mesozoic Research*, **1**, 151-186.
- GALLAGHER, W.B. 1991. Selective extinction and survival across the Cretaceous/Tertiary boundary in the northern Atlantic Coastal Plain. *Geology*, **19**, 967-970.
- GARDINER, B.G. 1993. Osteichthyes: basal actinopterygians. In: BENTON, M.J. (ed.) *The fossil record 2*. Chapman & Hall, London, 612-619.
- GARTNER, S. 1996. Calcareous nannofossils at the Cretaceous-Tertiary boundary. In: MACLEOD, N. & KELLER, G. (eds) *The Cretaceous-Tertiary mass extinction: biotic and environmental events*. W. W. Norton & Co., New York, 27-84.
- GASPARINI, Z., CHIAPPE, L.M. & FERNANDEZ, M. 1991. A new Senonian peirosaurid (Crocodylomorpha) from Argentina and a synopsis of the South America Cretaceous crocodiles. *Journal of Vertebrate Paleontology*, **11**, 316-333.
- GILLILAND, P.M. 1990. *The skeletal morphology and systematics of Recent and fossil holothurians with particular reference to the Triassic/Jurassic*. PhD thesis, University of Exeter.
- 1992. *The skeletal morphology, systematics and evolutionary history of holothurians*. Special Papers in Paleontology, **47**.
- GINSBURG, R.N., CANUDO, J.I., KELLER, G., MASTERS, B.A., OLSSON, R. K., ORUÉ-EXTEBARRIA, X. & SMIT, J. (in press). The Cretaceous-Tertiary boundary: the El Kef blind test. *Marine Micropaleontology*.
- GLAESSNER, M.F. 1937. Studien über Foraminiferen aus der Kreide und dem Tertiär des Kaukasus. I—Die Foraminiferen der ältesten Tertiärschichten des Nordwestkaukasus. *Problems in Paleontology, Moscow University Laboratory of Paleontology*, **2-3**, 349-410.
- GOLTMAN, E.V. 1988. The correlation of heterofacial Maastrichtian deposits of the Tadzhik Depression by radiolarians. *Doklady Akademii Nauk Tadzhikskoy SSR*, **31**, 202-206.
- GRAVESEN, P. 1979. Remarks on the regular echinoids in the Upper Maastrichtian and Lower Danian of Denmark. In: BIRKELUND, T. & BROMLEY, R.G. (eds) *Cretaceous/Tertiary boundary events symposium. I. The Maastrichtian and Danian of Denmark*. University of Copenhagen, 72-73.
- GRIGORESCU, D., WEISHAMPEL, D.B., NORMAN, D.B., SECLAMEN, M., RUSU, M., BALTES, A. & TEODORESCU, V. 1994. Late Maastrichtian dinosaur eggs from the Haneg basin (Romania). In: CARPENTER, K., HIRSCH, K.F. & HARNER, J.R. (eds) *Dinosaur eggs and babies*. Cambridge University Press, Cambridge, 74-87.
- HÅKANSSON, E., KJAER, C. R. & THOMSEN, E. 1996. Benthic recovery subsequent to the Cretaceous-Tertiary boundary—the European example. In: REPETSKI, J.E. (ed.) *Sixth North American Paleontological Convention Abstracts of Papers*. The Paleontological Society Special Publications, **8**, 156.
- HÅKANSSON, E. & THOMSEN, E. 1979. Distribution and types of bryozoan communities at the boundary in Denmark. In: BIRKELUND, T. & BROMLEY, R.G. (eds) *Cretaceous-Tertiary boundary events. I. The Maastrichtian and Danian of Denmark*. University of Copenhagen, Copenhagen, 78-91.
- HANSEN, H.J. 1990. Diachronous extinctions at the K/T boundary: a scenario. In: SHARPTON, V.L. & WARD, P.D. (eds) *Global catastrophes in Earth history: an interdisciplinary conference in impacts, volcanism, and mass mortality*. Geological Society of America, Special Papers, **247**, 417-423.
- , RASMUSSEN, K.L., GWOZDZ, R. & KUNZENDORF, H. 1987. Iridium-bearing carbon black at the Cretaceous-Tertiary boundary. *Bulletin of the Geological Society of Denmark*, **36**, 305-314.
- HAQ, B. 1991. Sequence stratigraphy, sea-level change and significance for the deep sea. *International Association of Sedimentologists, Special Publications*, **12**, 3-39.
- , HARDENBOL, J. & VAIL, P.R. 1987. Chronology and fluctuating sea levels since the Triassic. *Science*, **235**, 1156-1166.
- HARGRAVES, P.E. 1986. The relationship of some fossil diatom genera to resting spores. *Proceedings of the Eighth International Diatom Symposium*, 33-46.
- & FRENCH, F.W. 1983. Diatom resting spores: significance and strategies. In: FRYXELL, G.A. (ed.) *Survival strategies of the algae*. Cambridge University Press, Cambridge, 49-68.
- HARWOOD, D.M. 1988. Upper Cretaceous and Lower Paleocene diatom and silicoflagellate biostratigraphy of Seymour Island, Eastern Antarctic Peninsula. In: FELDMANN, R.M. & WOODBURN, M.O. (eds) *Geology and Paleontology of Seymour Island, Antarctic Peninsula*. Geological Society of America Memoirs, **169**, 55-129.
- & GERSONDE, R. 1990. Lower Cretaceous diatoms from ODP Leg 113, Site 693 (Weddell Sea). Part 2: resting spores, chrysophycean cysts, an endoskeletal dinoflagellate, and notes on the origin of diatoms. *Proceedings of the Ocean Drilling Program, Scientific Results*, **113**, 403-425.
- HECK, S.E., VAN & PRINS, B. 1987. A refined nannoplankton zonation for the Danian of the central North Sea. *Abhandlungen der Geologischen Bundesanstalten*, **39**, 285-303.
- HEDBERG, H. 1976. *International Stratigraphic Guide: A Guide to Stratigraphic Classification, Terminology, and Procedure*. John Wiley & Sons, New York.
- HEDGES, S.B., NUSSBAUM, R.A. & MAXSON, L.R. 1993. Caecilian phylogeny and biogeography inferred from mitochondrial DNA sequences of the 12S rRNA and 16S rRNA genes (Amphibia: Gymnophiona). *Herpetological Monographs*, **7**, 64-76.
- HOLLIS, C.J. 1991. *Latest Cretaceous to Late Paleocene Radiolaria from Marlborough (New Zealand) and DSDP Site 208*. PhD thesis, University of Auckland.
- 1993. Latest Cretaceous to Late Paleocene radiolarian biostratigraphy: a new zonation from the New Zealand region. *Marine Micropaleontology*, **21**, 295-327.
- 1996. Radiolarian faunal change through the Cretaceous-Tertiary transition of eastern Marlborough, New Zealand. In: MACLEOD, N. & KELLER, G. (eds) *The Cretaceous-Tertiary Mass extinction: biotic and environmental events*. W. W. Norton & Co., New York, 173-204.
- & HANSON, J.A. 1991. Well-preserved late Paleocene Radiolaria from Tangihua Complex, Camp Bay, eastern Northland. *Tane*, **33**, 65-76.
- HOOKE, J.J., MILNER, A.C. & SEQUEIRA, S.E.K. 1991. An ornithopod dinosaur from the Late Cretaceous of West Antarctica. *Antarctic Science*, **3**, 331-332.
- HOUSE, M.R. 1993. Fluctuations in ammonoid evolution and possible environmental controls. In: HOUSE, M.R. (ed.) *The Ammonoidea: environment, ecology, and evolutionary change*. Systematics Association Special Volumes, **13-34**.
- HSÜ, K.J. & MCKENZIE, J.A. 1985. A "strangelove" ocean in the earliest Tertiary. In: SUNDQUIST, E.T. & BROECKER, W.S. (eds) *Natural variations: Archean to present*. American Geophysical Union Monographs, **32**, 487-492.
- HUBER, B.T., HODELL, D.A. & HAMILTON, C.P. 1995. Middle-Late Cretaceous climate of the southern high latitudes: stable isotopic evidence for minimal equator-to-pole thermal gradients. *Geological Society of America Bulletin*, **107**, 1164-1191.
- HULBERT, S.H. & ARCHIBALD, J.D. 1995. No statistical support for sudden (or gradual) extinction of dinosaurs. *Geology*, **23**, 881-884.
- JABLONSKI, D. 1995. The biogeography of rebounds: comparisons among K-T bivalves. *Geological Society of America Abstracts with Programs*, **27**, A-164.
- & RAUP, D.M. 1995. Selectivity of end-Cretaceous marine bivalve extinctions. *Science*, **268**, 389-391.
- JAGT, J.W.M. 1995. Late Cretaceous and early Cainozoic crinoid assemblages from northeast Belgium and the southeast Netherlands. In: EMSON, R.H., SMITH, A.B. & CAMPBELL, A.C. (eds) *Echinoderm Research 1995*. A. A. Balkema, Rotterdam, 185-196.
- JEFFERY, C.H., in press, a. Carrying on regardless: changes in the Cretaceous echinoid genus *Cyclaster* at the Cretaceous-Tertiary boundary. *Proceedings of the 9th International Echinoderms Conference, San Francisco*. A. A. Balkema, Rotterdam.

- , in press. *b.* All change at the K–T boundary: echinoids from the Maastrichtian and Danian of the Mangyshlak Peninsula, Kazakhstan. *Palaeontology*.
- & SMITH, A.B., in press. Estimating extinction levels and changes in diversity and disparity of echinoids across the Cretaceous–Tertiary boundary. *Proceedings of the 9th International Echinoderms Conference, San Francisco*. A. A. Balkema, Rotterdam.
- JOHANSEN, M.B. 1987. Brachiopods from the Maastrichtian–Danian boundary sequence at Nye Kløv, Jylland, Denmark. *Fossils and Strata*, **20**, 1–99.
- JOHNSON, C.C. & KAUFFMAN, E.G. 1996. Maastrichtian extinction patterns of Caribbean province rudistids. *In: MACLEOD, N. & KELLER, G. (eds) The Cretaceous–Tertiary Mass Extinction: Biotic and Environmental Changes*. W. W. Norton & Co., New York, 231–274.
- JOHNSON, K.R. & GREENWOOD, D. 1993. High-latitude deciduous forests and the Cretaceous–Tertiary boundary in New Zealand. *Geological Society of America, Abstracts with Programs*, **25**, A-50.
- & HICKEY, L.J. 1990. Megafloreal change across the Cretaceous–Tertiary boundary in the northern Great Plains and Rocky Mountains, U.S.A. *In: SHARPTON, V.L. & WARD, P.D. (eds) Global catastrophes in Earth History: an interdisciplinary conference on impact, volcanism, and mass mortality*. Geological Society of America, Special Papers, **247**, 433–444.
- JOUSE, A.P. 1978. Diatom biostratigraphy on the generic level. *Micropaleontology*, **24**, 316–326.
- KAMINSKI, M.A. 1985. Evidence for control of abyssal agglutinated community structure by substrate disturbance: results from HEBBLE area. *Marine Geology*, **66**, 113–131.
- , GRASSLE, J.F. & WHITLATCH, R.B. 1988. Life history and recolonization among agglutinated foraminifera in the Panama basin. *In: GRADSTEIN, F.M. & RÖGEL, F. (eds) Proceedings of the Second International Workshop of Agglutinated Foraminifera*. Abhandlungen der geologischen Bundesanstalt (Wien), **41**, 229–244.
- KAUFFMAN, E.G. 1984. The fabric of Cretaceous extinctions. *In: BERGGREN, W.A. & VAN COUVERING, J.A. (eds) Catastrophes and Earth History: The New Uniformitarianism*. Princeton University Press, Princeton, 151–246.
- & JOHNSON, C.C. 1988. The morphological and ecological evolution of Middle and Upper Cretaceous reef-building rudistids. *Palaios*, **3**, 194–216.
- KELLER, G. 1988a. Biotic turnover in benthic foraminifera across the Cretaceous–Tertiary boundary at El Kef, Tunisia. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **66**, 153–171.
- 1988b. Extinction, survivorship and evolution of planktic foraminifera across the Cretaceous/Tertiary boundary at El Kef, Tunisia. *Marine Micropaleontology*, **13**, 239–263.
- 1989. Extended Cretaceous/Tertiary boundary extinctions and delayed population change in planktonic foraminiferal faunas from Brazos River, Texas. *Paleoceanography*, **4**, 287–332.
- 1993. The Cretaceous–Tertiary boundary transition in the Antarctic Ocean and its global implications. *Marine Micropaleontology*, **21**, 1–46.
- , BARRERA, E., SCHMITZ, B. & MATTSO, E. 1993. Gradual mass extinction, species survivorship, and long-term environmental changes across the Cretaceous–Tertiary boundary in high latitudes. *Geological Society of America Bulletin*, **105**, 979–997.
- & BENJAMINI, C. 1991. Paleoenvironment of the eastern Tethys in the Early Paleocene. *Palaios*, **6**, 439–464.
- , LI, L. & MACLEOD, N. 1995. The Cretaceous/Tertiary boundary stratotype section at El Kef, Tunisia: how catastrophic was the mass extinction? *Palaeogeography, Palaeoclimatology, Palaeoecology*, **119**, 255–273.
- & LINDINGER, M. 1989. Stable isotope, TOC and CaCO<sub>3</sub> record across the Cretaceous/Tertiary boundary at El Kef, Tunisia. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **73**, 243–265.
- KENNEDY, W.J. 1993. Ammonite faunas of the European Maastrichtian; diversity and extinction. *In: HOUSE, M.R. (ed.) The Ammonoidea: environment, ecology, and evolutionary change*. Systematics Association Special Volume, 285–326.
- KÉROURIO, P. & SIGÉ, B. 1984. L'aport des coquilles d'oeufs de dinosaïres de Laguna Umayo à l'âge de la Formation Vilquechico (Pérou) et à la compréhension de *Perutherium altiplanense*. *Newsletters on Stratigraphy*, **13**, 133–142.
- KIENEL, U. 1994. Di Entwicklung der kalkigen Nannofossilien und der kalkigen Dinoflagellaten-Zysten an der Kriede/Tertiär-Grenze in Westbrandenburg im Vergleich mit Profilen in Nordjütland und Seeland (Dänemark). *Berliner Geowissenschaftliche Abhandlungen, Reihe E*, **12**, 1–87.
- KIER, P.M. 1974. Evolutionary trends and their functional significance in the post-Paleozoic echinoids. *Paleontology Society Memoirs* **5** (*Journal of Paleontology*, **48**, supplement), 1–95.
- KITCHELL, J.A., CLARK, D.L. & GOMBOS, A.M. 1986. Biological selectivity of extinction: A link between background and mass extinction. *Palaios*, **1**, 504–511.
- KOZLOVA, G.E. 1983. Radiolarian complexes of Boreal regions in the lower Paleocene. *In: LYUBIMOVA, P.S. & MAYTYLYUK, E.V. (eds) The use of microfossils in the study of sediments from the continents and oceans (miscellaneous scientific reports)*. *Proceedings of the All Union Petroleum Scientific Research Institute for Geological Survey (VNIGRI)*. 84–112.
- KUHNT, W. & HESS, S. 1994. Benthic foraminifera (Sonne-95 cruise). *Berichte-Reports Geologisch-Paläontologisches Institut der Universität Kiel*, **68**, 215–220.
- & KAMINSKI, M.A. 1993. Changes in the community structure of deep water agglutinated foraminifera across the K/T boundary in the Basque basin (northern Spain). *Revista Española de Micropaleontología*, **25**, 57–92.
- LAMBERT, J. & THIÉRY, P. 1909–1925. *Essai de nomenclature raisonnée des échinides*. Clairmont.
- LARSON, A. & DIMMICK, W.W. 1993. Phylogenetic relationships of the salamander families: an analysis of congruence among morphological and molecular characters. *Herpetological Monographs*, **7**, 77–93.
- LI, G.-Q. 1994. *New osteoglossomorphs (Teleostei) from the Upper Cretaceous and Lower Tertiary of North America and their phylogenetic significance*. PhD thesis, University of Alberta.
- LIDGARD, S., MCKINNEY, F.K. & TAYLOR, P.D. 1993. Competition, clade replacement, and a history of cyclostome and cheilostome bryozoan diversity. *Paleobiology*, **19**, 352–371.
- LING, H. Y. 1991. Cretaceous (Maestrichtian) radiolarians: Leg 114. *In: CIESIELSKI, P.F. ET AL. (eds) Proceedings of the Ocean Drilling Program, Scientific Results*. The Ocean Drilling Program, College Station, Texas, 317–324.
- LIPPS, J.H. & HICKMAN, C.S. 1982. Origin, age, and evolution of Antarctic and deep-sea faunas. *In: ERNST, W.G. & MORRIS, J.G. (eds) The environment of the deep sea*. Prentice-Hall, Englewood Cliffs, N. J., 324–356.
- LIU, C. & OLSSON, R.K. 1992. Evolutionary radiation of microporiferate planktonic foraminifera following the K/T mass extinction. *Journal of Foraminiferal Research*, **22**, 328–346.
- MACELLARI, C.E. 1986. Late Campanian–Maastrichtian ammonite fauna from Seymour Island (Antarctic Peninsula). *Journal of Paleontology, Memoirs*, **18**, 1–55.
- MACLEOD, N. 1994. An evaluation of criteria that may be used to identify species surviving a mass extinction. *New Developments Regarding the K/T Event and Other Catastrophes in Earth History, LPI Contribution*, **825**, 75–77.
- 1995a. Cretaceous/Tertiary (K/T) biogeography of planktic foraminifera. *Historical Biology*, **10**, 49–101.
- 1995b. Graphic correlation of high latitude Cretaceous–Tertiary boundary sequences at Nye Kløv (Denmark), ODP Site 690 (Weddell Sea), and ODP Site 738 (Kerguelen Plateau): comparison with the El Kef (Tunisia) boundary stratotype. *Modern Geology*, **19**, 109–147.
- 1995c. Graphic correlation of new Cretaceous/Tertiary (K/T) boundary sections. *In: MANN, K.O. & LANE, H.R. (eds) Graphic Correlation*. Society for Sedimentary Geology Special Publications, **53**, Tulsa, 215–233.
- 1996a. Nature of the Cretaceous–Tertiary (K–T) planktonic foraminiferal record: stratigraphic confidence intervals, Signor–Lipps effect, and patterns of survivorship. *In: MACLEOD, N. & KELLER, G. (eds) The Cretaceous–Tertiary mass extinction: biotic and environmental changes*. W. W. Norton & Co., New York, 85–138.
- 1996b. Stratigraphic completeness and planktic foraminiferal survivorship across the Cretaceous–Tertiary (K/T) boundary. *In: MOGULEVSKY, A. & WHATLEY, R. (eds) Microfossils and Oceanic Environments*. University of Wales, Aberystwyth, 327–353.
- 1996c. K–T Redux. *Paleobiology*, **22**, 311–317.
- 1996d. Testing patterns of Cretaceous–Tertiary planktonic foraminiferal extinctions at El Kef (Tunisia). *In: RYDER, G., FASTOVSKY, D. & GARTNER, S. (eds) The Cretaceous–Tertiary Event and Other Catastrophes in Earth History*. Geological Society of America, Special Papers, **307**, 287–302.
- & KELLER, G. 1991. How complete are Cretaceous/Tertiary boundary sections? A chronostratigraphic estimate based on graphic correlation. *Geological Society of America Bulletin*, **103**, 1439–1457.
- & — 1994. Comparative biogeographic analysis of planktic foraminiferal survivorship across the Cretaceous/Tertiary (K/T) boundary. *Paleobiology*, **20**, 143–177.
- MADDOCKS, R.F. 1985. Ostracoda of the Cretaceous–Tertiary contact sections in central Texas. *Gulf Coast Association of Geological Societies Transactions*, **35**, 445–456.
- MALCHUS, N. 1990. Revision der Kreide-Austern (Bivalvia: Pteriomorpha) Aegyptens (Biostratigraphie, Systematik). *Berliner Geowissenschaftliche Abhandlungen, Reihe A*, **125**, 1–231.

- MARIN, I.I. & STOYKOVA, K.H. 1994. Cretaceous-Tertiary boundary events in the area of Bjala, eastern Bulgaria—biostratigraphical results. *Geologica Balcanica*, **24**, 3–22.
- MARINCOVICH, L., BROUWERS, E.M., HOPKINS, D.M. & MCKENNA, M.C. 1990. Late Mesozoic and Cenozoic paleogeographic and paleoclimatic history of the Arctic Ocean basin, based on shallow-water marine faunas and terrestrial vertebrates. *In: The Arctic Ocean Region. The Geology of North America*, **1**, Geological Society of America, Boulder, 403–426.
- MARSHALL, C.R. 1995. Distinguishing between sudden and gradual extinctions in the fossil record: predicting the position of the Cretaceous-Tertiary iridium anomaly using the ammonite fossil record on Seymour Island, Antarctica. *Geology*, **23**, 731–734.
- MATTEUCCI, R., SCHIAVINOTTO, F., SIRNA, G. & RUSSO, A. 1982. Palaeoenvironmental significance of Maastrichtian biological communities in the Pachino area (Sicily) and preliminary data on their distribution in the Mediterranean Upper Cretaceous. *In: MONTANARO GALLITELLI, E. (ed.) Palaeontology, essential of historical geology*. S.T.E.M. Mucchi, Modena, 77–96.
- MCGOWAN, G. & EVANS, S. 1995. Albanerpetontid amphibians from the Cretaceous of Spain. *Nature*, **373**, 143–145.
- MILLER, K.G. 1982. Cenozoic benthic foraminifera: case histories of paleoceanographic and sea-level changes. *In: BROADHEAD, T.W. (ed.) Foraminifera, notes for a short course*. University of Tennessee, Studies in Geology No. **6**, 107–126.
- MILNE, D.H. & MCKAY, C.P. 1982. Response of marine plankton communities to a global atmospheric darkening. *In: SILVER, L.T. & SCHULTZ, P.H. (eds) Geological implications of impacts of large asteroids and comets on the Earth*. Geological Society of America Special Papers, **190**, 297–303.
- MILNER, A.R. 1993. Amphibian-grade Tetrapoda. *In: BENTON, M.J. (ed.) The fossil record 2*. Chapman & Hall, London, 663–677.
- MOSKVIN, M.M., SOLOVYEV, A.N. & ENDELMAN, L.G. 1980. [Class Echinoidea.] *In: MENNER, V.V. (ed.) [Evolution and change of invertebrates at the boundary of the Mesozoic and Cenozoic]*. Izdatel'stvo 'Nauka', Moskva [in Russian], 116–167.
- MOUSSAVIAN, E. & VECSEI, A. 1995. Paleocene reef sediments from the Maiella carbonate platform, Italy. *Facies*, **32**, 213–222.
- MOURIER, T., BENGSTON, P., BONHOMME, M., BUGE, E., CAPETTA, H., CROCHET, J.-Y., FEIST, M., HIRSCH, K.F., MOULLADE, M., NOBLET, C., PONS, D., REY, J., SIGÉ, B., TAMBAREAU, Y. & TAQUET, P. 1988. The Upper Cretaceous-Lower Tertiary marine to continental transition in the Bagua basin, northern Peru. *Newsletters on Stratigraphy*, **19**, 143–177.
- MUSACCHIO, E.A. 1990. Non-marine Cretaceous ostracodes from Argentina and the paleobiogeographical relationships. *In: WHATLEY, R.C. & MAYBURY, C.A. (eds) Ostracoda and Global Events*. Chapman & Hall, London, 557–569.
- NELSON, J.S. 1994. *Fishes of the world*. John Wiley & Sons Inc., New York.
- NEWELL, N.D. 1962. Paleontological gaps and geochronology. *Journal of Paleontology*, **36**, 592–610.
- NICHOLS, D.J. & FLEMING, R.F. 1990. Plant microfossil record of the terminal Cretaceous event in the western United States and Canada. *In: SHARPTON, V.L. & WARD, P.D. (eds) Global catastrophes in Earth history: an interdisciplinary conference on impacts, volcanism, and mass mortality*. Geological Society of America Special Papers, **247**, 445–455.
- NIELSEN, K.B. 1909. Brachiopoderne i Danmarks Kridtfaejring Det Kogelige. *Danke Videnskabernes Selskabs Skrifter*, **7**, 129–178.
- 1914. Some remarks on the brachiopods in the Chalk of Denmark. *Meddelelser fra Dansk Geologisk Forening*, **4**, 287–296.
- NISHIMURA, A. 1986. Paleocene radiolarians at Site 384, DSDP. *News of Osaka Micropaleontologists, Special Volume*, **7**, 87–93.
- 1992. Paleocene radiolarian biostratigraphy in the northwest Atlantic at Site 384, Leg 43, of the Deep Sea Drilling Project. *Micropaleontology*, **38**, 317–362.
- NOETLING, F. 1897. Fauna of the Upper Cretaceous (Maestrichtian) of the Mari Hills. *Memoirs of the Geological Survey of India, Palaeontologica Indica, Series 16*, 1–80.
- NORELL, M.A. 1992. Taxic origin and temporal diversity: the effect of phylogeny. *In: NOVACEK, M.J. & WHEELER, Q.D. (eds) Extinction and phylogeny*. Columbia University Press, New York, 89–118.
- OLSSON, R.K. & LIU, C. 1993. Controversies on the placement of Cretaceous-Paleogene boundary and the K/P mass extinction of planktonic foraminifera. *Palaios*, **8**, 127–139.
- PANG, Q. & WHATLEY, R.C. 1990. The biostratigraphical sequence of Mesozoic non-marine ostracod assemblages in northern China. *In: WHATLEY, R.C. & MAYBURY, C.A. (eds) Ostracoda and Global Events*. Chapman & Hall, London, 239–250.
- PATTERSON, C. 1993. Osteichthyes: Teleostei. *In: BENTON, M.J. (ed.) The fossil record 2*. Chapman & Hall, London, 621–656.
- PATTERSON, C. & SMITH, A.B. 1987. Is periodicity of mass extinctions a taxonomic artefact? *Nature*, **330**, 248–251.
- & — 1989. Periodicity in extinction: the role of systematics. *Ecology*, **70**, 802–811.
- PERCH-NIELSEN, K. 1979. Calcareous nannofossils from the Cretaceous between the North Sea and the Mediterranean. *International Union of Geological Sciences, Series A*, **6**, 223–272.
- PERCIVAL, S.F. & FISCHER, A.G. 1977. Changes in calcareous nannoplankton in the Cretaceous-Tertiary biotic crisis at Zumaya, Spain. *Evolutionary Theory*, **2**, 1–35.
- PEYPOUQUET, J.-P. 1983. *Krithe* and *Parakrithe* in the Kef section (northeast Tunisia) around the Cretaceous-Tertiary boundary: paleohydrological implications. *In: MADDOCKS, R.F. (ed.) Applications of Ostracoda*. University of Houston, Houston, 510–519.
- PEYRT, D., LAHODYNSKY, R. & DURAKIEWICZ, T. in press. Deep-water agglutinated foraminiferal changes and stable isotope profiles across the Cretaceous/Paleogene boundary in the Rotwandgraben section, Eastern Alps (Austria). *Palaeogeography, Palaeoclimatology, Palaeoecology*.
- POSPICHAL, J.J. 1994. Calcareous nannofossils and the K/T boundary, El Kef: No evidence for stepwise, gradual, or sequential extinctions. *Geology*, **22**, 99–102.
- 1995. Cretaceous/Tertiary boundary calcareous nannofossils from Agost, Spain. *In: FLORES, J.A. & SIERRA, F.J. (eds) Proceedings of the 5th International Nannoplankton Association Conference*. University of Salamanca, Salamanca, Spain, 185–217.
- , in press. Calcareous nannoplankton mass extinction at the Cretaceous/Tertiary boundary: an update. *In: RYDER, G., FASTOVSKY, D. & GARTNER, S. (eds) The Cretaceous-Tertiary Event and Other Catastrophes in Earth History*. Geological Society of America, Special Papers, **307**.
- POSSELT, H.J. 1894. Brachiopoderne i den dansk Kridtformation. *Danmarks Geologiske Undersogelse*, **2**, 1–59.
- RASMUSSEN, H.W. 1950. Cretaceous Asteroidea and Ophiuroidea with special reference to the species found in Denmark. *Danmarks Geologiske Undersogelse*, **77**, 1–134, pls 1–18.
- 1961. *A monograph on the Cretaceous Crinoidea*. Biologiske Skrifter det Kongelige Danske Videnskabernes Selskab, **12**.
- 1972. Lower Tertiary Crinoidea, Asteroidea and Ophiuroidea from northern Europe and Greenland. *Kongelige Danske Videnskabernes Selskab Biologiske Skrifter*, **19**, 1–83, pls 1–14.
- RAUP, D.M. & BOYAJIAN, G.E. 1988. Patterns of generic extinction in the fossil record. *Paleobiology*, **14**, 109–125.
- & SEPKOSKI, J.J., JR. 1984. Periodicity of extinctions in the geologic past. *Proceedings of the National Academy of Sciences*, **81**, 801–805.
- REISS, Z. 1957. The Bilamellidea, nov. superfamily, and remarks on Cretaceous Globorotaliids. *Contributions of the Cushman Foundation for Foraminiferal Research*, **8**, 127–145.
- ROCEK, Z. & NESSOV, L.A. 1993. Cretaceous anurans from central Asia. *Palaeontographica Abteilung A*, **226**, 1–54.
- ROMAN, J. 1984. Les échinidés et la crise Crétacé-Tertiaire. *Bulletin de la Section des Sciences 1984*, **6**, 133–147.
- ROMEIN, A.J.T. 1979. Lineages in Early Palaeogene calcareous nannoplankton. *Utrecht Micropaleontological Bulletin*, **22**, 1–231.
- ROSEN, B.R. 1988. From fossils to earth history: applied historical biogeography. *In: MYERS, A.A. & GILLER, P.S. (eds) Analytical biogeography: an integrated approach to the study of animal and plant distributions*. Chapman & Hall, London, 437–481.
- & TURNSEK, D. 1989. Extinction patterns and biogeography of scleractinian corals across the Cretaceous/Tertiary boundary. *In: JELL, P.A. & PICKETT, J.W. (eds) Fossil Cnidaria 5. Memoirs of the Association of Australasian Palaeontologists*, **8**, 355–370.
- SCHINDEWOLF, O. 1962. Neokatastrophismus? *Deutsch Geologische Gesellschaft Zeitschrift Jahrgang*, **114**, 430–445.
- SCHMITZ, B., KELLER, G. & STENVALL, O. 1992. Stable isotope and foraminiferal changes across the Cretaceous-Tertiary boundary at Stevns Klint, Denmark: arguments for long-term oceanic instability before and after bolide-impact event. *Palaeoceanography, Palaeoclimatology, Palaeogeography*, **96**, 233–260.
- SCHOCH, R.M. 1986. *Phylogeny reconstruction in paleontology*. Van Nostrand Reinhold Co., New York.
- SHEEHAN, P.M. 1985. Reefs are not so different—they follow the evolutionary pattern of level-bottom communities. *Geology*, **13**, 46–49.
- , FASTOVSKY, D.E., HOFFMANN, R.G., BERGHAUS, C.B. & GABRIEL, D. 1991. Sudden extinction of the dinosaurs: Latest Cretaceous, Upper Great Plains, U.S.A. *Science*, **254**, 835–839.

- SHIMANSKII, V.N. & SOLOVYEV, A.N. 1982. [*The Mesozoic-Cenozoic boundary in the organic development of the world.*] Izdatel'stvo 'Nauka', Moskva. [in Russian].
- SIGNOR, P.W., III & LIPPS, J.H. 1982. Sampling bias, gradual extinction patterns and catastrophes in the fossil record. *In*: SILVER, L.T. & SCHULTZ, P.H. (eds) *Geological Implications of Impacts of Large Asteroids and Comets on the Earth*. Geological Society of America Special Papers, **190**, 291–296.
- SKELTON, P.S., GILL, E., ROSEN, B.R. & VALLDEPERAS, F.X. in press. Corals and rudists in the Late Cretaceous: a critique of the hypothesis of competitive displacement. *VII International Symposium on Fossil Cnidaria and Porifera, Madrid, September 12–15*.
- SLOAN, R.E., RIGBY, J.K., VAN VALEN, L.M. & GABRIEL, D. 1986. Gradual dinosaur extinction and simultaneous ungulate radiation in the Hell Creek Formation. *Science*, **232**, 629–633.
- SMITH, A.B. 1994. *Systematics and the Fossil Record: Documenting Evolutionary Patterns*. Blackwell, London.
- , MORRIS, N.J., GALE, A.S. & ROSEN, B.R. 1995. Late Cretaceous (Maastrichtian) macrofossil assemblages and palaeoenvironments from a Tethyan carbonate platform succession, Oman Mountains. *In*: PHILIP, J. & SKELTON, P.W. (eds) *Palaeoenvironmental models for the benthic association of Cretaceous carbonate platforms in the Tethyan Realm. Palaeogeography, Palaeoclimatology, Palaeoecology*, **119**, 155–168.
- & PATTERSON, C. 1988. The influence of taxonomic method on the perception of patterns of evolution. *Evolutionary Biology*, **23**, 127–216.
- SOHL, N.F. 1987. Cretaceous gastropods, contrasts between Tethys and the temperate provinces. *Journal of Paleontology*, **61**, 1085–1111.
- SPEIJER, R.P. & VAN DER ZWANN, G.T. 1996. Extinction and survivorship of southern Tethyan benthic foraminifera across the Cretaceous/Palaeogene boundary. *In*: HART, M.B. (ed.) *Biotic recovery from mass extinction events*. Geological Society Special Publication No. **102**, 245–258.
- STANLEY, G.D. & CAIRNS, S.D. 1988. Constructional azooxanthellate coral communities: an overview with implications for the fossil record. *Palaios*, **3**, 233–242.
- STRELNIKOVA, N. I. 1975. Diatoms of the Cretaceous Period. *Third symposium on Recent and fossil diatoms, Nova Hedwigia, Supplement*, **53**, 311–321.
- STILLWELL, J.D., FORDYCE, R.E. & ROLFE, P.J. 1994. Paleocene isocrinids (Echinodermata: Crinoidea) from the Kauru Formation, South Island, New Zealand. *Journal of Paleontology*, **68**, 135–141.
- STOKES, R.B. 1979. An analysis of the ranges of spatangoid echinoid genera and their bearing on the Cretaceous/Tertiary Boundary. *In*: CHRISTENSEN, W.K. & BIRKELUND T. (eds) *Cretaceous/Tertiary boundary events symposium. I. Proceedings*. University of Copenhagen, 78–82.
- STOTT, L.D. & KENNETT, J.P. 1990. Antarctic Paleogene planktonic foraminiferal biostratigraphy: ODP Leg 113, sites 689 and 690. *Proceedings of the Ocean Drilling Program, Scientific Results*, **113**, 549–569.
- STRONG, C.P., HOLLIS, C.J. & WILSON, G.J. 1995. Foraminiferal, radiolarian and dinoflagellate biostratigraphy of Late Cretaceous to middle Eocene pelagic sediments (Muzzle Group) at Mead Stream, Marlborough, New Zealand. *New Zealand Journal of Geology and Geophysics*, **38**, 165–206.
- SULLIVAN, R.M. 1987. A reassessment of reptilian diversity across the Cretaceous–Tertiary boundary. *Contributions in Science*, **391**, 1–26.
- SURLYK, F. & JOHANSEN, M.B. 1984. End-Cretaceous brachiopod extinctions in the chalk of Denmark. *Science*, **223**, 1174–1177.
- SWEET, A.R., BRAMAN, D.R. & LERBEKMO, J.F. 1990. Palynofloral response to K/T boundary events; A transitory interruption within a dynamic system. *In*: SHARPTON, V.L. & WARD, P.D. (eds) *Global Catastrophes in Earth History*. Geological Society of America, Special Papers, **247**, 457–469.
- SWINBURNE, N.H.M. 1990. *The extinction of rudist bivalves*. D Phil Thesis, Open University, Milton Keynes.
- TAYLOR, J.D., MORRIS, N.J. & TAYLOR, C.N. 1980. Food specialization and the evolution of predatory prosobranch gastropods. *Palaeontology*, **23**, 375–409.
- TAYLOR, P.D. 1993. Bryozoa. *In*: BENTON, M.J. (ed.) *The fossil record 2*. Chapman & Hall, London, 465–489.
- & LARWOOD, G.P. 1988. Mass extinctions and the pattern of bryozoan evolution. *In*: LARWOOD, G.P. (ed.) *Extinction and survival in the fossil record*. Clarendon Press, Oxford, 99–119.
- THIERRY, J. & NÉRAUDEAU, D. 1994. Variation in Jurassic echinoid biodiversity at ammonite zone levels: stratigraphical and palaeoecological significance. *In*: DAVID, B., GUILLE, A., FÉRAL, J.-P. & ROUX, M. (eds) *Echinoderms through time*. A.A. Balkema, Rotterdam, 901–909.
- THIERSTEIN, H. R. 1981. Late Cretaceous nannoplankton and the change at the Cretaceous–Tertiary boundary. *In*: WARME, J.E., WINTERER, E. & DOUGLAS, R.G. (eds) *The Deep Sea Drilling Project: a decade of progress*. Society of Economic Paleontologists and Mineralogists, Special Publications, **32**, 355–394.
- THOMAS, E. 1990. Late Cretaceous–Early Eocene mass extinction in the deep sea. *In*: SHARPTON, V.L. & WARD, P.D. (eds) *Global Catastrophes in Earth History*. Geological Society of America, Special Papers, **247**, 481–495.
- THOMSEN, E. 1976. Depositional environment and development of Danian bryozoan biomicrite mounds (Karlbly Klint, Denmark). *Sedimentology*, **23**, 485–509.
- TROELSON, J.C. 1957. Some planktonic foraminifera of the Type Danian and their stratigraphic importance. *U.S. National Museum Bulletin*, **215**, 125–131.
- VAN DER HAM, R. 1988. Echinoids from the early Palaeocene (Danian) of the Maastricht area (NE Belgium, SE Netherlands): preliminary results. *Mededelingen van de Werkgroep voor Tertiaire en Kwartaire Geologie*, **25**, 127–161.
- , DE WIT, R.W., ZUIDEMA, G. & VAN BIRGELEN, M. 1987. Zeeëgels uit het Krijt en Tertiair van Maastricht, Luik en Aken. Een atlas van de zeeëgels uit het Campanin, Maastrichtin en Danin van Zuid-Limburg en aangrenzende delen van België en Duitsland. *Publicaties van het Natuurhistorisch Genootschap in Limburg*, **36**, 1–96.
- VAROL, O. 1989. Palaeocene calcareous nannofossil biostratigraphy. *In*: CRUX, J.A. & VAN HECK, S.E. (eds) *Nannofossils and their applications*. Ellis Horwood, Chichester, 267–310.
- VISKOVA, L.A. 1994. The dynamics of diversity of Gymnolaemata around the Cretaceous-Paleogene crisis. *In*: *Fossil and living Bryozoa of the Globe*. All-Russian Paleontological Society, Perm, 61.
- WARD, P.D. 1995a. The K/T Trial. *Paleobiology*, **21**, 245–247.
- 1995b. After the fall: lessons and directions after the K/T debate. *Palaios*, **10**, 530–538.
- & KENNEDY, W.J. 1993. Maastrichtian ammonites from the Biscay region (France, Spain). *Paleontological Society Memoirs*, **34**, 1–58.
- , —, MACLEOD, K.G. & MOUNT, J.F. 1991. Ammonite and inoceramid bivalve extinction patterns in Cretaceous/Tertiary boundary sections of the Biscay region (southwestern France, northern Spain). *Geology*, **19**, 1181–1184.
- WARREN, A.A., KOOL, L., CLEELAND, M., RICH, T.H. & RICH, P.V. 1991. Early Cretaceous labyrinthodont. *Alcheringa*, **15**, 327–332.
- WEISHAMPEL, D.B. 1990. Dinosaurian distribution. *In*: WEISHAMPEL, D.B., DODSON, P. & OSMÓLSKA, H. (eds) *The Dinosauria*. University of California Press, Berkeley, 63–139.
- WELLNHOFER, P. 1991. *The illustrated encyclopedia of Pterosaurs*. Salamander Books, London.
- WERNER, C. & RAGE, J.-C. 1994. Mid-Cretaceous snakes from Sudan. A preliminary report on an unexpectedly diverse snake fauna. *Comptes Rendus de l'Académie des Sciences, Paris*, **319**, 247–252.
- WHATLEY, R. 1990. Ostracoda and global events. *In*: WHATLEY, R. & MAYBURY, C. (eds) *Ostracoda and Global Events*. Chapman Hall, London, 3–24.
- WIDMARK, J.G. & MALMGREN, B.A. 1992. Benthic foraminiferal changes across the Cretaceous-Tertiary boundary in the deep sea; DSDP Sites 525, 527, and 465. *Journal of Foraminiferal Research*, **22**, 81–113.
- WILLIAMS, M.E. 1994. Catastrophic versus noncatastrophic extinction of the dinosaurs: testing, falsifiability, and the burden of proof. *Journal of Paleontology*, **68**, 183–190.
- WORNARDT, W.W. 1972. Stratigraphic distribution of diatom genera in marine sediments in western North America. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **12**, 49–72.
- WRIGHT, C.W. (WITH CALLOMON, J.H. & HOWARTH, M.K.). 1986. Treatise on invertebrate paleontology. Part L. Mollusca (revised), 4. The Geological Society of America and the University of Kansas, 362.
- WU, X., BRINKMAN, D.B., RUSSELL, A.P., DONG, Z., CURRIE, P. J., HOU, L. & CUI, G. 1993. Oldest known amphibaenian from the Upper Cretaceous of Chinese Inner Mongolia. *Nature*, **366**, 57–59.
- YE, C. 1993. Ostracode communities and their paleoecological environments for the Cretaceous-Tertiary from southern Tibet, PR China. *In*: MCKENZIE, K.G. & JONES, P.J. (eds) *Ostracoda in the Earth and Life Sciences*. Balkema, 668–669.