Reports

End-Cretaceous Brachiopod Extinctions in the Chalk of Denmark

Abstract. *The results of a detailed study of the brachiopods of the most complete Cretaceous-Tertiary boundary in Denmark, Nye Kløv, show an extinction pattern for this marine invertebrate group compatible with that reported for pelagic foraminifera and coccoliths and with the impact scenario. The extinction is abrupt, coinciding with the Maastrichtian-Danian boundary. There is no warning in the form of decreasing density, decreasing diversity, or early extinction of specialized groups. The basal few meters of the Danian are almost devoid of brachiopods, and a Danian brachiopod fauna starts almost as abruptly as the Maastrichtian fauna disappeared. The new fauna is similar to the Maastrichtian as regards density and diversity, and at maximum six species are common to both stages. The northwest European Maastrichtian chalk is composed mainly of the remains of coccoliths and pelagic foraminifera. The mass extinction of these groups led to a total cessation of chalk production. The chalk is overlain by a thin clay bed deposited partly under anoxic conditions. This combination of anoxia and clay deposition coupled with a cessation of productivity led to the extinction of specialized groups such as the chalk brachiopods. The surviving species included forms that could survive in well-aerated shallow marine waters on substrates other than chalk.*

The discovery of an apparently worldwide iridium anomaly at the Cretaceous-Tertiary boundary (*1*, *2*) has led to a shift in emphasis from the biotic to the geochemical and geophysical aspects of the end-Cretaceous mass extinction (*3*). Although detailed studies of the extinction pattern have been presented for several groups of marine microplankton (*4*), precise data are lacking for virtually all marine invertebrate groups.

Most sections that have been studied fail to meet the criteria necessary to illuminate the detailed nature of extinction patterns. The most important of such features are more or less continuous sedimentation and few or no facies changes across the boundary, accompanied by minimum diagenetic dissolution and minimum destruction of fossils in transport. Preferably, the fossil groups that are chosen for study should have a high density and diversity.

We have investigated the brachiopod fauna from the section Nye Kløv (Denmark), which approaches this ideal except for the occurrence of the thin Fish Clay at the boundary and the absence of brachiopods in the basal Danian (*5*). Supplementary material has been obtained from virtually all other Danish localities exposing the Cretaceous-Tertiary boundary.

The brachiopods from the Maastrichtian chalk of northwest Europe are extremely well documented (*6–10*). Most of the species are micromorphic, reaching only a few millimeters in adult length (*8*). They are represented by 10 to 20 species and up to several thousand individuals in each sample weighing between 5 and 10 kg (*6–8*). In Denmark the total number of Maastrichtian species is about 50. The earliest Tertiary, Danian brachiopods received considerable attention in the early 20th century (*11*), and the paleoecology of the brachiopods from the coral and bryozoan mound facies at the Danian type locality, Fakse, was described by Asgaard (*12*). On the basis of studies of the Maastrichtian brachiopods and a review of literature, museum material, and scattered data on the Danian brachiopods, Surlyk concluded (*9*) that there were few if any species common to the two stages. However, the possibility was mentioned that a few Maastrichtian species straddled the boundary to become extinct in the basal Danian (*9*, *13*). Recently the taxonomy and paleoecology of the early Danian fauna of Nye Kløv was studied by Johansen (*14*); she examined material from a large number of densely spaced bulk samples (Fig. 1). The sample series also included the highest part of the Maastrichtian.

During the Late Cretaceous, the Danish Basin received great thicknesses of uniform chalk with a rather sparse benthic fauna. In the Maastrichtian alone, about 500 m were deposited in the axial part of the basin where Nye Kløv is situated (*15*). This contrasts markedly with the situation over the adjacent structural highs, where more condensed chalks with occasional hardgrounds, marked lithological changes, and extremely rich benthic faunas were deposited. Stevns Klint, which exposes the Maastrichtian-Danian boundary over 12 km of cliff and which together with Fakse constitutes a composite Danian type section, is such a locality (*16*). It is thus somewhat unfortunate that the Stevns Klint section has been selected for most of the biotic and geochemical studies across the boundary.

We obtained the brachiopods of Nye Kløv by washing bulk samples of chalk weighing between 1 and 20 kg. The samples were collected in a detailed measured section (Figs. 1 and 2). The washing method involves boiling and deep-freezing in a supersaturated Glauber's salt solution. After repeating this process about 15 times, we washed the sample through a 0.25-mm sieve with hot water. The dried residue was finally sieved by hand into three size fractions, 0.25 to 0.5 mm, 0.5 to 1 mm, and > 1 mm, which were then examined for the millimeter-sized brachiopods under a binocular microscope. The specimens were then determined as to species. Even small fragments can normally be safely determined because of the extremely good preservation of shell ornamentation combined with the knowledge that has been obtained by the determination of more than 100,000 specimens of Maastrichtian chalk of northwest Europe (*7–9*, *17*).

A range chart of all brachiopod species found in Nye Kløv (*14*) is shown in Fig. 1. The Maastrichtian part of the sequence contains 26 species, all of which are well known from contemporaneous strata in the nearby localities Kjølbygård and Bjerre (*17*). Several additional species are known from the highest Maastrichtian in the more shallow-water, benthos-rich chalk of Stevns Klint (*7*, *8*). The Danian part of the Nye Kløv section contains 35 species, which can be subdivided into three groups (*14*):

1) Five species have a long Cretaceous record and are restricted to the basal Danian clay bed, the Fish Clay. They were almost certainly contained in

reworked pebbles of Maastrichtian chalk which occur commonly in the Fish Clay, as they have never been found higher in the Danian sequence. They are accordingly not included in the Danian fauna in the following treatment.

2) Six of the species are common to the Maastrichtian and the Danian and represent forms that have crossed the boundary.

3) The remaining 24 species appear for the first time in the Danian, and most of the species are new.

The true indigenous Early Danian brachiopod fauna in Nye Kløv is thus represented by about 30 species, only six of which also occurred in the Maastrichtian. The specific assignment of three of these six species is uncertain, and they may well represent new Danian species.

On the generic or higher level, the taxonomic composition of the fauna is markedly different from the Maastrichtian to the Danian Stage. The Maastrichtian fauna is dominated by cancellothyridid brachiopods (genera related to the genus *Terebratulina*). In Nye Kløv this group includes eight species of the genera *Terebratulina, Rugia, Gisilina*, and *Meonia*. Next in importance is a more homogeneous group of five species belonging to the genus *Argyrotheca*. In the Danian the situation is reversed. The dominant genus is *Argyrotheca*, which is represented by nine species, whereas the cancellothyridid group includes seven species.

The Maastrichtian brachiopod fauna was highly specialized, and seven main adaptive groups are recognizable (*11*): group 1, minute species attached with a pedicle and able to utilize very small hard substrates; group 2, medium to very large species attached with a pedicle and confined to large hard substrates; group 3, medium-sized species attached directly to the sediment with a rooted type pedicle; group 4, medium to large free-living species with pedically attached juvenile stages; group 5, burrowing species; group 6, cementing species able to utilize very small substrates and essentially free living as adults; and group 7, cementing species confined to large hard substrates.

Group 1 overwhelmingly dominates in the Maastrichtian, but the free-living species are also important. This pattern is even more marked in the Danian, where the minute forms comprise 66 percent of all species. In contrast, an important component of the group of free-living species consisting of hemispherical forms has disappeared (Fig. 3).

The six species that cross the boundary belong to groups 1, 3, and 6 and are able to use very small substances as substrates, such as skeletal fragments, notably bryozoans. Furthermore, they represent relatively featureless forms which seem to be nonspecialized and which occur in large numbers throughout the Maastrichtian as a basic stock.

The most specialized species, in particular the secondarily free-living forms (Fig. 3), became extinct at the boundary, and the surviving species could not form the basis for an exploitation of all the

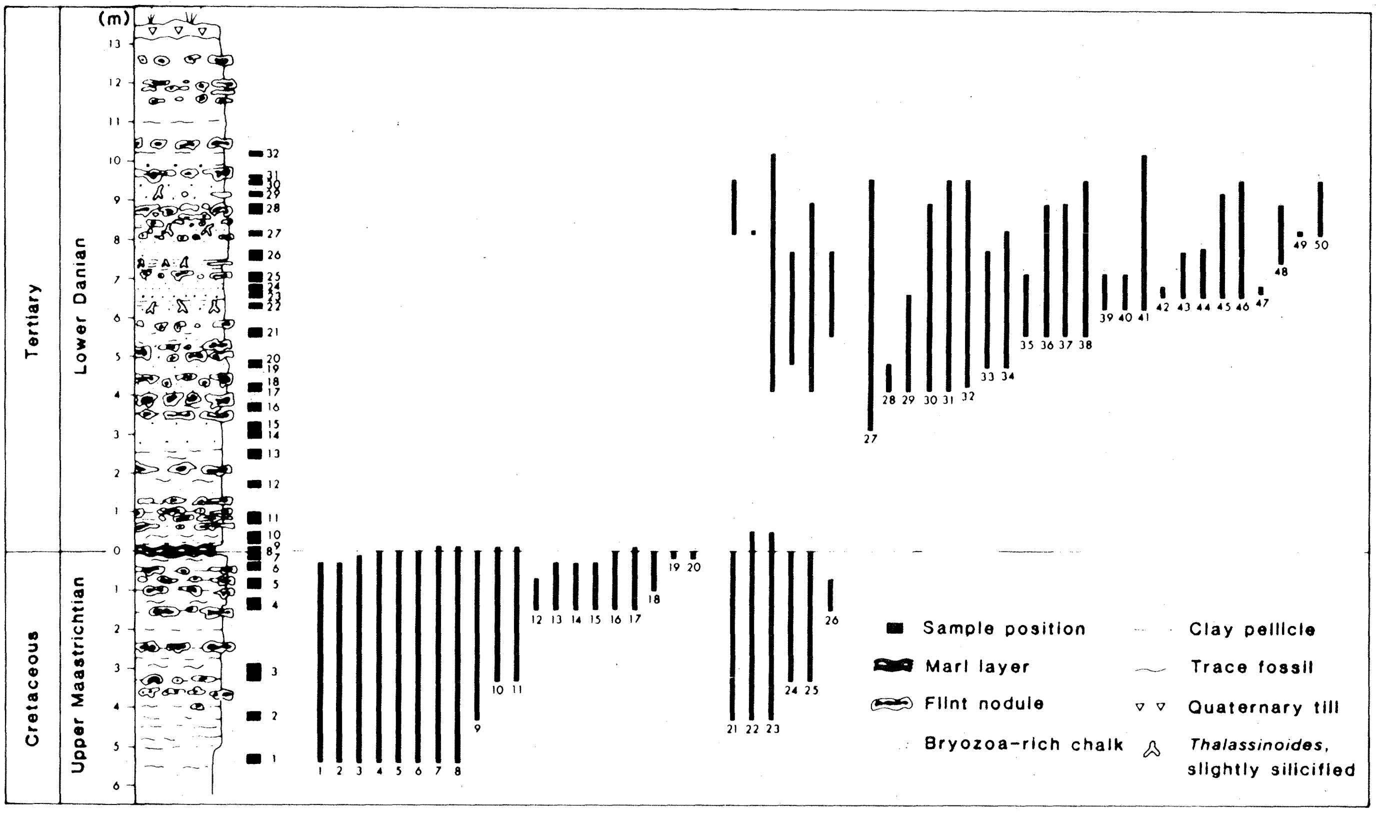


Fig. 1. Range chart of brachiopod species in the Cretaceous-Tertiary boundary sequence at Nye Kløv [modified from Johansen (*14*)]: *1*, *Cretirhynchia* sp.; *2*, *Magas chitoniformis*; *3*, *Gisilina jasmundi*; *4*, *Scumulus inopinatus*; *5*, *Kingena pentangulata*; *6*, *Leptothyrellopsis* (?) sp.; *7*, rhynchonellid sp.; *8*, *Argyrotheca bronnii*; *9*, *Terebratulina faujasii*; *10*, *Meonia semiglobularis*; *11*, *Isocrania* aff. *costata* (1); *12*, *Argyrotheca danica*; *13*, *Carneithyris subcardinalis*; *14*, *Rugia* aff. *tenuicostata*; *15*, *Scumulus* (?) sp.; *16*, *Rugia acutirostris*; *17*, *Terebratulina gracilis*; *18*, *Crania* aff. *craniolaris*; *19*, *Argyrotheca coniuncta*; *20*, *Craniscus* sp.; *21*, *Terebratulina longicollis*, *T.* aff. *longicollis*; *22*, *Aemula* cf. *inusitata*; *23*, *Terebratulina chrysalis*; *24*, *Isocrania costata*; *25*, *Argyrotheca stevensis*; *26*, *Argyrotheca hirundo*/*A.* aff. *hirundo*; *27*, rhynchonellid sp.; *28*, *Argyrotheca* sp. 4; *29*, *Argyrotheca* n. sp. aff. *bronnii*; *30*, *Gwyniella* n. sp.; *31*, *Rugia* n. sp. 1; *32*, *Cryptopora* n. sp.; *33*, *Argyrotheca* n. sp. 5; *34*, *Crania tuberculata*; *35*, *Platidia* sp.; *36*, *Argyrotheca* n. sp. 1; *37*, *Isocrania* aff. *costata* (2); *38*, *Argyrotheca* n. sp. 2; *39*, *Argyrotheca* n. sp. aff. *stevensis*; *40*, *Dalligas* (?) sp.; *41*, *Carneithyris* (?) sp.; *42*, *Isocrania* sp. 3; *43*, *Cretirhynchia* sp.; *44*, *Rugia* n. sp. 2; *45*, *Terebratulina* aff. *rigida*; *46*, *Neoliothyrina* (?) sp.; *47*, *Rugia* (?) sp.; *48*, *Argyrotheca* n. sp. 3; *49*, *Crania* sp.; *50*, *Terebratulina* n. sp. The majority of the Danian species are new (*14*).

vacant niches. It is remarkable, however, that the species diversity is virtually the same in the two stages.

The species of group 1 increase in importance in the Danian; this finding suggests either an increasing niche subdivision or a larger number of available microhabitats. There is some evidence in support of the latter suggestion, as the Danian includes more diverse sediment types, including layers richer in bryozoans and other small potential substrates than the uniform Maastrichtian chalk.

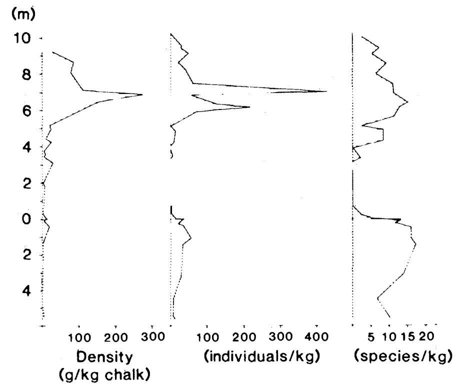
It is clear from Fig. 1 that the extinction was abrupt, and even on a millimeter scale it coincides with the top of the Maastrichtian. It is also highly significant that there are no early warning signals in the form of a gradual decrease in species diversity or even population structures at the end of the Maastrichtian. This picture is the same in all other boundary localities in Denmark that have been investigated (*7–9, 17*).

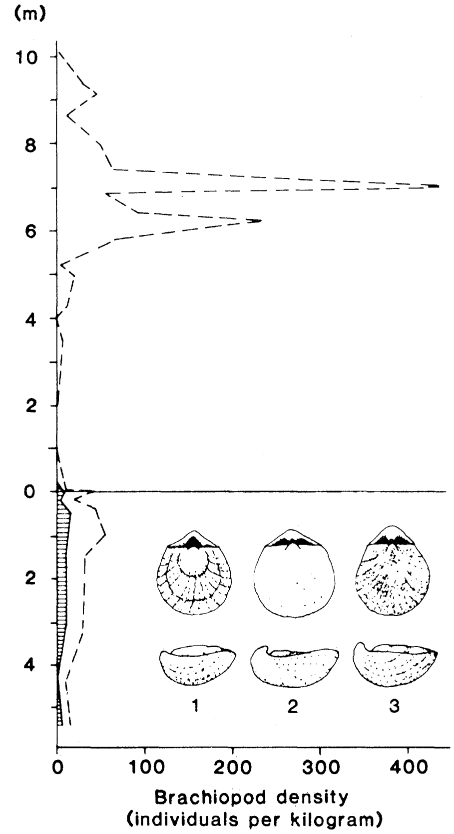
Minor environmental fluctuations eventually leading to a major crisis can, however, easily be envisaged to have influenced the benthic fauna without causing extinction of any species. The effects of such fluctuations would be expected to appear in the population structures of the individual species.

There is a clear correlation between the size-age distribution of a living population and the resulting death assemblage. Size-frequency studies of the fossil brachiopod populations can thus give important information on the dynamics of the living population (*8, 18*). Each of the Maastrichtian brachiopod species is characterized by a distinct type of size-frequency distributions in all samples. Virtually all the group 1 species have a strongly right-skewed curve with a large number of juveniles and few if any fully grown specimens (*8*). The Nye Kløv section has relatively low densities of all species, and it is thus difficult to construct meaningful size-frequency curves.

We have carried out a size-frequency analysis of the two most abundant species, *Meonia semiglobularis* and *Terebratulina longicollis*. The histograms from the individual samples are remarkably uniform. We have compared them to published size-frequency histograms for the same species from other Maastrichtian samples (*8*). Both species show size-frequency distributions that are remarkably similar to the distributions from the other Maastrichtian samples. Figure 4 shows the size-frequency distribution of *T. longicollis* compared to that of populations from two different stratigraphic levels. It is clear that the Maastrichtian brachiopod fauna at Nye Kløv thrived well until the very end of the stage. No decrease in density, diversity, or changes in population structures can be observed when the Maastrichtian-Danian boundary is approached. It can thus be safely concluded that no major ecological crisis was initiated before the time of the youngest preserved Maastrichtian at Nye Kløv. The end-Cretaceous extinction is real and abrupt, without any apparent warning signals.

This extinction pattern suggests a common cause with the oceanic microplankton extinction and is compatible with the impact scenario envisaged by Alvarez *et al.* (*1*). The extremely rich brachiopod fauna of the northwest European Maastrichtian chalk sea was highly specialized to this particular macrohabitat, and only very few of the species occur in other more shallow marine facies. When it is remembered that chalk consists mainly of the remains of coccoliths and pelagic foraminifera, it becomes immediately clear that the mass extinction of these groups led to a total cessation in the production of chalk. The top surface of the chalk is overlain by the Fish Clay, the basal layers of which show that the conditions at the bottom were anoxic. The chalk facies is restricted to the relatively deeper, more offshore parts of the northwest European shelf sea. The combined effects of productivity cessation, anoxia, and beginning clay deposition caused an almost





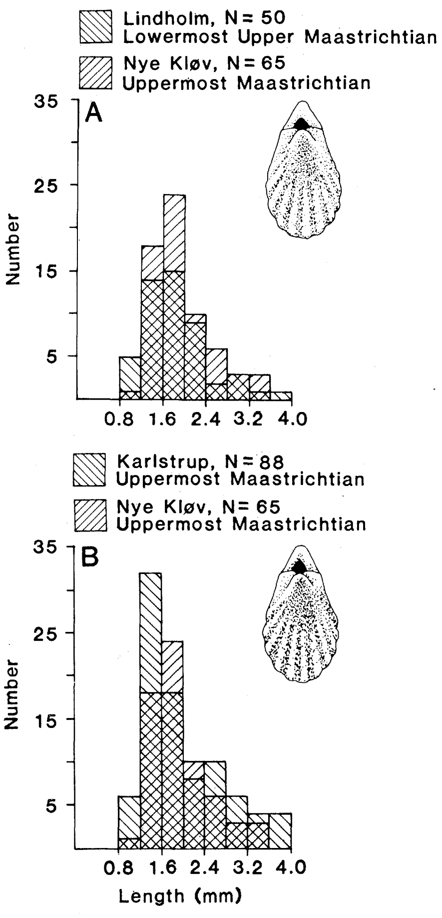


Fig. 2 (top left). Diagram showing the density of skeletal fragments (= washing residue), brachiopod density (individuals per kilogram), and brachiopod diversity (species per kilogram) in a series of samples across the Cretaceous-Tertiary boundary at Nye Kløv (see Fig. 1) [modified from Johansen (*14*)]. Fig. 3 (bottom left). Frequency and extinction of three species of free-living hemispherical brachiopods in the Nye Kløv section. The dashed line shows the variation in the total number of brachiopod specimens in the section (compare Fig. 2) [modified from Johansen (*14*)]. Fig. 4 (right). Size-frequency distribution of *Terebratulina longicollis* from Nye Kløv superimposed on the corresponding distributions of two populations from the lowermost Upper Maastrichtian (Lindholm) and the uppermost Maastrichtian (Karlstrup), respectively. All distributions are characterized by high juvenile mortality.

instantaneous destruction of a unique macrohabitat, the immediate effect of which was the extinction of faunal groups that were specialized and restricted to the chalk substrate, such as the chalk brachiopods. The surviving species included forms that could survive in well-aerated shallow marine waters in other types of substrate.

When chalk deposition eventually resumed, adaptive radiation within surviving groups led to a rapid restoration of the chalk macrohabitat. The Maastrichtian and Danian chalks had uniform properties as substrates for benthic animals. Sedimentologically they are, however, quite different. The Danian chalk is composed of the remains of a whole new plankton flora and fauna. The shelly benthos is almost totally different on the species level as regards the most specialized groups, whereas other groups with wider substrate tolerance continue less changed across the boundary.

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Terminal Cretaceous Extinctions in the Hell Creek Area, Montana: Compatible with Catastrophic Extinction

Abstract. *Inaccurate stratigraphic correlations in the Hell Creek area, Montana, have led to the assumption that transitional vertebrate faunas (Bug Creek Anthills) exist in the latest Cretaceous, refuting a catastrophic turnover at the Cretaceous-Tertiary boundary. Establishment of the transitional faunas in Paleocene channels that cut down through the Cretaceous-Tertiary boundary renders the terrestrial faunal record compatible with the marine record and with catastrophic extinction.*

Since the discovery of iridium abundance anomalies at the Cretaceous-Tertiary (K/T) boundary at various sites (*1*) and the subsequent verification of the presence of an iridium anomaly at others (*2*), many investigations have been undertaken, culminating in several symposia (*3, 4*). Although not all investigators agree with the asteroid-impact theory (*5–8*), the evidence in its favor has steadily increased (*4, 9*). The marine fossil record across the K/T boundary appears to be in accord with an impact-induced mass mortality and mass extinction and with a subsequent recovery, as demonstrated by the planktonic foraminiferal record (*10*).

Some vertebrate paleontologists and paleobotanists studying the terrestrial sequence of the western interior of the United States (*6–8*) have presented a different picture of the K/T boundary turnover, which is inconsistent with a catastrophic impact model. They argue that the record shows gradual replacement of the latest Cretaceous vertebrate faunal communities by new faunas already below the K/T boundary. However, new data that we collected on a field trip to Montana, as guests of W. A. Clemens and his co-workers, show otherwise. We argue here that the terrestrial record, on the contrary, is consistent with the model of catastrophic turnover and that both terrestrial and marine extinctions are probably due to the same catastrophe.

Smit and ten Kate (*9*) presented a scenario for marine plankton extinctions (shown slightly modified in Fig. 1). A succession of five phases is hypothesized in a catastrophic faunal turnover resulting from an asteroidal impact:

1) Before the impact equilibrium conditions existed for several million years at the end of the Cretaceous.

2) An asteroidal impact led to mass mortality and mass extinctions and to the deposition of an iridium-enriched fallout stratum.

3) This was followed by a period of indirect and delayed effects, leading to a period of stressed ecological conditions, in which secondary extinctions took place. These extinctions continued for 1,000 to 15,000 years after impact, during deposition of the so-called boundary clay (*10*). No new species are known to have appeared in this period.

4) The origination of new species and the radiation of pioneering faunas, dominated by short-living opportunistic spe-

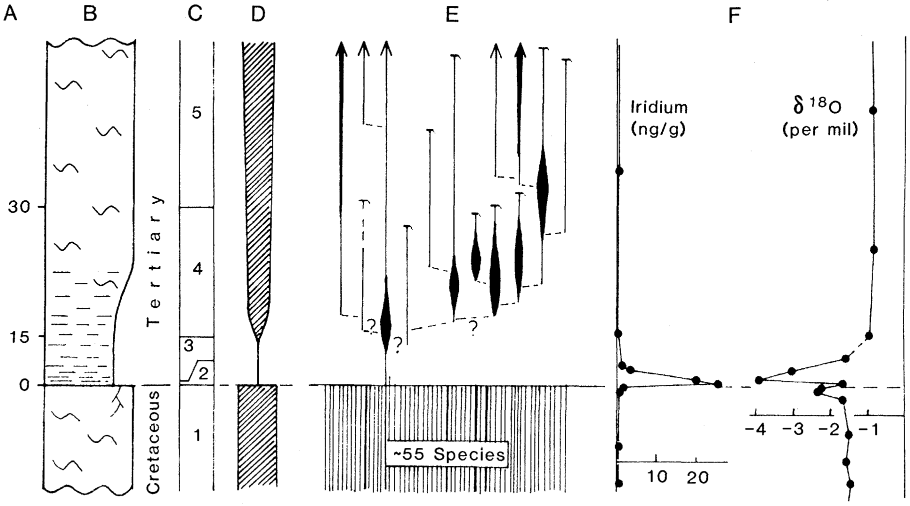

Fig. 1. Marine events at the K/T boundary, as illustrated by planktonic foraminifera (*9*). (A) Age (in 10^3 years) from the K/T boundary. (B) Lithology. (C) Subdivision in phases of the faunal events. (D) "Biomass" estimated on the basis of species and specimen density. (E) Lineages and relative abundances of planktonic foraminiferal species (*10*). (F) Iridium profile and $\delta^{18}O$ isotope profile relative to the Pee Dee belemnite standard (*9, 10*).