



III JORNADAS DE PALEONTOLOGIA

Leioa (Vizcaya), Octubre de 1987

ANA - MÁRQUEZ

III JORNADAS DE PALEONTOLOGIA

PALAEONTOLOGY AND EVOLUTION: EXTINCTION EVENTS

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DE
Ana Márquez

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CONFERENCE ON

PALAEONTOLOGY AND EVOLUTION: EXTINCTION EVENTS

PALEONTOLOGIA Y EVOLUCION: FENOMENOS DE EXTINCION

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Y los siete ángeles que tenían las siete trompetas se dispusieron a tocarlas.

El primer ángel tocó la trompeta, y hubo granizo y fuego mezclados con sangre, que fueron lanzados sobre la tierra; y la tercera parte de los árboles se quemó, y se quemó toda la hierba verde.

El segundo ángel tocó la trompeta, y como una gran montaña ardiendo en fuego fue precipitada en el mar; y la tercera parte del mar se convirtió en sangre.

Y murió la tercera parte de los seres vivientes que estaban en el mar, y la tercera parte de las naves fue destruida..

El tercer ángel tocó la trompeta, y cayó del cielo una gran estrella, ardiendo como una antorcha, y cayó sobre la tercera parte de los ríos, y sobre las fuentes de las aguas.

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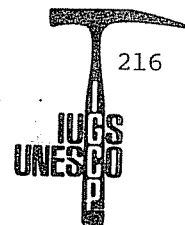
MAMMAL EXTINCTIONS IN THE VALLESIAN (UPPER MIOCENE)

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ABSTRAC: The term Vallesian was created by CRUSAFONT (1950) to designate the first European Mammalian palaeofaunas containing the equid Hipparion, the remainder of the Mammal faunas being composed of typical elements coming from the Middle Miocene such as Micromeryx, Euprox, Sansanosmilus, Pseudaelurus, Listriodon, etc. Thus, the Aragonian-Vallesian boundary did not imply a strong change among the European Miocene faunas (AGUSTI, 1978; AGUSTI et al., 1983). On the contrary, the Lower Vallesian/Upper Vallesian transition truly corresponds to an important crisis. In this boundary it can be observed the disappearance of most of the Artiodactyl Aragonian forms such as Protragocerus, Miotragocerus, Listriodon, Hyo-therium, Parachleuastochoerus, etc. Among the Rodents, this crisis affects the family Eomyidae and most of the Cricetid and Glirid species. On the other hand, a number of eastern elements appear in the area. This is the case of the suid Schizochocerus and the murid Progonomys. Other eastern forms were Tragoportax, Graecoryx, Adcrocuta, Paramachairodus, Microstonyx, etc. Most of these elements are typical forms of the next Mammal stage, the Turolian. Thus, whereas the Lower Vallesian fauna is a typical Aragonian one although with Hipparion, after the Middle Vallesian event, the Upper Vallesian faunas are already largely Turolian in character. The possible factors involved in this extinction event are discussed.

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FAUNAL REPLACEMENT IN PLIOCENE-PLEISTOCENE TRANSITION

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It should be pretentious in my case, to start a dissertation on the global critical events that are currently understood when one speaks of mass extinctions. Global, all category, penecontemporaneous extinctions are extraordinary phenomena just because, more commonly, the components of a fauna replace each other with moderate rates, below the degree of a catastrophe. The purpose of this talk is to expose a case study of faunal replacement, occurred in less than 2 million years (My) in a small, changing subcontinent.

More than eighty species of a Subclass, Mammalia, Eutheria, all large sized, that are classified in 48 genera are taken into consideration. The words "large size" are here taken in a broad sense.

The time span studied was the Pliocene-Pleistocene transition, that is the duration of the Matuyama magnetic chron, with just a small margin added on both sides; in other words from 2.6 Ma to 0.6Ma, the time covered by middle-and upper Villafranchian faunae, in Late Pliocene, plus the Early Pleistocene and just what is considered the beginning of Middle Pleistocene. The fossil assemblages of

38 sites were studied, of Italy, Spain, France, Great Britain and the two Republics of Germany. Faunal lists of these sites have been updated and/or revised; the respective dates have also been discussed and ascertained in search of the closest approximation range. The 38 sites are grouped into equivalent time slices. The resolution is of 100 Ka to 200 Ka. No one over the 86 species considered is known to last the time span considered.

The curves representing the relative faunal stability or changes are matched with that of ocean paleotemperatures, with vegetation stages in Western Europe and with episodes of geodynamic diastrophism, in a search of eventual deterministic relationships. The taxa taken into consideration belong of the Ungulates, namely Proboscidiens, Perissodactyla, Artiodactyla plus Primates and Carnivores. The term "large" Mammals is used in this study conventionally as including animals of a size larger than that of a cat. The smaller mammals, Mustelidae included equally as large rodents, are not counted for the purpose of this study, for two reasons: first, because they are not preserved in many sites with fossil remains of large mammals due to common taphonomic conditions and, second, because the small vertebrates may have a different behavior relate to the dynamic of ecosystems. A study like this can be done with small sized mammals and also with non-therian vertebrates, and with other groups of organisms; but it should be a subject for separate studies. One more reason is that the record of Rodentia is being improved very fast recently, so that it will quite soon allow a similar study with a better degree of resolution.

The present analysis deals with oryctocenoses or fossil assemblages. The representative value of the assemblages is discussed. The analysis is duplicated at two different taxonomic levels, namely at the level of genera and at a level of lower category. At this lower level species are counted, but in several cases subspecies are distinctively taken into account. These are the cases in which successive subspecies replace each other in time, so that such subspecies have a significance in biostratigraphy equally as sequential, or anagenetic taxa recognized as species in other genera. For instance, the former is the case of successive subspecies of Equus stenonis and progressive forms of Mammuthus meridionalis; these have a value comparable to that of the sequential species of Homotherium or of Eucladoceros, relate to biostratigraphical and to paleoecological problems. We speak in the first case of "genera" and in the latter of specific/subspecific taxa, or simply "taxa" for abbreviation sake. On the other hand, two or more "species" are counted as only one, if at least one of them is not well defined, or is not clearly distinguishable. In total, 48 genera and 86 lesser taxa have been considered. As many as 11 genera living before -2.5My were still living after the period studied and 10 exist in modern faunal assemblages; none of the species of large mammals living 2.5 Million years ago is found in early Middle Pleistocene assemblages.

Sites with quite poor faunal representation, or with dubious identification, and those, whose stratigraphic position and/or faunal content has not been revised, are excluded from the following accountings. Radiometric ages and other accurate means for dating have been admitted only after serious criticism.

Some of the 38 sites retained for the present accounting are penecontemporaneous to each other; these are counted as only one and representing the same paleofauna, since chronologic diversity is difficult to assess and faunal differences among them are minimal. Such are the cases of Etouaires and Villarroja, Roccaneyra and Montopoli, Saint-Vallier and Pueblán de Valverde, Chilhac and Le Coupet, and other like these. In such cases, if a taxon is present in one of these sites record and not in the one which is penecontemporaneous of the former, one can suppose without fallacy, that it should be considered as a common occurrence, and that its absence on a faunal list is simply due to randomness in either fossilizing processes or fossil collecting. The 38 sites have therefore been regrouped into less than 20 paleofaunal-representing associations. These are, on the other hand, diversely distributed; so that there is a larger number of sites known and there are closer successive fossil associations at the beginning of the Matuyama, and around the Matuyama/Brunhes inversion, than in Early Pleistocene times, between say, -1.3 My and -1 My.

If we attempt to appreciate differences in rhythm, or rating the amounts of any kind of events per time unit, we need to regroup again our data into divisions of equal durations. That is why, the faunal record is here presented in the form of assemblages corresponding to time slices of equal duration.

We have therefore divided the time span considered (near 2 million years) in regular, arbitrary slices of 250 thousand years. Each of these time slices includes two or more of the studied faunal assemblages. Those time

Intervals between the faunal assemblages recorded in the mentioned sites are centered on both sides of the following dates: -2.5 My, -2.25 My, -2.0 My, -1.75 My, -1.50 My, -1.25 My, -1.0 My, -0.75 My. Extinctions recorded as last occurrences in the respective preceding unit and new appearances recorded as earliest occurrences in the respective next unit may have actually occurred near those dates with a maximum error of $\pm$ c. 100.000 years, with a high probability. This is the resolution level that we can attain for those large mammals, in this part of the Old Continents, and in that part of the Late Cenozoic, with a high reliability. Although the detail of changes in short intervals between several well known faunal assemblages is not reflected, the eventual biases due to particular taphonomic conditions of a site are eliminated, and the collections from comparatively poorer and/or approximately dated sites can be taken into account, as complementing the record from other penecontemporaneous site. This division is, as said, artificial, does not pretend to have any biostratigraphic meaning, as it is introduced with the only purpose of estimating rates of change, that is amounts of variation related to unvariated durations.

Certainly, extinctions may have occurred within the proposed "time slices", that is between the ages of deposition of two different fossil assemblages which are included in one of our divisions. Similarly, some of the arrivals of new recorded taxa for an interval, may have either immigrated or been originated within the following time slice. This kind of lacunes and error margins are due to the discontinuous condition of the fossil record of the terrestrial Vertebrates under study.

The interval designed by the time plane -2.5 My runs in fact from more than -2.7 My (likely c.-3My), a prudent age estimation for the Les Etouaires fauna, to no much less than -2.3 My. The latter is a figure close to the age for Pardines fossil vertebrates; this together with the assemblages of Saint-Vidal and La Roche-Lambert contain some faunal elements that are still unknown at Montopoli and Roccaneyra. These two sites are well dated as very close to -2.45 My.

The faunal record of Saint-Vallier and Puebla de Valverde sites apparently is so complete and representative that one can take the central value of the range of approximation for its age, as a limit for the confidence interval of the faunal changes immediately before and after it. Therefore we assume that faunal replacement occurred between the Montopoli-Pardines and related records on one side and the faunal representation of Saint-Vallier should have occurred, with acceptable probability, between -2.35 and -2.1 My. This interval is designed here by the roughly central value of -2.25 My.

Similarly, the time plane of -2.0 My, is convenient for introducing regular time divisions, what helps making comparisons and estimating rates of change, and at the same time is a somewhat central value for the time span between -2.1 My and -1.85 My, in which the faunal changes distinguishing Saint-Vallier from Olivola faunal assemblages should have occurred. This central value falls with high confidence between the fossil assemblages of Senèze and Chilhac, for which the dates of ca -2.05/2.0 My and -1.9 My are very reliable.

The age of -1.75 My is similarly a good central value for the time span between -1.85 My, maximum estimated age

for the Olivola assemblage, and -1.6 My, a fairly good approximation for the basal boundary of the Pleistocene, and the minimum acceptable as a date of the Peyrolles and Tasso assemblages.

The division at -1.5 My separates well the assemblages of Tasso and Farneta, and stays as a good approximation for changes occurred between the assemblages related to Peyrolles, with a date of c. -1.56 My and those represented by Sinzelles dated closest to -1.35 My. Division of -1.25 My can be not far from the date of most changes occurred between the Sinzelles age and that of Venta Micena. The age of the latter stays unknown, but very approximately should be above -1.1 My and below -1.3 My. Quite roughly those changes may be supposed to have occurred between -1.35 My and -1.05 My.

The most characteristic and the richest records of the fossil faunal division following that of Venta Micena are those of Ponte Galeria, Solihac and Voigstedt. For these, the well established age of the Solihac site is near -0.83 My. The changes between Venta Micena, and Solihac and related sites should have occurred between -1.2 My and -0.85 My. Our a priori division at -1. My gives a fairly approximative central value, that shortly preceeds the fossil assemblages of Vallonet, Mosbach I and Calatrava 1.

Finally, the interval, that we design as around -0.75 My, may be narrowly bracketed between -0.8 My and -0.6 My. The record of the adjacent time slices is very complete, and the sites are abundant.

The record is fairly good, in general, with an average of 25 taxa and 24 genera of large Mammals per time-slice. There are no relevant deviations in general. Only the Sinzelles and Farneta division have a comparatively poor record (Figure 1, I; Figure 2, XII). The number of specific and subspecific taxa is higher than the average in the last two divisions, not so the number of genera represented. This is due to an active speciation of several genera, e.g. Ursus, Dicerorhinus, Equus, Megaceros, not to bias in the record.

A few trivial taxa are missing in the record of the majority of the defined complexes. A trivial taxon, relate to a particular faunal complexe, is one that exists at least in the preceding and in the following assemblages. In two assemblages, namely that of Saint-Vallier and related sites (-2.25 My to -2 My) and Casa Frata, Peyrolles, Almenara (-1.75 My to -1.5 My), there are no such trivial taxa missing. In some cases, all or a majority of the missing taxa are carnivores, namely in the Montopoli, Roccaneyra, Pardines assemblage or assemblage 2 (c. -2.5 My to c. -2.25 My), and in the assemblage 8, that of Vallonet, Mosbach I, Solihac, Ponte Galeria and correlated (-1 My to -0.74 My). In the Sinzelles, Farneta assemblage both, trivial Carnivora and Ungulata are missing (Figure 1, II). The record of Ungulates appears more regular than the one of Carnivores (Table I, Figure 1, III); it is regularly increasing with a light deviation due to trivial taxa missing in the Sinzelles, Farneta and in the Venta Micena assemblages. The subtotal of Cervoidea plus Bovoidea is quite constant indeed, the range being 9 to 12 taxa averaging 10 taxa. The slight decay of the record in the Sinzelles, Farneta complex may reflect an actual faunal crisis. Missing Carnivora and Primates is a bias due to taphonomic conditions in the formation of

sites, somewhat frequent in sites originated without anthropic influence.

According to the evidence exposed in the precedent sentences, the recorded oscillation of the Bovid vs. Cervid dominance is reliable (Table I, Figure 1, IV). This relationship is expressed as the percentage of Bovid taxa to the subtotal of taxa of these two families. The oscillation of the alternative dominance of Bovids vs. Cervids has been mentioned as a climatic indicator (Figure 1, V). In our case this view is strengthened to some extent. The dominance of Cervids in early Villafranchian assemblage 1 (Etouaires, Villarroja) is recovered in the Early Pleistocene assemblage 6 (Sinzelles); after an oscillation, it is surpassed in assemblages 8,9. These are correlated with the Early to Middle Pleistocene transition of the conventional stratigraphic language. The predominance of Bovids in Late Pliocene is continued in Early Pleistocene, but with fluctuations and gradual decay. Major inflections occur c. -2.5 My and near -1.5 My. These oscillations cannot be matched with the oxygen isotope curves of ocean paleotemperatures, their resolution or frequency being looser; these are more comparable to those of the classical glacial interglacial cycles and to palynological divisions.

Two extinction maxima occurred, around -2.5 My and near -1.5 My. Both events are reflected taking into account genera as well as the taxa of lesser rank. The fluctuations are quite sharp in the first case (Table I). Over a total of 48 genera recorded, some 21 are lost in two million

years : an average of slightly over 10 per million years.

Not all the extinction cases counted for (see Table I) are true extinctions. Among the genera, Papio, Nyctereutes, Acinonyx, Tapirus and Gazella survived either in Africa or in other continents and are still alive. Chasmaportetes did not survive very long in Africa (until -1.5 My, approximately), almost the same as Megantereon; Hipparion lasted in Africa longer than in Europe in a subgenus quite peculiar and well characterized, Stylohipparion. Therefore, with respect to a global record, the generic extinction figures of the intervals -2.5 My, -1.75 My, and -1.5 My should be lowered one unit; those of the -2 My interval are nul. Not so, if we speak here of "extinctions" meaning the disappearance from the record at a continental, or widely regional, level. The "regional" losses are, in our studied period, 5; the true, total generic extinctions are 14.

In our case, one cannot speak of mass extinction of species or subspecies. In each of the eight periods of 0.25 My along two million years studied, the last quotations of specific or subspecific taxa vary from 4 to 9 (Figure 1, VIII). The extinction rates for intervening intervals are distributed within a range of 11.8% to 28.1%. The last index is the only one that could be said to approach the qualification of a catastrophe; it occurs at the interval of -1.5 My, the one following the faunal complexes of Casa Frata, Peyrolles, Almenara 1. Remember that the record of the next stage is deficient.

In fact, a general trend of specific or subspecific replacement is seen all along the Early Pleistocene, with extinction rates above the average. One can say that from near -1.8 My to near 0.9 My there has been an almost constant or gradual screening of species.

The disappearance of up to 5 genera (barely a 20%) occurs in one interval, that of c. -2.5 My. In two successive intervals the loss of 4 genera is observed, making a total of 8 disappearances in less than half a million years. These two maxima of generic extinctions are immediately followed by intervals without a single generic loss. A double rhythm is here out of question: a major loss of genera is straight followed by a short stage of stability, at a generic level, compatible with specific change. Then the disappearances of genera restart and more or less gradually increase up to a new maximum (Figure 2, XIV).

The above referred maxima of generic extinctions are not quite spectacular, although conspicuous. The highest percentages observed are 18.5 at the interval near -2.5 My and the two figures 13.3 and 15.4 obtained for the two successive intervals of -1.75 My and -1.5 My around the Pliocene-Pleistocene Boundary (Figure 2, XVI). May we recall that the global figure for the end of Blancan in North America, near -1.9 MY, relate to a period of almost one million years, is of 11 lost over 43 (c. 25%) Mammalian genera comparable to ours by their size. The events I am recalling here stay very far from deserving the qualification of catastrophic, or "mass extinction", as is the case established on the Rancho La Brea record. Up to 33 out of 57 genera, comparable to those here considered, that is a 56% became extinct after Rancho La Brea time of deposition, that is, in less than 20,000 years. Similar or no much lesser figures could be obtained for the Recent extinctions in Eurasia, South America and Madagascar. The gentle, birhythmic mood of generic extinctions in the case we are considering could respond to a more general, may we say normal pattern.

The overall faunal replacement and its opposite faunal stability are reflected by the number and percentage of trivial taxa (Table I; Figure VI, VII), and also by an index, or Rate of Faunal Change (RFC) according to either genera or minor taxa (Table I; Figures 2, XV; 1, IX).

Faunal assemblages 3 and 9 are the most conservative, according to the amount of trivial taxa, while assemblage 7, namely that of Venta Micena, is affected by a strong instability, a turnover could be said (Figure 1, VI).

Three maximal percentages (Table I; Figure 1, VII) of trivial taxa above 60% are recorded at the assemblages 3, 6, 9; and three low average rates (between 47% and 48%) at assemblages 2, 5, 8, the minimum (34.5%) being that of assemblage 7. The change index, or RFC referred to intervals between faunal assemblages grouped into time spans of equal duration, shows for the account of genera two maxima (Figure 2, XV): one around -2.5 My, and other protracted at c. -1.75 My and c. -1.5 My (Figure 2, X). A moderate maximum comes near -1 My. Taking into account the specific and subspecific taxa, the turnovers, with a RFC index above 55%, occur near -2.5 My and near -1.0 My. Faunal remaking has apparently been gradual and protracted along the Early Pleistocene after a maximum of faunal stability around -2.0 My, with up to 90% of surviving genera and 73.5% of surviving taxa. Rates of stability similar to these are found for the beginning of the Brunhes chron, that is, the Cromer-Early Elster complex, equivalent to oxygen isotopic curves 19 to 15. Replacement of species and genera are coincident in the first part of the time studied; a very high rate of specific turnover occurs near -1 My, more than half a million years later than the preceding maxima of change at generic level.

An input of new genera occurs immediately after the maximum of generic extinction of the c.-2.5 My interval. The increasing figures are 3 and 4 new genera for the faunal assemblages 2 and 3, respectively. The percentual rates of renewal are 11.1 at the c.-2.5 My and 14.3 at the -2.25 My intervals (Table I; Figures 2, XIII and XVII).

The curves of generic renewal are less regular and the variations are less sharp than those of extinctions. The renovation following the second maximum of extinction is protracted all along the Early Pleistocene with a slight fluctuation. After a stop with only 1 new recorded genus in assemblage 4, a sequence of 3,2,3,4 new recorded genera occurs in assemblages 5 to 8, respectively. The renovation rates at the corresponding intervals are: 10% around -1.75 My; 7.7% at the next interval; 12% c.-1.25 My, and 11.8% at the -1 My interval. After a more or less protracted epoch of increasing rates of genera newly introduced, a time follows in which the input of new genera in the faunas is drastically reduced: this is the case in assemblages 4 (Chilhac) and 9 (Isernia, Süssenborn, lower Atapuerca). The renovation rates in the corresponding intervals of -2 My and -0.75 My are equally minimal, 3.4%. A sort of a double rhythm is also conspicuous in the renewal of genera.

If we take into consideration the taxa of lesser rank (Figure 1, IX) there is also an oscillation, but with different degree in the increasing-decreasing slopes along the sequence. The maxima of first recorded appearance of species and subspecies occur in assemblage 21, (Roccaneyra, Montopoli), with a number of 10, and successively in assemblages 7 and 8 with 11 and 15 respectively. Origination of species and specialisation of subspecies -anagenetic in some cases, splitting in others- appears as a complementary mechanism for the renovation of faunas, which is additional to the migration-extinction balance.

Change and stability alternate in two complete cycles during the time span considered. In these two cycles the extinctions and the new faunal elements (introduced either by immigration or by evolution) appear to compensate each other in some way, giving the impression of a constantly and smoothly oscillating equilibrium, within moderate rates of change. True catastrophic breaks are not seen in this period (Figures 1,X; 2, XV).

One can see that the maxima of change occur when more or less higher levels of both extinction and renovation overlap. This is the case of the interval c.-2.5, when a high rate of extinction is accompanied by new appearances above the average, and similarly that of the -1.75 My interval. This is also the case with the high rate of overall change at specific level near -1. My, due to an extensive event of speciation.

Let us move now to investigate the eventual relationships of the pattern of faunal replacement discussed in the preceding sentences with other sequences, or cycles of events on Earth's crust and lighter envelopes. Matching of these sequences has been eased thanks to the accuracy reached in geochronometric techniques in recent years, and to the increased maturity in the use of these for dating and correlating sequences of events, that left their imprint in rock surfaces and in sedimentary formations.

The curves of extinction, renewal and faunal replacement for large mammals in Western and Central Europe from -2.6 My to -0.6 My have been matched: (a) to a sequence of diastrophic events recorded both in Central Italy and in Spain; (b) to the magnetostratigraphic scale; (c) to the palinostratigraphic stages established for central-western Europe; (d) to the climatic phases established by Emiliani and revised by Shackleton for the oceanic paleotemperatures inferred from the fluctuations of oxygen isotopes (see Figures 1,2).

The first maximum of faunal turnover coincides with or slightly precedes the end of the paleomagnetic Gauss chron, and the early major climatic deterioration that is commonly correlated with the beginning of the Praetiglian paleobotanical unit. It follows and partially coincides with the Acquatraversan unconformity of Italian authors, likely also with the suggested age for the Iberomanchegan 2 diastrophic phase. Our faunal event is no older than -2.7 My and no younger than -2.4 My. For the end of the Gauss we may accept an average date between -2.5 My and -2.45 My. Montopoli fossils occur in a regressive facies consequent and partly coincident to a sharp tilting. Again, -2.5 My to -2.4 My is the age more widely recognized for a general severe cooling, which is reflected in the Praetiglian floral change.

The second, protracted maximum of change at generic level, with increasing slope at specific level, starts not earlier than -1.85 My, that is after Chilhac and Coupet, and ends certainly earlier than -1.4 My, that is before Farneta. This time span includes two of the divisions practically adopted in this study, both of them with equal rate of faunal change for genera. These dates include the Olduvai subchron, with late tiglian flora and the span of

the Eburonian floral assemblage; they also include a protracted epoch with warm climate and a long phase with dominant cold temperatures according to the oxygen curves. In fact, signs of declining temperatures are seen since near -1.84/1.81 My; the general decline is accentuated near -1.75 My, and quite sharply at -1.61, that is at the end of the Olduvai subchron and quite closely to the base of the Pleistocene. The Aullan unconformity in Central Italy is dated as between -1.7 My and -1.4 My, just following the Olivola faunal assemblage. Most likely, the cooling recorded at Olivola is not the Eburonian, but that of the oscillations that occurred near -1.8 to -1.75 My.

The third faunal crisis, less severe for generic than for specific change, and mostly consisting on speciation events, starts with Untermassfeld and Venta Micena, that is not earlier than the Sinzelles minimum age (-1.3 MY); it reaches a climax before the deposition time of Vallonet and Mosbach I, that is no later than -1.0 My. These two dates are just bracketing the dominantly warm (should say very warm) epoch that includes the Waalian and the oxygen isotope optima 25 to 37, with two significant cold to fresh interphases: 32 between -1.2 and -1.15 My, and 26 between approximately, -1.05 and 1.03 My. These dates precede the Cassian unconformity in Italy.

We therefore should recognize that two maior events of faunal replacement are related with a trend of climatic deterioration, and that these precisely occur during and are pronounced at the end of a time of normal magnetic polarity; the third and the latest, on the contrary, runs exactly with high and ameliorating temperatures, along a time of reverse polarity almost exclusively. The sign of the latter, nevertheless, differ from that of the former ones.

two, since that one is characterized for species renovation, the other two by generic substitution. One could therefore think on an almost generalized speciation event related to an ecological diversification at the end of Early Pleistocene. It is also noteworthy, that the intervals with highest rates of faunal stability are the one around -2. My and the other c.- 0.75 My. The first includes the beginning of the Tiglian with a very cold phase following a warm stage c.-2.2 My, with a sharp end at -2.1 My. The second corresponds to several fluctuations of paleotemperatures starting from very cold (curve 22) up to the temperate, short warm phase of curve 19, that is, exactly the end of the Matuyama chron of reverse polarity. Another time interval with high rate of stability is that from -1.4 My to maybe -1.2 My, corresponding to a trend of improving thermal conditions, from curve 39 to 33, temperate to warm, and coincident with early Waalian.

Let us conclude that changes in the faunal composition of large Mammals are apparently related in some way with variations of climate, not following in detail every oscillation of temperature, but rather in correspondence with envelopping curves and as affected by durable trends. A correspondence of accentuated faunal instability with phases of crustal disequilibrium is not constant. Regression of sea level and consequent erosion in land in this period, can be related to increase of ice caps, at least partially; elevation of mountain chains and of continental masses may contribute to cooling at least in temperate latitudes. In fact, the Acquatraversa erosive phase is contemporaneous with the Praetiglian cold phase; the Aulla unconformity corresponds to the Eburonian and late Olduvai, and the Cassia may well correlate with the Menapian (curve 22).

Lowering of sea level and relative elevation of lowlands can favour migrations and competition of species. Isolation, on the other side may influence local and anagenetic specialisation.

The long rank fluctuations, such as the classic glacial-interglacial cycles, the floral stages and the stability/replacement cycles in the faunal composition -as we can estimate from the big mammals-, may be a result of feeding-back effect and additional inputs of the atmospheric and astronomic variables. These effects respond for fluctuations in faunal composition of the magnitudes seen in this case, but could also be responsible for more critical disequilibria, like those of catastrophic or mass extinctions in other circumstances.

With regard, particularly, to the extinction events -that is the subject of our present common concern-, the disappearance of 5 (18.5%) genera including that of 9 (26.5) species of the large mammals of the Early Villafranchian faunal of Etouaires and Villarroja before the Montopoli, Roccaneyra and Pardines, between -2.7 My and -2.4 My, could be related to either a crustal diastrophism or a severe climatic deterioration, or both. The disappearance of 8 genera between Chilhac-Olivola and Sinzelles-Farneta, that is in two time slices of a quarter of a million years, between -1.8 My and -1.4 My, with an extinction rate of 13.3% and 15.4% in each interval, is related to progressive climatic deterioration along the dominantly warm to temperate phase during the Olduvai subchron, and to the sharp fall in oceanic paleotemperature near -1.61 My, with 9 subsequent cold phase. This extinction event also runs contemporary to the Aullan erosive epoch, to Eburonian cold floral stage and to a

vegetational zonal change in the Mediterranean, according to recent investigations of SUC (1987). The extinction rates for specific taxa in the same intervals (c.-1.7 My and c.- 1.5 My) are 19.4% and 28.1% respectively. We cannot confirm here the model described by D. WEBB for North America, in which the major extinction events occurred at the end of glacial cycles. Extinction of species and subspecies is protracted after the Venta Micena time until the begining of Middle Pleistocene, with 9 and 6 last quotations in these time slices, respectively, what means extinction rates of 20.9% and 15% for their following intervals. Generic losts in these are less significant. In fact, the passage from Early to Middle Pleistocene is absolutely conservative and bears the mark of faunal stability. It corresponds to a time slice of improving climate after a sharp fall of temperatures from warm to very cold that occurred at 0.82 My, just after the date of the Solihac fossil record. A considerable amount of new recorded genera, at the Jaramillo and late Matuyama times, possibly related, al least in part, withe Cassia erosional phase, can be responsible for an intrafaunal stress influencing specification and splitting of ecosystems.

To all appearances, both extinction events and major faunal crises, in the case studied, are coincident with last records of normal magnetic polarity. Wheter or not is there any cause-effect, or deterministic relationship can be a subject for further research.

I am sure that this story of the faunal replacements in Late Pliocene and Early Pleistocene does not provide for us an answer to the problem of generalized extinctions and true critical turnovers in faunal composition that occurred several times in the History of Life. But let me suppose that this attempt of accurately describing a non-catastrophic case of faunal replacement may help, as a reference fact not empty of usable information.

III JORNADAS DE PALEONTOLOGIA
PALEONTOLOGIA Y EVOLUCION: FENOMENOS DE EXTINCION

EXTINCIONES EN LA FAMILIA EQUIDAE (PERISSODACTYLA, MAMMALIA) SUBSECUENTES A LOS CAMBIOS CLIMATICOS

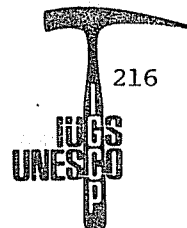
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RESUMEN: El actual conocimiento de los cambios climáticos globales nos permite inferir su influencia en la extinción o extinciones de asociaciones o grupos faunísticos. En la familia Equidae podemos deducir la extinción tanto de Anchitherium como de Hipparion en base a cambios climáticos. El reemplazo de la asociación faunística de Anchitherium por la de Hipparion en torno a 13-12 M.A. en el área Mediterránea puede relacionarse con la crisis climática del Serravaliense que implica un período menos cálido y más seco; e incluso podría estar ligado a un evento tectónico responsable de la separación del Tetis-Paratetis (DEMARCO, 1985). Por otra parte la extinción de Hipparion parece estar enlazada al primer enfriamiento ocurrido alrededor de 3,0-2,5 M.A. (ALBERDI, 1987).

ABSTRACT: The present knowledge of global climatic changes allows the authors to infer their influence on the extinction(s) of assemblages or faunistic groups. In the Equidae family, the extinctions of bot Architherium and Hipparion may be deduced on the base of climatic changes. The replacement of the Anchitherium faunal assemblage by the Hipparion assemblage, about 13-12 M.A. in the Mediterranean area, may well be related to the Serravallian climatic crisis. During this crisis there was a less warm period and drier conditions. It may also be related to a tectonic event, which separated the Tethys from the Paratethys (DEMARCO, 1985). On the other hand, the extinction of Hipparion appears to coincide with the first cold period, approximately 3.0-2.5 M.A. (ALBERDI, 1987).



III JORNADAS DE PALEONTOLOGIA
PALEONTOLOGIA Y EVOLUCION: FENOMENOS DE EXTINCION

MIGRATIONS AND EXTINCTIONS OF MICROMAMMALS DURING THE OLIGOCENE AND MIOCENE IN SPAIN

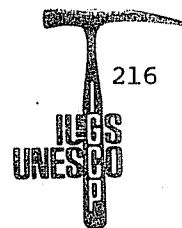
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ABSTRACT: In this paper it is demonstrated that migrations and extinctions of small mammals in the Oligocene and Miocene continental faunas of Spain are related to climatic events. In some cases tectonic events may have played a role. During the Late Oligocene and the Oligocene/Miocene boundary interval no large scale climatic and/or Paleoeological events took place, and consequently immigration and extinction phenomena are not frequent. In the Early Miocene a cooling trend sets in and the entry of various taxons of northern origin is observed. Afterwards, during a warming-up trend and large scale tectonic movements in the Mediterranean area (Early Aragonian, which may be correlated to the Late Burdigalian) a massive immigration of modern cricetids (hamsters) and other small mammals is observed. This is followed by a successive disappearance of various micromammals taxons, when temperatures reach tropical values in a relatively dry environment. Several of these species migrate to S-Germany where they are found in more modern faunas. During the cooling trend of the Late Aragonian (comparable to the Serravalian) again it is observed that small mammals of northern origin migrate into Spain.



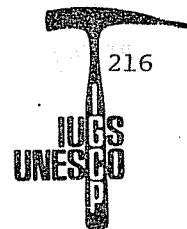
III JORNADAS DE PALEONTOLOGIA
PALEONTOLOGIA Y EVOLUCION: FENOMENOS DE EXTINCION

BACKGROUND AND MASS EXTINCTION OF THE MICROMORPHIC BRACHIOPODS FROM THE NORTHWEST EUROPEAN UPPER CRETACEOUS CHALK.

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ABSTRACT: The very detailed biostratigraphy, monotonous lithology and, in general, uniform depositional environment spanning about 23 million years, are features characteristic of the Upper Cretaceous chalk of northwestern Europe. They make this area an excellent frame for a study of the evolutionary patterns of a fossil group. The micromorphic brachiopods are well preserved, presents high diversity and density and have been transported very little, if at all. They are well documented on the species-level, and in each sample numerous generations of each species are represented. Furthermore, they show high environmental tolerance and wide biogeographic distribution. The material provides a unique possibility of following the brachiopod fauna from its early colonization of the chalk in the Coniacian, through reaching an absolute optimum in Maastrichtian, through its sudden end-Maastrichtian devastation and up to its Lower Danian recolonization of the chalk. 85 species are recorded from the Coniacian-Lower Danian and of these 60 appear during the Upper Cretaceous. 30 species occur in the Lower Danian and of these 25 are new. Through the Upper Cretaceous the number of species increases gradually, the rate of speciation being relatively low and the rate of extinction even lower, both varying only a little. Coinciding with the Maastrichtian-Danian boundary 70% of the species become extinct. Among these are the short-ranging, highly specialized, free-lying hemisphaerical forms. In the Lower Danian a new fauna forms through rapid adaptive radiation within surviving long-ranging, morphologically conservative forms.



Mass extinctions in the fossil record of late
Palaeozoic and Mesozoic tetrapods

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ABSTRACT. The fossil record of tetrapods is very patchy because of the problems of preservation in terrestrial sediments in particular, and because vertebrates are rarely very abundant. However, the fossil record of tetrapods has the advantages that it is easier to establish a phylogenetic taxonomy than for many invertebrate groups, and there is the potential for more detailed ecological analyses.

The diversity of tetrapods increased during the Devonian, the Carboniferous, and the Permian, but it remained roughly constant during the Triassic, the Jurassic, and the Early Cretaceous. Overall diversity then began to increase in the Late Cretaceous, and continued to do so during the Tertiary. The rapid radiation of "modern" tetrapod groups - frogs, salamanders, lizards, snakes, turtles, crocodiles, birds and mammals - was hardly affected by the celebrated end-Cretaceous extinction event.

Major mass extinctions amongst tetrapods took place in the Early Permian, Late Permian, the Early Triassic, the Late Triassic, and at the end of the Cretaceous. Many of these events appear to coincide with the major mass extinctions amongst marine invertebrates, but the tetrapod record is largely equivocal with regard to the recent theory of cyclicity of mass extinctions. Some data, on the Permo-Triassic events, is very much against the cyclical model, since the events are irregularly spaced in time. However, the absence of mass extinctions amongst Jurassic and Cretaceous tetrapods, apparent evidence against cyclicity, may be explained by the relatively patchy fossil record during those periods.

INTRODUCTION

Most studies on mass extinctions so far have focussed on the fossil record of marine invertebrates (e.g. Raup and Sepkoski 1982, 1984, 1986; Jablonski 1986; McKinney 1986). A smaller number of studies have used the fossil record of vascular plants (Niklas *et al.* 1983) and non-marine vertebrates (Benton 1985a, b), and there has been an implicit assumption that these records are poorer. Indeed, the fossil record of marine invertebrates generally has the advantages of abundant specimens, good stratigraphic control, closely spaced samples, uniform preservation quality, broad geographic distributions, and a mature taxonomy.

The aims of this paper are to consider the problems and the advantages of the fossil record of tetrapods of the late Palaeozoic and Mesozoic, and to outline what has been learnt from it about mass extinctions.

THE NATURE OF THE THE FOSSIL RECORD OF TETRAPODS

Scope

The first tetrapods, according to most recent classifications (e.g. Romer 1966; Carroll 1977; Smithson 1985; Panchen and Smithson 1988) are the Ichthyostegalia (Ichthyostegidae, Acanthostegidae), known first from the Famennian Stage (c. 365 Myr.) of the Late Devonian. There are earlier records of tetrapods from the Devonian, based on footprints, but skeletal remains only are considered here. The tetrapods radiated during the Carboniferous into nine or more major lineages of labyrinthodont amphibians which were generally bulky carnivores and piscivores that lived near water, and lepospondyl amphibians that were often smaller and more varied in their modes of life. One labyrinthodont lineage led to the amniotes, the clade of tetrapods that moved away from a dependence on the water.

The first amniotes, and thus the first reptiles, according to most recent classifications (e.g. Romer 1966; Carroll 1982; Heaton and Reisz 1986) are the Protorothyrididae (= Romeriidae), known first from the Moscovian Stage (c. 300

Myr.) of the Late Carboniferous. During the remaining 15 Myr. or so of the Carboniferous, the early amniotes diversified into a number of additional lineages - the Araeoscelidia and the "Pelycosauria", the most primitive groups of the Diapsida and Synapsida respectively. These two amniote clades dominated tetrapod evolution from the Late Carboniferous to the present day. The Diapsida radiated during the Permian and Triassic, and gave rise to sphenodontians, the ancestors of lizards and snakes, crocodilians and dinosaurs in the Triassic, and birds in the Jurassic. The Synapsida radiated in the Permian and Triassic as the mammal-like reptiles, and gave rise to the mammals towards the end of the Triassic. The mammals remained at low diversity during most of the Mesozoic but began to radiate strongly in the Late Cretaceous, well before the end-Cretaceous event.

The labyrinthodont amphibians continued, in reduced numbers, through the Permian, Triassic, and Early to Middle Jurassic. The modern amphibians (Lissamphibia) apparently arose in the Permian or Early Triassic, and gradually increased in diversity during the Mesozoic, but they never became abundant.

The diversity and importance of the major tetrapod groups are indicated in the phylogenetic tree in Fig. 1. This is based on recent cladistic analyses, although these leave many doubtful relationships, and familial diversity is indicated.

In all, there are 858 families of living and extinct non-marine tetrapods, and 58 families of exclusively marine tetrapods (Benton 1987a, b), giving a total of 916 families. The figures for late Palaeozoic and Mesozoic families are 338 non-marine, and 32 exclusively marine, giving a total of 370 (see Table 1).

Quality of the fossil record of tetrapods

The relative incompleteness of the fossil record of tetrapods has been described by many authors (e.g. Pitrat 1973; Bakker 1977; Carroll 1977; Olson 1982; Padian and Clemens 1985; Benton 1985a, b, 1987a). The record of the non-

marine tetrapods, which make up the vast bulk of all tetrapods, is particularly poor. Some stratigraphic stages, for example the Aalenian (Middle Jurassic), have yielded no identifiable tetrapod fossils at all anywhere in the world, and other stages [e.g. Gzelian (Carboniferous); Toarcian, Bajocian, Callovian, Oxfordian (Jurassic); Berriasian - Aptian, Cenomanian - Santonian (Cretaceous)] have yielded very few remains.

The incompleteness of the fossil record of terrestrial tetrapods has been characterised in another way by Padian and Clemens (1985, p. 82). Most dinosaur genera are known only from a single stratigraphic stage which would suggest, in a literal reading of the fossil record, that the dinosaurs experienced total generic mass extinction 24 or 25 times during their history. However, at the family level, there is only the one final K-T mass extinction event since dinosaur families generally span more than one stage.

It is possible to estimate the completeness of the tetrapod record in a broad way by examining the numbers of families present per stage. The Simple Completeness Metric (SCM, Paul 1982; Benton 1987a, b) compares the numbers of families that are known to be present compared to the numbers that ought to be present. The SCM is based on the fact that tetrapod families span several stratigraphic stages. The family may be represented by fossils throughout its entire duration, or there may be gaps spanning one or more stratigraphic stages where fossils are absent. Jablonski (1986) has termed this the Lazarus Effect, where a taxon apparently disappears, and then reappears higher up in the sequence. The more incomplete the fossil record is for a particular stage, the more Lazarus (hidden) taxa there will be. The SCM ranges from 0% (no fossils at all, e.g. Aalenian) to 100% (all families represented by fossils); e.g. Viséan, Ufimian, Scythian). Most other stages have SCM values between 50 and 100%, but values fall below 50% in the Early-Middle Jurassic (Toarcian-Bajocian), the Late Jurassic (Oxfordian), and the Late Cretaceous (Turonian-Santonian).

Advantages of the fossil record of tetrapods

The fossil record of tetrapods is not as hopeless for studies of mass extinction as has often been assumed. It has a number of advantages over the record of marine invertebrates, and these are noted briefly below.

(1) There is a high probability of identifying clades. Rates of evolution, extinction, origination, and so on, should apply to monophyletic groups (sensu Hennig 1966; that is, holophyletic groups, sensu Ashlock 1971) only, and not to paraphyletic groups (groups that had a single ancestor, but exclude some of the descendants of that ancestor). This is because monophyletic groups (clades) have a unique history that exists and is to be discovered, whereas paraphyletic groups may start off with a unique history, but their boundaries are adjusted a posteriori, and they are in part a human invention (Cracraft 1981). For example, the well-known "Class Reptilia" is paraphyletic. That is, all reptiles derive from a single common ancestor (or the group could be defined in that way by juggling some early groups between "Amphibia" and "Reptilia"). However, the group "Reptilia" does not include all of the descendants of that ancestor (Aves and Mammalia are excluded). The boundary line between reptiles and birds, or reptiles and mammals is an arbitrary cut-off, and the line could be moved up and down depending on which synapomorphy is regarded as defining. This means that the upper limit of Reptilia is not fixed by any positive attribute, only by the absence of a synapomorphy. The lower limit of "Reptilia", and of clades, is also arbitrary in one sense, in that it can be drawn at many different levels, but it depends on a positive attribute, the acquisition of a synapomorphy, which defines an evolutionary event.

The finding of clades for macroevolutionary studies depends on cladistic analysis. Vertebrates have proved highly amenable to this technique, as have only a few invertebrate groups (e.g. echinoderms, arthropods). This suggests that it may be hard to define cladistic families for the bulk of the record of fossil invertebrates. The significance of this problem has been highlighted by Patterson

and Smith (pers. comm. 1987), who find that as much as 76% of the standard data set on fossil echinoderms and fish (Sepkoski 1982), used in most recent studies of mass extinctions, is invalid because the families are paraphyletic, polyphyletic, monogeneric, or monospecific. A reanalysis of a cladistically-based data set of marine animals would probably yield rather different patterns of extinction. A study of this sort on "pre-cladistic" and cladistic data sets of non-marine tetrapods (Maxwell and Benton 1987) has shown considerable, but unpredictable, changes in the patterns of extinction. This study suggested that, from 1966 to 1986, the major improvements in our knowledge of the past distribution of tetrapods stemmed more from the rigorous identification of monophyletic groups than from the discovery of new fossils. These improvements may not be possible in most of the fossil records of marine invertebrates because of the problems of cladistic analysis.

(2) Tetrapods offer great scope for ecological analysis. Many detailed studies of the functional morphology and palaeoecology of single species (autecology) of fossil tetrapods have been carried out, and these often allow detailed reconstructions of their modes of life. Studies have also been made of whole faunas (synecology). This work offers potentially great contributions to detailed palaeobiological interpretation of aspects of extinction events. It may be possible, for example, to compare "extinction-prone" and "extinction-resistant" taxa for a broad range of potential ecological correlates: size, diet, position in food chains, locomotory adaptations, reproductive mode, growth rate, habitat preference, geographic distribution, and so on. Tetrapods may lend themselves more readily to detailed ecological analysis than many marine invertebrates. This work is facilitated by our knowledge of the ecology of modern terrestrial vertebrates, which is greater than that of modern marine invertebrates.

(3) The generic- and species-level taxonomy of tetrapods is a mature branch of systematics. Because Homo sapiens is a non-marine tetrapod, zoologists have devoted more attention to the systematics of mammals, birds, reptiles and

amphibians than they have to the systematics of brachiopods, annelids, pogonophorans or hyolithids. Our understanding of the relationships and the bounds of living tetrapod species is probably more mature than that of any other group of organisms. This should allow more confident extrapolation of such concepts into the past, and thus better identification of fossil genera and species, better censuses of these taxa, and better phylogenetic reconstructions, thereby improving the usefulness of such data for macroevolutionary research.

TETRAPOD FAMILY DIVERSITY ANALYSIS

Several authors have recently plotted graphs of the diversity of tetrapod families and orders through time (e.g. Charig 1973; Pitrat 1973; Bakker 1977; Thompson 1977; Olson 1982; Padian and Clemens 1985; Colbert 1986). However, these graphs have been based largely on data from Romer (1966) and Harland et al. (1967), the classic source works. More recent studies (Benton 1985a, b, 1987b) have been based on a new compilation of data on families of non-marine tetrapods (Benton 1987a,b). These new compilations differ significantly from those derived from Romer (1966) and Harland et al. (1967) in several ways:

(1) New records up to the end of 1985 are included. This has affected the date of origination or extinction of as many as 50% of families.

(2) The latest cladistic classifications have been incorporated, as far as possible, and attempts have been made to test that all families are clades. This has caused significant rearrangements of families of late Palaeozoic and Mesozoic reptiles in particular, by amalgamations and redistributions of genera into monophyletic taxa.

(3) The stratigraphic resolution of family distributions has been improved. As far as possible, the dates of origination and extinction of each family have been determined to the nearest stratigraphic stage, usually by examination of the primary literature. The stage is the smallest practicable division of geological time for this compilation (relevant stage lengths vary from

2-19 Myr. in length, with a mean duration of 6 Myr.). This allows more detailed analysis than simply relying on the Lower, Middle and Upper divisions of geological periods in Romer (1966) and elsewhere.

The new compilations of data on fossil tetrapod family diversities have been used for a variety of graphs and calculations. A small number of families that are based on single species or single genera have been omitted.

The diversity of non-marine tetrapods has increased through time, with a particularly rapid acceleration in the rate of increase from the Late Cretaceous (Campanian) onwards (Fig. 2; Benton 1985a,b). Three major diversity assemblages have been identified (Benton 1985b), which appeared to dominate for a time, and then gave way to another: I (labyrinthodont amphibians, "anapsids", mammal-like reptiles) dominated from Late Devonian to Early Triassic times; II (early diapsids, dinosaurs, pterosaurs) dominated during the Mesozoic; and III (the "modern" groups - frogs, salamanders, lizards, snakes, turtles, crocodiles, birds, mammals) have dominated from Late Cretaceous times to the present day.

There appear to be six declines in diversity (Fig. 2, nos. 1-6) that are attributable to mass extinction events, four of which fall in the late Palaeozoic to Mesozoic interval. The other drops (Early Jurassic, end-Jurassic, mid-Cretaceous) probably indicate mainly a change in the quality of the fossil record (Benton 1985a, b), and mass extinctions cannot be assumed here. These three episodes correspond to times when the SCM described above gives particularly low values.

Extinction and origination rates were calculated stage by stage for non-marine tetrapod families based on the new data set. Total extinction (R_e) and total origination (R_g) rates were calculated as the number of families that disappeared or appeared, respectively, during a stratigraphic stage, divided by

the estimated duration of that stage (Δt):

$$R_e = \frac{E}{\Delta t} \text{ and } R_s = \frac{S}{\Delta t},$$

where E is the number of extinctions and S is the number of originations. Per-taxon extinction (r_e) and origination (r_s) rates were calculated by dividing the total rates by the end-of-stage family diversity D (Sepkoski 1978):

$$r_e = \frac{1}{D} \cdot \frac{E}{\Delta t} \text{ and } r_s = \frac{1}{D} \cdot \frac{S}{\Delta t}.$$

The per-taxon rates can be seen as the "probability of origin" or the "risk of extinction". In these calculations, the recent summary geological time scale of Palmer (1983) was used for stage lengths in Myr.

The graphs of total rates (Fig. 3) for amniote families show great fluctuations in both origination and extinction rates. There is no clear correlation of high extinction rates with all mass extinction events. Of the highest rates, those in the Artinskian, Tatarian, "Rhaetian", Maastrichtian, Rupelian, and Late Miocene correspond to mass extinctions 2, 3, 4, 5 and 6 (Fig. 2) respectively. Equally high, or higher, total extinction rates in the Ufimian (Late Permian), Tithonian (Late Jurassic), Coniacian (Late Cretaceous), Thanetian (Late Palaeocene), Ypresian (Early Eocene), Bartonian - Priabonian (Middle - Late Eocene), Pliocene and Pleistocene do not match any of the drops in amniote diversity that have been ascribed to mass extinctions.

The total origination rates (Fig. 3) generally track the total extinction rates quite closely. Peaks in both rates may be produced in part by episodes when the fossil record is better than usual, corresponding to particular Fossil-Lagerstätten, such as the Sakamena Group (Late Permian) and the Solnhofen

Limestone (Tithonian). The improvement in the record boosts the apparent number of family originations and extinctions (Hoffman and Ghisold 1985).

The per-taxon rates remove this bias in part. When extinction and origination rates are recalculated relative to the numbers of taxa available (Fig. 4), the rates do not track each other so closely, although "Lagerstätten peaks" remain in the Ufimian, Tithonian and Coniacian. There are particularly high per-taxon extinction rates at times of mass extinctions corresponding to the Artinskian, Tatarian, and "Rhaetian" events (nos. 1, 2, 3: Fig. 2). Per-taxon extinction rates are barely elevated at the times of the Maastrichtian, Rupelian, or Late Miocene mass extinctions (nos. 4, 5, 6: Fig. 2). These mass extinctions correspond to depressed per-taxon origination rates (Fig. 4), as noted by Benton (1985b).

MASS EXTINCTIONS

The history of non-marine tetrapods has apparently been punctuated by at least six mass extinction events (Fig. 2; Benton 1985b), together with up to seven other possible extinction events. These had widely differing effects, ranging from a 58% drop in family diversity for the Early Permian event to a 2% drop for the Late Miocene event. It has already been argued (Benton 1987b) that the fossil record of tetrapods is generally not complete enough to test the hypothesis of periodicity of mass extinctions (Raup and Sepkoski, 1984, 1986), but data from the Triassic record appear to contradict the idea (Benton 1986a, 1987b).

The four extinction events in the late Palaeozoic to Mesozoic interval, together with the other possible events, are summarised briefly below, with notes on the groups that became extinct, and those that survived. More details of reptile extinctions is given in Benton (1987b).

Early Carboniferous (Serpukhovian): four families of amphibians died out at the boundary between the Early and the Late Carboniferous:

Labyrinthodontia: Proterogyrinidae, Eoherpetontidae;

Lepospondyli: Adelogyrinidae, Acherontiscidae.

This may correspond to the end-Namurian marine event noted by Sepkoski and Raup (1986, p. 23), by Saunders and Ramsbottom (1986), and by others. The small number of tetrapod families lost (and each of them is of low diversity) gives lower than normal extinction rates (Figs. 3, 4). This cannot be regarded as a well-supported tetrapod extinction event.

Late Carboniferous (Kasimovian-Gzelian): two families of tetrapods died out:

Lepospondyli: Ophiderpetontidae, Tuditanidae.

The suggested end-Carboniferous extinction event (Sepkoski and Raup 1986, p. 23) is even less convincing for tetrapods. Only two families of rather rare Lepospondyli disappeared, and the extinction rates were low during both stages (Figs. 3, 4).

Early Permian (Artinskian): fifteen families died out during this event (no. 1: Fig. 2):

Labyrinthodontia: Saurerpetontidae, Trematopsidae, Archeriidae;

Lepospondyli: Urocordylidae, Hapsidopareiontidae, Ostodolepidae,

Lysorophidae;

"Anapsida": Protorothyrididae, Bolosauridae, Mesosauridae;

Diapsida: Araeoscelididae;

Synapsida: Eothyrididae, Edaphosauridae, Ophiacodontidae,

Sphenacodontidae.

There were six families of labyrinthodont amphibians that are known to have survived into the succeeding Kungurian Stage (Trimerorachidae, Eryopidae, Dissorophidae, Archegosauridae, Seymouriidae, Diadectidae) two of Lepospondyli (Keraterpetontidae, Gymnarthridae), and only three of reptiles (Captorhinidae, Caseidae, Varanopidae). This extinction then had its greatest effect on the

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reptiles, and it marked the sharpest decline in the formerly dominant pelycosaurs (early synapsids). Artinskian extinction rates are high, but not excessively so.

Late Permian (Tatarian): twenty seven families of tetrapods died out at the end of the Permian (event no. 2: Fig. 2).

Labyrinthodontia: Dvinosauridae, Melanosauridae, Rhinesuchidae,

Kotlassidae, Lanthanosuchidae, Chroniosuchidae;

"Anapsida": Captorhinidae, Millerettidae, Pareiasauridae;

Diapsida: Weigeltisauridae, Younginidae, Tangasauridae;

Synapsida: Ictidorhinidae, Gorgonopsidae, Dromasauridae,

Endothiodontidae, Cryptodontidae, Aulacocephalodontidae,

Dicynodontidae, Pristerodontidae, Cistecephalidae,

Diictodontidae, Moschorhinidae, Whaitsiidae, Silphestidae,

Procynosuchidae, Dviniidae.

The end-Permian event had a decisive effect on the amphibians, wiping out six families, and leaving only three survivors that crossed the Permo-Triassic boundary (Uranocentrodontidae, Benthosuchidae, Brachyopidae). It also caused the end of many major reptilian families, and particularly a large number of formerly dominant mammal-like reptiles. The six or seven families that survived into the Triassic rapidly radiated into new forms, but the synapsids had begun to lose their dominance to the diapsids.

The extinction rates for the Tatarian are fairly high (Figs. 3, 4), but not as high as those in the Ufimian, the first stage in the Late Permian, when there was not a drop in tetrapod family diversity.

Early Triassic (Scythian): there was another smaller extinction event about 5 Myr. later, at the end of the Scythian Stage, when thirteen tetrapod families died out:

Labyrinthodontia: Lydekkerinidae, Uranocentrodontidae,

Benthosuchidae, Rhytidosteidae,

Trematosauridae, Indobrachyopidae;

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Diapsida: Proterosuchidae, Euparkeriidae;

Synapsida: Emydopidae, Kingoriidae, Ictidosuchidae,

Scaloposauridae, Galesauridae.

The event really affected only the amphibians, since reptilian diversity remained roughly constant as a result of a high origination rate at the time. There was a small mass extinction of marine invertebrates at this time also (Raup and Sepkoski 1984, 1986).

Late Triassic (Carnian - "Rhaetian"): The three stages of the Late Triassic, the Carnian, Norian and "Rhaetian" (or two, if the "Rhaetian" is included in the Norian) span 18-25 Myr., depending upon which of the current time scales is employed. Raup and Sepkoski (1984, 1986) have argued that the Late Triassic extinction consisted of a single event, but Benton (1986a, b) has identified at least two phases of extinction in the fossil record of tetrapods (no. 3: Fig. 2), as well as in that of ammonoids and other groups.

The first, and larger, extinction event occurred at the end of the Carnian Stage. Ten families of tetrapods died out:

Diapsida: Thalattosauridae, Trilophosauridae, Rhynchosauridae,

Proterochampsidae;

Synapsida: Kannemeyeriidae, Chiniquodontidae;

"Euryapsida": Nothosauridae, Simosauridae, Cymatosauridae,

Henodontidae.

The second, smaller, Late Triassic extinction event, at the Triassic-Jurassic boundary ("Rhaetian") was marked by the loss of eight families:

Labyrinthodontia: Capitosauridae, Plagiosauridae;

"Anapsida": Procolophonidae;

Diapsida: Phytosauridae, Aetosauridae, Rauisuchidae,

Ornithosuchidae;

"Euryapsida": Placochelyidae.

These extinctions, although few in number, do seem to have some significance. The last of the thecodontians (four families) disappeared on land, as did the last of the placodonts in the sea. Most of the "modern" groups of amniotes had appeared during the preceding 12-17 Myr. of the Norian Stage: the Testudines, the Crocodylia, and the Mammalia, as well as the Pterosauria, and the Dinosauria in the Carnian. At one time it was thought that the end of the Triassic saw the termination of the formerly abundant labyrinthodont amphibians and the mammal-like reptiles, but these two groups continued in greatly reduced diversity until the Bathonian and Callovian (both Middle Jurassic) respectively.

Both the Carnian and the "Rhaetian" events are associated with peaks in total and per-taxon extinction rates of tetrapod families (Figs. 3, 4), but the peaks are higher for the latter event.

Jurassic - Cretaceous events: Raup and Sepkoski (1984, 1986) and Sepkoski and Raup (1986) have identified three probable extinction events that affected marine animals between the "Rhaetian" and the K-T events. These additional extinction events, with dates of the ends of the stages from Palmer (1983), are:

Jurassic: Pliensbachian (193 Myr.)

Tithonian (144 Myr.)

Cretaceous: Cenomanian (91 Myr.)

The data on tetrapod families are particularly weak during parts of this time interval (see above). There are indeed declines in family diversity in the non-marine tetrapod data (Fig. 2) after the Pliensbachian, Tithonian, and Cenomanian, with the decline after the Tithonian standing out best. There are also slight peaks in total (Fig. 3) and per-taxon (Fig. 4) extinction rates in the Pliensbachian and Cenomanian, with a more marked peak in the Tithonian. At present, the tetrapod data are not good enough to decide either way about the occurrence of these postulated extinction events.

Late Cretaceous (Maastrichtian): The Cretaceous-Tertiary boundary (K-T) event is surely the best known mass extinction, and not least for its effects on

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the reptiles (dinosaurs, pterosaurs and plesiosaurs all died out then). However, in relative terms at least, the percentage loss of families of tetrapods as a whole (no. 4: Fig. 2) was less than for the two Permian events and the Late Triassic events already described. The total extinction rate for the Maastrichtian (Fig. 3) is higher than any before it, but the per-taxon rate for tetrapods (Fig. 4) is not so impressive, being lower than the "Rhaetian", Pliensbachian and Coniacian rates, for example. The decline in tetrapod family diversity at the K-T boundary is caused partly by a slightly elevated extinction rate, and partly by a low origination rate (Benton 1985 b).

Thirty-six families of tetrapods died out at the K-T boundary:

Diapsida: Crocodylia: Uruguaysuchidae, Notosuchidae, Goniopholididae;

Pterosauria: Pteranodontidae, Azhdarchidae;

Dinosauria: Coeluridae, Ornithomimidae, Dromaeosauridae,

Sauromnithoididae, Oviraptoridae, Elmsauridae, Megalosauridae,

Dryptosarridae, Tyrannosauridae, Camarasauridae, Diplodocidae,

Titanosauridae, Hypsilophodontidae, Hadrosauridae,

Pachycephalosauridae, Nodosauridae, Ankylosauridae,

Protoceratopsidae, Ceratopsidae;

Sauria: Mosasauridae;

Aves: Baptornithidae, "Enantiornithes", Lonchodytidae, Torotigidae;

Mammalia: Marsupialia: Pediomyidae, Stagodontidae;

"Euryapsida": Plesiosauria: Elasmosauridae, Cryptocleididae, Polycotylidae.

The K-T event was clearly taxonomically selective: certain major groups became completely extinct during Maastrichtian times: the Pterosauria (2 families), the Dinosauria (19 families) and the Plesiosauria (3 families). Other groups were less affected - turtles, crocodilians, lizards, snakes, birds and mammals (although two out of three marsupial families died out). Indeed, the mammals continued to radiate without any obvious pause right through the K-T boundary.

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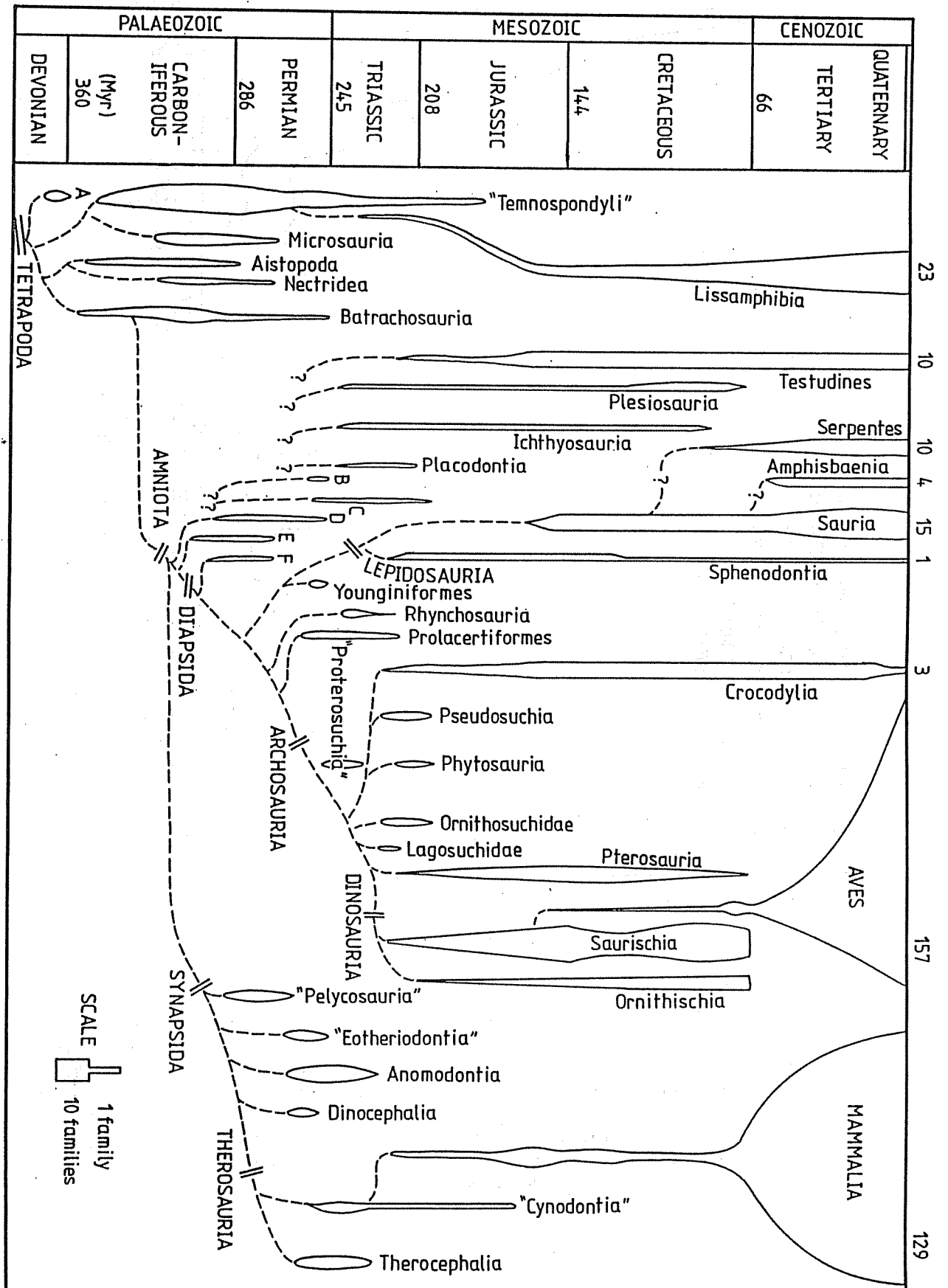
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Table 1

Numbers of families of Late Palaeozoic and Mesozoic tetrapods, based on data in Benton (1987a, b). Note: some of these families cross *into* the Tertiary.

	<u>non-marine</u>	<u>exclusively marine</u>	<u>total</u>
Amphibia	85	0	85
Reptilia	205	32	237
Aves	13	0	13
Mammalia	<u>35</u>	<u>0</u>	<u>35</u>
TOTAL	338	32	370

Fig. 1.- Phylogenetic tree of the Tetrapoda, showing relationships, stratigraphic duration, and diversity of each group. The major groups are indicated as balloons that show the known stratigraphic range by their height, and the relative numbers of families present by their width (see scale in bottom right-hand corner). Relationships of the groups are indicated by dashed lines on the basis of recent cladistic analyses (e.g. Gaffney 1980; Kemp 1982; Benton 1984, 1985c; Smithson 1985; Panchen and Smithson 1985; Gauthier 1986; Heaton and Reisz 1986). Abbreviations: A, Ichthyostegalia; B, Pareiasauria; C, Procolophonia; D, Captorhinidae; E, Protorothyrididae; F, Araeoscelidia.



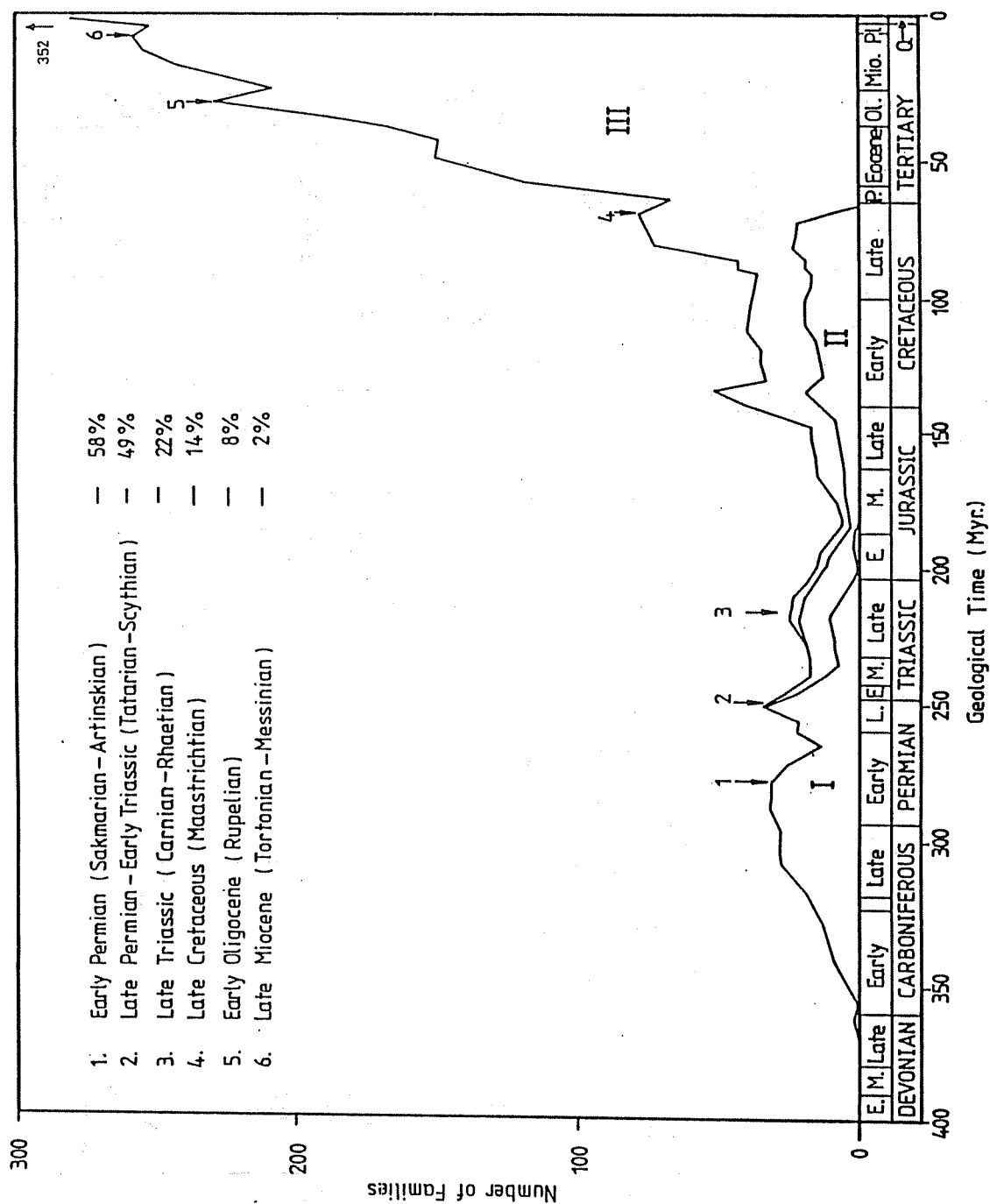


Fig. 2.- Standing diversity with time for families of non-marine tetrapods. The upper curve shows total diversity with time, and six apparent mass extinctions are indicated by drops in diversity, numbered 1-6. The relative magnitude of each drop is given in terms of the percentage of families that disappeared. The time scale is that of Palmer (1983). Three assemblages of families succeeded each other through geological time: I, II, III (see text for details). Abbreviations: Carb., Carboniferous; Dev., Devonian; Trias., Triassic.

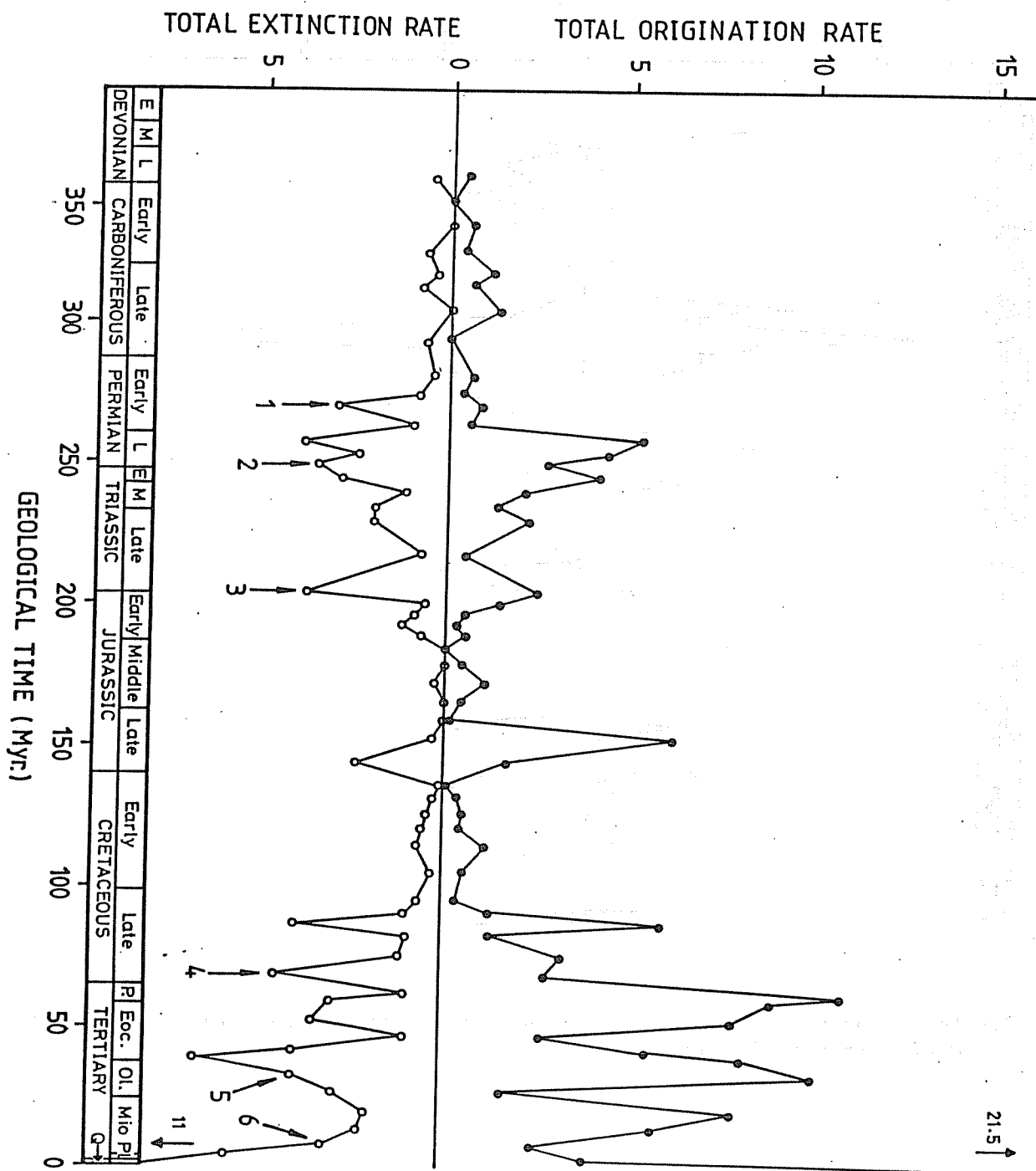


Fig. 3.- Total rates of origination and extinction for families of amniotes, calculated stage by stage for 56 stages between the Late Devonian and the Pleistocene. The Miocene was divided into Early, Middle and Late units only, and the Pliocene was treated as a single time unit.

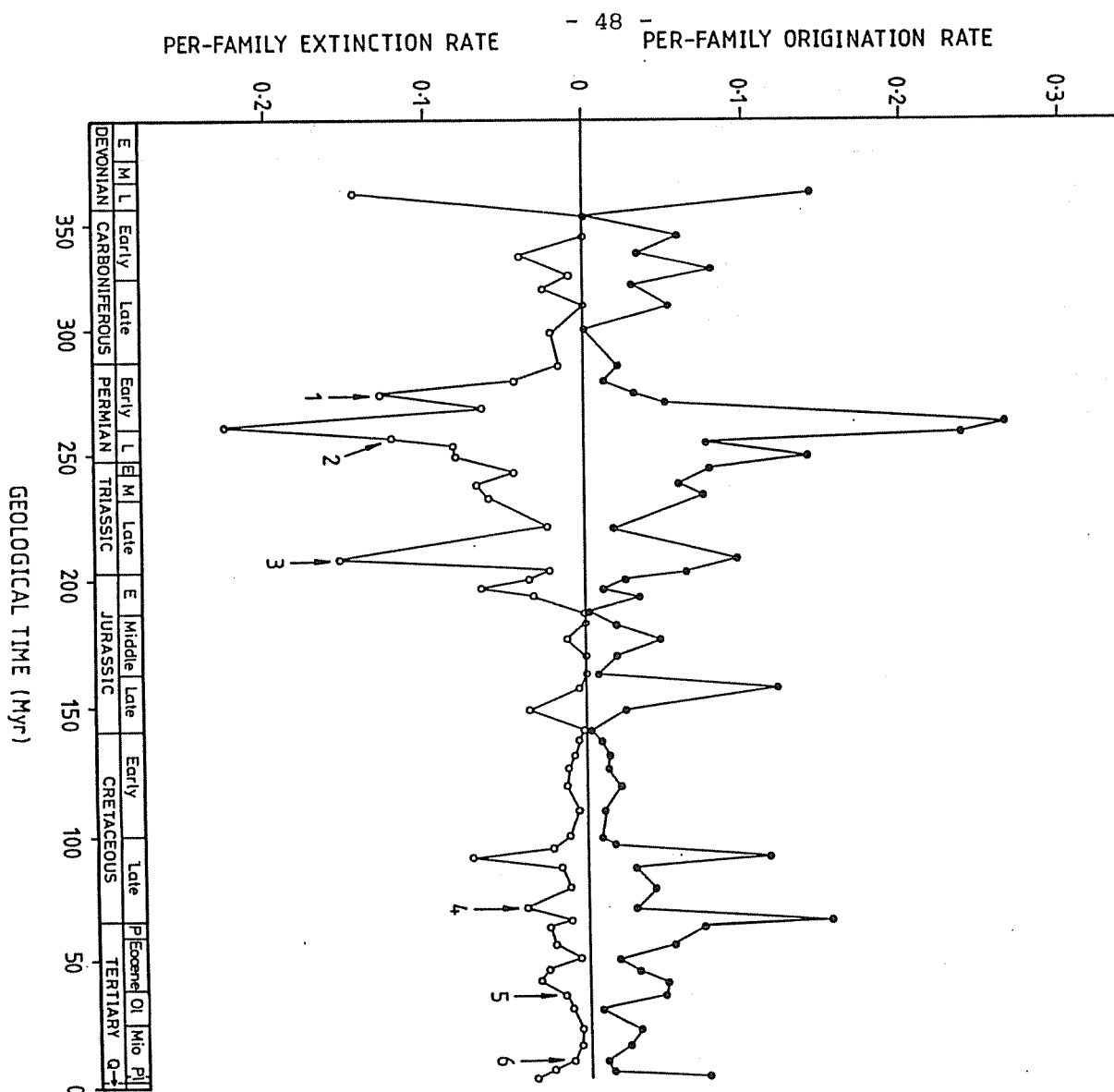
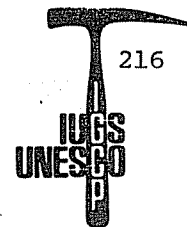


Fig. 4.- Per-taxon rates of origination and extinction for families of amniotes. Conventions as in Fig. 3.



III JORNADAS DE PALEONTOLOGIA
PALEONTOLOGIA Y EVOLUCION: FENOMENOS DE EXTINCION

EVOLUTIONARY CRISIS WITHIN THE ORDOVICIAN ACROTRETIDS (INARTICULATE BRACHIOPODS)

Gertruda BIERNAT & Wieslaw BEDNARCZYK

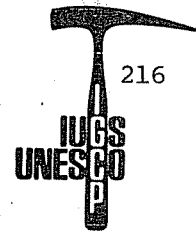
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ABSTRACT: Acrotretids (sensu Rowell, 1965) have been a dynamically developed group during the Cambro-Ordovician times and became extinct by the end of Ordovician except the Scaphelasma line which continued up to the Silurian (Artiotreta) and the Torynelasma line going on to the Silurian (Artiotretella) and even up to the Devonian (Opsiconidion). In Poland, this group much diversified in the Ordovician, is known to occur in the time span comprising the Middle Cambrian-Silurian. The peak of their maximum differentiation is observed in the Lower Ordovician (Upper Tremadocian-Llanvirnian). This being confirmed by the following genera: Ditreta, Conotreta, Paratreta, Eurytreta, Spondylotreta, Myotreta, Pomeraniotreta, Scaphelasma, Ephippelasma, Torynelasma. Only some forms continued i.e. Conotreta -to the Upper Ordovician (Caradocian) and Opsiconidion, a member of torynelasmatids- to the Silurian. A similar evolutionary line is to be observed outside Poland, in the Balto-Scandia (Sweden, Estonia including the Leningrad environs) probably in Bohemia and also at Kazakhstan (USSR) and Nevada (USA). It seems that, basing on the palaeogeographical data, the radiation and diversity and subsequent steep extinction of acrotretids could have been caused by changes of climate, sea-level in connection with the glaci-eustatic events during Ordovician and fluctuations in the rate of sea-floor spreading.

PHANEROZOIC EXTINCTIONS: HOW SIMILAR ARE THEY TO EACH OTHER?

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ABSTRACT

A brief account of the major Phanerozoic extinction events suggests that each one has a flavor all its own. Major extinction events involving varied combinations of different taxonomic levels, such as many classes, or many orders, or many families, and the varied impacts on community structure in varied combinations are what is referred to here by "flavor." Most of the evidence discussed is taken from the relatively well sampled, marine, level bottom environment. Recent evidence developed by Kauffman and a few others suggests that extinctions take place over a geologically brief interval of time in which more stenotopic taxa are eliminated, followed by an abrupt termination of the more abundant, higher biomass eurytopes, during community collapse. Adaptive radiations too, appear to take place during a geologically brief interval (up to a few million years) rather than "instantaneously" in ecologic time (less than a thousand years). This suggests that "instantaneous" extra terrestrial events are not likely to have influenced the gradual phase of either extinctions or adaptive radiations in any very important manner. Long term extra-terrestrial events that potentially resulted in terrestrial climatic gradient changes might have been significant. However, the more instantaneous community collapse, high biomass effects, might involve other factors, including certain types of extra terrestrial events. The decoupling, non-coincidence in time of the extinction events and adaptive radiations in varied parts of the global ecosystem, such as the marine and nonmarine environment, does not support a concept of "instantaneous" extraterrestrial influences. It is concluded that we still have little understanding of the specifics involved in any major extinction event or adaptive radiation on land or sea. Many of our paleontologic and geologic data have been collected in such an inadequate manner as to make new sampling mandatory if we are to attain a better understanding of these problems.

KEY WORDS: Extinctions, adaptive radiations, community evolution, decoupling.

"Those who cannot remember the past
are condemned to repeat it."
George Santayana (The Life of Reason)

INTRODUCTION

D'Orbigny (1849-1852, 1850-1852) compiled the original biostratigraphic synthesis that made him the Father of Biostratigraphy, and provided the foundation for future studies on extinctions and adaptive radiations. Following Cuvier, d'Orbigny employed a catastrophist interpretation (1849-1852, v. 2, pp. 252-254) of the biostratigraphic facts. We no longer subscribe to this view, for which many paleontologists have substituted a neocatastrophist-evolutionary attitude. However, we are still faced with trying to understand what are basically the same data.

Most of the major extinction events have, of course, been recognized for a century or more (see Newell, 1956, 1963, 1967, for incisive summaries). The relative ease with which the earlier paleontologists and biostratigraphers had recognized the major extinctions was largely based on the presence of major biofacies and biomass (communities of modern parlance) changes across the boundaries combined with significant taxonomic changes; there was much more to this recognition process than a mere change of taxa at the boundaries (Newell, 1967). After most of the Treatise on Invertebrate Paleontology and Osnovy Paleontologii volumes became available, it was reasonable to compile stratigraphic range data for varied taxonomic levels in order to test earlier conclusions about the major extinction events. Valentine (1969) and Raup (1972) performed this compiling service, although arriving at somewhat different conclusions about the significance of the compilations, as might have been predicted given the nature of the basic information. Furthermore, it was reasonable to continue to try to refine these data with both additional information and varied statistical techniques. The authors of these later papers eventually were able to recognize most of the major extinctions noted previously by biostratigraphers and paleontologists well before the advent of the Treatise and the Osnovy. We owe a debt of gratitude to these compilers for having called these basic paleontologic, evolutionary problems to the attention of the biologists. But, the recent spate of papers alleging periodicity of extinctions in the post-Paleozoic marine fossil record (see Sepkoski and Raup, 1986, for a typical example), based on statistical treatments of similar basic data, involves a large measure of defective data while at the same time not agreeing with the major biostratigraphic breaks (see Patterson and Smith, ms., for a critique and summary; also, Ager, ms.; House, 1987). Patterson and Smith reject the alleged periodicity in the Late Permian to present family data. As is discussed below, additional to the basic criticisms provided by Patterson and Smith, I conclude on a paleoecologic basis that most data points compiled by the extinction-periodicity advocates result from taphonomic "noise" on the one hand, and the basic inadequacy of most fossil samples for recovering rare taxa on the other hand. Jaeger's (1986) thoughtful review of the extinction problem raises serious doubts about both the alleged "instantaneous" and "periodic" aspects of the problem.

As I have suggested before (1986), it is crucial that we now advance our understanding of the extinction and adaptive radiation problems involved if we are to find any real solution for them. To accomplish this, we must employ sampling methods that emphasize the ecostratigraphic rather than just the stratigraphic. By "ecostratigraphic," I mean the study of extinctions and adaptive radiations from within individual community types (community groups; see Boucot, 1983). We need to find out whether communities as a whole are subject to extinction and subsequent adaptive radiation; or whether it is only the more "sensitive" taxa in a community that are subject to these processes. Mere compilation of miscellaneous taxa will not achieve this goal if the taxa are divorced from their community context. We must analyse the system, part by part. We must keep separate the data of the level bottom community from those of the reef complex of communities, of the pelmatozoan thicket, the bryozoan thicket, and the sponge forest. In fact, we must separate all data bearing on the shelf communities from those of the bathyal, planktonic, and pelagic communities. Finally, we must--obviously--keep nonmarine data--both freshwater and terrestrial--separate from marine data.

HOW NOT TO RECOGNIZE EXTINCTIONS

At the outset it needs to be stated that the term "extinction" is employed by paleontologists in a manner distinct from the dictionary definition. We refer to a statistical phenomenon in which varying percentages of the biota, never the total biota in the Cuvierian sense, became extinct at different times in the past. Because of this situation Newell (1963) and Teichert (1985) preferred the term "crisis" rather than "extinction." Some workers prefer the term "extinction event." We are not, of course, referring to the terminal extinction of individual lineages, or to the name changes within individual, evolving lineages.

The best way to obscure extinction events, and to be able to overlook totally the lower level extinction events, is to continue to prepare summaries featuring the "known" stratigraphic ranges of ecologically miscellaneous taxa--families, genera, and species. It is necessary to keep in mind that most generic and specific "extinctions" are merely bookkeeping changes reflecting the evolution of one taxon into another, not true extinctions. This attitude assumes that the "known" ranges of all, or even most published taxa are of equal value, a position that the experienced taxonomist finds unrealistic (Newell, 1986, for example). It has been clear for many years, even during the last century, that the published stratigraphic ranges of the presently described fossils are of highly variable quality. For example, Teichert (written comm., 1987) points out that 25% of the pelmatozoan families are monogeneric; i.e., they probably represent a very fortuitous sample for which the "known" stratigraphic ranges are obviously far below the true ranges, because they are also largely endemic, relatively uncommon units whose reported ranges tend to be minimal. Excluding monotypic taxa and those restricted to a single stage cannot eliminate this problem. Enlarging one's sample size does

not improve the reliability. One must keep in mind that the skeletonized echinoderms have a very low preservational potential that almost guarantees that the known stratigraphic ranges of most taxa will be very minimal. It is, therefore, amazing that many compilers make no serious attempt to evaluate the reliability of the varied components in their samples. This approach defeats a priori the purpose of the study! The first rule of statistical analysis is to prepare if possible, where some understanding is available, a proper evaluation of the sample and its components, and then to consider how best to weight these components. One should decide on the basis of this body of knowledge how best to discard certain components because of their statistical unreliability. This is particularly true when dealing with natural history data of the biostratigraphic sort, where we have more than a little real understanding of varied controls over the nature of the data. These samples should not be viewed in some sort of statistical vacuum; to do so would not be objective, it would be to discard intentionally the experience and understanding gained by many generations of paleontologists.

I have emphasized (1986) that the term "Background Extinction Rate" is largely a sampling artifact. It is a combination of taphonomic "noise" plus the all too common small size of most fossil collections. The taphonomic "noise" results from the uncritical use of many well-skeletonized taxa that are so poorly articulated that they are most commonly preserved as indeterminate fragments.

For example, consider the Echinodermata. The overwhelming majority of the generic and familial stratigraphic ranges within this phylum are obviously gross underestimates, because of the ease with which most taxa disaggregate into unidentifiable particles. The compilers have made no attempt to deal with this problem. Because of this taphonomic defect, as well as related ecologic questions, most echinoderm taxa probably should be eliminated from the analyses of compilations, with the exception of a few taxa such as the numerically abundant, cosmopolitan, infaunal, irregular urchins (present in Mortensen's old Subclass Irregularia).

The sampling bias part of the problem involves the fact that with both living and extinct taxa the great majority belong to the endemic category (Boucot, 1975a), which is characteristically represented by relatively uncommon specimens. The compilers have uncritically lumped together the taxa represented by these poorly sampled, commonly endemic, rare taxa, whose reported stratigraphic ranges may be far short of what community paleoecology suggests should be their true ranges, with the far more numerous, more cosmopolitan taxa whose known ranges approximate their true ranges (Boucot, 1983). This uncritical procedure produces both noise and artifact.

Furthermore, the compilers make no attempt to evaluate their data in terms of what is now known about community evolution (Boucot, 1983). This may happen because most paleontologists do not subdivide their data ecologically. I am also referring here to the all too common practice of lumping together stratigraphic data from evolutionarily largely decoupled parts of the marine ecosystem such as the reef community complex and the level bottom environments (an

example of this practice is McKinney [1987]). Workers who would never think of combining stratigraphic range data from the nonmarine and marine environments for the purpose of recognizing extinctions and adaptive radiations seem to feel free to lump together the data of the level bottom shelf with those of the reef community complex, the pelmatozoan thicket, the bryozoan thicket, and the sponge forest, not to mention the pelagic and planktonic complexes. This failure, or refusal, to make an effort to analyse the distinctly different parts of the ecosystem, in terms of independent times of adaptive radiation and terminal extinction, needlessly blurs the record, giving a false sense of what might actually have occurred. Additional to this failure to consider sample reliability in terms of community paleoecologic understanding is the failure to consider the biogeographic reliability of the sample, i.e., whether a complete community complement has been recovered from the known biogeographic units, as well as whether the available communities have been adequately sampled. It is clear that overall diversity at lower taxonomic levels, in some cases extending up to and including the familial, is positively correlated with numbers of provincial units (I have commented on this some time ago: Boucot, 1975b).

It is clear that softbodied taxa should not be considered for the purpose of recognizing extinction events or adaptive radiations, and indeed few include them in their compilations. However, rare taxa for which stratigraphic sampling is still woefully inadequate (Boucot, 1986), and for which it is clear that "known range" seldom even approaches "true range," are still being included by most compilers in their summaries (McKinney [1987] is a typical example). Needless to say, such a major sampling error introduces substantial noise and potential artifacts into the conclusions--leading in no small part to the fallacious concept of a "Background Extinction Rate." However, use of the ecostratigraphic concepts of community evolution provides a more balanced means of evaluating all taxa, whether rare or abundant, in both slowly evolving and rapidly evolving lineages that have similar stratigraphic ranges within the many coeval community groups belonging to each ecologic-evolutionary unit (Boucot, 1983, Fig. 1).

From what we have learned about community evolution it is clear that there will be a continuing "extinction" rate of both genera and species, but particularly species, within the evolving taxa characteristic of every community group (this type of "extinction" is mere name changing, not extinction in the commonly accepted sense [Boucot, 1983, 1986]). Within any major portion of the global ecosystem, such as the level bottom, the plankton, the reef complex of communities, pelmatozoan thickets, and the like, there is good evidence that there is no background extinction rate at the family and higher levels. New families are NOT being continually introduced and removed from extant community groups. There are inevitably a few families that appear later and disappear earlier than the bracketing ecologic-evolutionary unit boundaries, but most of these are families represented by rare genera and species (this is an artifact caused by inadequate sampling).

The stratigraphic ranges of the benthic non-level bottom ecologic units are overall far less well known than those of the level

bottom units. For example, the stratigraphic ranges of the varied pelmatozoan thicket communities are very poorly known, and little attempt has been made to synthesize the currently available data. If one adds to this the rarity of the taxa within such communities (largely because of the ease with which most of these organisms are disarticulated beyond recognition), it is little wonder that they contribute a great deal to the artifact of "Background Extinction Rate."

Sepkoski (1986) suggests that genus-level compilations through time are a far more sensitive means of detecting extinctions than is the case with familial and higher level units. I strongly disagree. In many cases genera within a family tend to grade into each other, as anyone who has ever tried to assign a species to a genus is painfully aware. I am indebted to Sepkoski for providing me with a copy of his articulate brachiopod generic data. Consideration of his data shows that the known disappearance time for each genus is treated as an "extinction," which involves the assumption that there has been a very low level of evolutionary change within families from one genus to another. Examination of Sepkoski's data convinces me that well over three-quarters of these "extinctions" are merely name changes within evolving lineages (i.e., these are not true extinctions). This is not surprising. Sepkoski (1986) apparently ignored generic changes in evolving lineages as contrasted with terminations of generic lineages which seriously flaws his approach. Anyone involved with the study and description of genera and species understands that most genera are merely convenient "cubbyholes" for groups of relatively similar species that are parts of continuously evolving groups. This basic fact is exemplified in Simpson's (1953) concept of Quantum Evolution. Quantum evolution is an apology for the almost invariable absence of species and genera intermediate between families. I (1986) have discussed the tendency for a higher level of generic terminations at the end of ecologic-evolutionary units rather than within them. There is also a tendency for taxonomists to employ more generic terms than needed just above and below period, series, and stage boundaries. That is, the normal human tendency for some of us to "see" things where they "should" be results in different names for the same genus above and below a boundary. Generic compilations also introduce a biogeographical artifact in that times of increasing provincialism, themselves commonly decoupled from extinctions or adaptive radiations (Boucot, 1983), see a marked increase in generic and specific diversity (Boucot, 1978, diacladogenesis) owing to intensive allopatric speciation.

Finally, the stratigraphic range compilers, despite defective noisy data, have been able to recognize the major extinction events first identified in the last century. Attempts by them to recognize the host of lesser extinction events by employing these data fail. This is exemplified in Sepkoski's (1986) work, with his alleged minor event at the Pennsylvanian-Permian boundary. I conclude that this is an artifact produced by employing generic data based on the all too common tendency to change generic and specific terms at "major" boundaries. Anyone familiar with the deliberations involved in the selection of the Pennsylvanian-Permian boundary decision made at the 1937 International Geological Congress in Moscow would be puzzled to

learn that a well defined extinction event was supposed to have been present (see Mudge and Yochelson, 1962, for a mass of information dealing with the boundary). One should also note Sepkoski's inability to recognize the minor extinction event at the Silurian-Devonian boundary, or that within the Emsian (Boucot, 1985).

MARINE HISTORY & RECOGNITION OF EXTINCTION EVENTS

The marine fossil record is by far our most complete. Therefore, any account of extinction, and of the companion problem of adaptive radiation, must emphasize the marine. There is, of course, a spectrum of both extinction events and adaptive radiations, from the major global events, to minor events, as well as to regional events. In this brief summary I stress the major events.

In terms of numbers of specimens, the marine record is largely one of the level bottom environments. However, in terms of numbers of taxa, many with poorly known stratigraphic ranges, the non-level bottom environments contribute a very significant fraction to the taxic total (think here of the pelmatozoan and bryozoan thicket taxa from the family to the species). Therefore, it is natural that most conclusions should be based on level bottom data, because of the significantly higher level of sample reliability, and from the more common taxa within the level bottom sample.

First, I review the major extinctions recognized to date in the level bottom marine record. I attempt to summarize their major characteristics. I then comment on some of the potential correlations of these extinction events with varied geological phenomena such as regression-transgression, global climatic gradients, intervals of orogeny, levels of provincialism, and the like. I also emphasize the major adaptive radiations that follow some, but not all, of the major extinction events. Community continuity and termination at times of extinction are discussed. Finally, I discuss briefly some of the minor extinction events affecting the level bottom environment, plus the adaptive radiations generating the reef environments *de novo* during the Phanerozoic, following extensive intervals when the reef environment was absent (also see Newell, 1971, and Sheehan, 1985).

In 1983 I discussed briefly the well known Phanerozoic extinction events that have affected the marine level bottom environments. They are the end of the Ediacarian, end of the Early Cambrian, end of the younger Cambrian biomes (including that at the end of the Cambrian), end of the Early Ordovician (about the end of the Arenigian), end of the Ordovician (the "old" Ordovician-Silurian boundary point for which the Zone of *Glyptograptus persculptus* formed the base of the Silurian, rather than the "new" boundary point for which the overlying Zone of *Akidograptus acuminatus* forms the base), mid-Late Devonian (Frasnian-Famennian boundary), end of the Permian, end of the Triassic, and end of the Cretaceous. In the 1983 paper I set up what were termed "Ecologic-Evolutionary Units" that conform in many respects to the *Etages* of d'Orbigny (1850-1852) insofar as both reflect the points in the stratigraphic record where major, geologically abrupt changes in the level bottom environment biota are

obvious.

END OF THE EDIACARIAN (Fig. 1): Thanks largely to Glaessner's pioneering studies (summarized in 1979 and 1984), we now have a considerable body of information concerning the enigmatic level bottom, softbodied fauna of the Ediacarian. There has been a great deal of concern about the phyletic affinities of many of the puzzling taxa. We are clearly far from resolving these concerns today. Yet, nearly everyone involved is in agreement that the species, genera, families, probably most superfamilies, and possibly most orders, appear to have no direct, post-Ediacarian continuations. Whether or not these extinctions were rapid or slow on a geologic time scale is unknown, owing to the small number of localities; in fact, it may never be known. However, the magnitude of the potential event is obvious. This extinction event does not give any insight into the behavior shown by varied communities and biogeographic units just before the extinction event. There are still far too few data even to begin to think seriously about Ediacarian biogeography or communities (Glaessner, 1984; Donovan, 1987a). The reason for citing this potential event is that it might just be the greatest of the Phanerozoic extinctions.

END OF THE EARLY CAMBRIAN (Fig. 1): Biotically, the Early Cambrian is in many ways the most distinctive Phanerozoic time interval. It has yielded about three to four times as many phylum to subclass level units as any post-Early Cambrian interval. I mention "phylum to subclass" because of the intrinsic difficulty in deciding how best to classify so many of the Cambrian higher taxa. The archaeocyathids are a typical example, having been assigned at one time or another to the Porifera and Coelenterata, as well as to a unique phylum (Hill, 1972, provides a useful account). The skeletal morphology of the Archaeocyatha is clearly too distinctive to permit their easy placement in any post-Cambrian higher taxon, whereas total ignorance of their soft anatomy and tissues probably precludes certainty on this point for the foreseeable future. Yet, all agree that they represent a high level taxon. Brasier (1986) has provided a brief summary of the many taxa appearing near the basal Cambrian boundary. This prominent earliest Early Cambrian, Tommotian interval adaptive radiation is still essentially unexplained. Whether or not there was an extinction event of any magnitude at the end of the Tommotian is still undecided because of inadequate sampling. Many of the "unique" Tommotian smaller shelly fossil taxa are now beginning to appear in the post-Tommotian (Brasier, 1986). Many of these "unique" taxa still have poorly known upper ranges owing to varied sampling problems, chiefly being the lack of enough acid treatment of the younger rocks. The fact that the Archaeocyatha have lingered on in a few very restricted locales into the Late Cambrian does not detract from their essential terminal Early Cambrian extinction nearly everywhere. It is common to consider the Early Cambrian as a time of "experimentation" insofar as higher taxa are concerned.

In terms of lower taxa, such as the family, syntheses of the Early Cambrian are inadequate for making detailed comparison with

later intervals; the sample also is very small. This fact is reflected in no small part by the overwhelming Lower Cambrian dominance of trilobite taxa (not to mention specimens). The Cambrian relative abundance of so-called "small shelly fossils" is still hard to estimate.

In addition to the many higher taxa, chiefly represented (with the exception of the Archaeocyatha) by very few genera, species, or even specimens, most lower level taxa involved in the extinction event are trilobites. This may be partly a sampling artifact owing to the fact that the abundant inarticulate brachiopods of the Cambrian as a whole are still poorly known.

Palmer (written comm., 1987) points out that "In the Lower Cambrian it is relatively easy to recognize olenellids, agnostoids, corynexochids and ptychoparioids (ordinal or superordinal groups), or species. Some family or superfamily divisions are becoming recognizable by the end of the Lower Cambrian (Zacanthoididae, Dorypygidae), and the ptychoparioids on the different continents are developing their own biogeographic aspects. (The biogeographic differentiation is there for most groups, except for maybe small shelly fossils about which we are just beginning to develop knowledge, right from the start.) Within the regions, however, there are few very clearcut intermediate level taxa. The family, superfamily and generic classification is thus relatively messy.

During the Middle Cambrian, genera become increasingly clearcut, but many supergeneric groupings are commonly disputed.

During the Late Cambrian, Family-level taxa become increasingly clearcut.

In Ordovician and younger Paleozoic rocks the superfamily level taxa (asaphids, phacopids, calymenids) become quite clear.

The impression is that through the early Paleozoic differentiation of superspecific taxa becomes increasingly better at increasingly higher taxonomic levels with time. The exception is the ordinal or superordinal levels, which are distinct from the very beginning....."

Most survivors of the Early Cambrian extinction event are represented in the shelf margin equivalent region by the well known agnostid and specialized polymeroid facies, commonly preserved in black shales, Palmer's "Outer Detrital Belt" (Palmer, 1977). This shelf margin to offshelf survival phenomenon continued through the Cambrian and Early Ordovician, and even to the end of the Ordovician insofar as these major trilobite groups are concerned. There are hints in the post-Ordovician record that this phenomenon of selective survival, which takes place close to the shelf margin, continued into the Late Devonian (Pedder, 1982). Sepkoski (1987) also considered this possibility. In fact, the differential survivorship of shelf-margin to offshelf taxa may provide clues about evolutionary decoupling of this part of the ecosystem from the level bottom benthos on the rest of the shelf (in fact, most of the shelf). This tendency

for greater offshelf survivorship may be correlated with the greater likelihood for elimination of varied shelf environments (and their stenotopic taxa) during intervals of major regression. But, it must be kept firmly in mind (Boucot, 1983) that there is no correlation between widespread regression and extinction. For example, the global regression characterizing most of the Early Devonian occurs at a time of great increase in generic and specific level diversity brought on by greatly increased provincialism. The correlation between regression and extinction is selective, suggesting that factors additional to regression are heavily involved here.

Causation: The cause of the terminal Early Cambrian extinction event is still unknown. At about this time, the global climatic gradient increased (Boucot, 1983), with a parallel increase in the level of provincialism. Globally, little important, well-dated orogeny, took place at this time. The factor(s) involved in the appearance of mineralized skeletons at the beginning of the Cambrian are as unknown as ever; they are equal in significance to the appearance of the soft bodied metazoans in the Ediacaran, and second only to the appearance of life itself in terms of the fossil record.

Communities: It is very clear that communities, trilobite communities in particular, were almost completely reorganized immediately following the Early Cambrian, except for the shelf margin agnostid and polymeroid facies, and that the first skeletonized communities were organized at the beginning of this interval.

END OF THE CAMBRIAN (Fig. 1): The Middle Cambrian-Late Cambrian ecologic-evolutionary unit opened with a period of adaptive radiation, at least as far as the numerically and taxonomically dominant shelf trilobites were concerned. Regardless of how one views Palmer's (1984) four Middle and Late Cambrian biomes, four major extinction events are clearly recognizable during this interval (Palmer, written comm., 1987, comments that most of the biome boundaries have not yet been recognized outside of North America, and that high levels of platform provincialism during the Cambrian may be partly responsible), at least on the North American Craton (Ludvigsen and Westrop, 1985, regard them as stages in the traditional sense). They seem, however, to be extinction events prominent mostly at the family to species level, with few superfamilies or higher taxa involved (Palmer, 1984). The terminal Late Cambrian event also affected the newly arrived nautiloid cephalopods (Chen and Teichert, 1983) at the family and lower levels; keep in mind, however, that the Cambrian nautiloids are poorly known at present outside of China. The newly diversified and numerically more abundant articulate brachiopods saw the bulk of their genera become extinct, as was also the case with the gastropods. (We still have inadequate information about the inarticulate brachiopods.)

Many other higher taxa lived during the Middle-Late Cambrian, but their stratigraphic ranges and overall record are too poorly known to shed much light on the extinction question.

Causation: There are no good correlations of the terminal Cambrian extinction event with global regression-transgression (Ludvigsen et

al., in press, make a good case for the absence of major regressive activity in the Cambrian-Ordovician boundary interval), orogeny (an essentially anorogenic interval), and with changing levels of global provincialism or climatic gradient. No evidence favoring extra-terrestrial "events" has been produced at any of the Late Cambrian biomere boundaries (Orth et al., 1984). Palmer (1981) emphasizes that the two important North American Cambrian regressions do not correlate with any of his biomere boundaries. It is still unclear whether the North American Cambrian biomere boundaries, and their extinctions, are global in extent.

Communities: The benthic communities of the latest Cambrian were largely replaced in the earliest Early Ordovician, along with the lower level taxa (Ludvigsen and Westrop, 1983). Community reorganization also occurred with the earlier biomeres.

END OF THE EARLY ORDOVICIAN (Fig. 1): The important extinction event occurring at the end of the Early Ordovician has, strangely enough, received very little publicity from those who seek major extinctions. The event is well known to the biostratigrapher. A number of families in certain groups terminate (gastropods, articulate brachiopods, nautiloids, and trilobites being among the most prominent). However, the principal characteristic of this extinction event was an almost total community reorganization that affected the shelf depth level bottom benthos shoreward of the shelf margin region with its agnostid-olenid type faunas. After this event, trilobite numerical abundance became subdominant for the first time since the post-Tommotian appearance of the group. This was also the event following which several nearshore environments previously dominated by gastropods and nautiloids, shared that position with other groups, including the first numerically abundant bivalves, as well as a few brachiopods. The abundance of stromatolites (*Cryptozoon*) of the Cambrian-Early Ordovician nearshore region decreased drastically at this time, never again to assume their former dominance. In many ways the Early Ordovician Ecologic-Evolutionary Unit III (Boucot, 1983), is a "halfway station" between the overwhelmingly trilobite-dominated benthos of the Cambrian and the more varied benthos of the post-Early Ordovician, although very distinct from both. In fact, after Early Ordovician time, no one group ever dominated again, except for the bivalve-dominated Early Triassic interval (Ecologic-Evolutionary Unit IX) (Boucot, 1983). The Early Ordovician began with an adaptive radiation involving several new family level units affecting such groups as the trilobites, brachiopods, gastropods, and nautiloids, but very little above that level. A few new higher taxa such as the conulariids and the pelagic graptoloid graptolites were involved in this adaptive radiation event.

Causation: The cause is difficult to pinpoint. A prominent, probably worldwide regression did take place near the beginning of the Llanvirnian (Lindstrom and Vortisch, 1982). Orogeny, provincialism, and global climatic gradients do not correlate very well, high or low, with the terminal Early Ordovician extinction event.

Communities: An almost total community reorganization took place at

the Early-Middle Ordovician boundary, with the appearance of far more varied communities above, as well as the extinction of most older community types below. Massive community reorganization of this magnitude also took place at the beginning of both the Early and Middle Cambrian, the beginning of the Carboniferous, the beginning of the Middle Triassic, and the beginning of the Jurassic.

END OF THE ORDOVICIAN (Fig. 1): The faunal composition of Ecologic-Evolutionary Unit IV (Boucot, 1983) is markedly different from its predecessor. Within that unit were the first appearance and subsequent adaptive radiation of the corals (both tetracorals and tabulates), as well as the radiation of the bivalves, gastropods, stony bryozoans ostracodes, crinoids and other major palmitozoan groups, and articulate brachiopods. The overall relative abundance of the trilobites decreased again, as did the inarticulate brachiopods. Almost all the community types are new.

The terminal Late Ordovician extinction event was one of the three most profound to affect the level bottom environment. A very large number of families, as well as many orders and superfamilies, from most of the benthic megafossil groups were involved. The plankton, including graptolites and acritarchs, also were greatly affected. The reef community complex of the Middle and Late Ordovician was totally extinguished. Most of the genera and species terminate. However, during this extinction event in about the Benthic Assemblage 4-5, outer shelf to upper bathyal position, some taxa survived very well, particularly within the Dicelospira-Skenidioides Community Group. The more cosmopolitan and commonly more eurytopic taxa (as judged by presence in numbers of communities, and shoreline to shelf margin distribution) generally survived, as is commonly the case in most extinctions. The taxonomic uniqueness of each major extinction event is attested to by Teichert's (written comm., 1987) comment that "The end Ordovician is not a big extinction event for the cephalopods." He points out that many higher nautiloid taxa pass through this interval, whereas others disappeared well before. For many other benthic and planktonic groups, however, it is a major event. Whether or not such taxonomic uniqueness of each of the major extinctions has a "cause or causes" as contrasted with being merely a chance event is currently unknown. However, there is no denying the taxonomic uniqueness of each major extinction event in terms of relative effects at different taxonomic levels.

Causation: In terms of cause, attention has commonly been directed to the glacial maximum within the late Ashgillian. The cause of the extinction, however, is unlikely to have been glaciation because many taxa survived well into the glacial interval, within their appropriate climatic zone. Just as with the Pleistocene there is no 1:1 correlation between rapid extinction and rapid regression correlated with the onset of widespread continental glaciation that reaches sealevel. In fact, this Ordovician extinction was delayed considerably after the onset of glaciation. However, it must be pointed out that here, as with almost all extinction events, we lack a careful, stratigraphically controlled account (centimeter-by-centimeter work in many sections that include as many community types

as possible) of the timing of the varied extinctions. Moreover, the relations between the extinctions and specific communities have not been well documented. Evidence for extraterrestrial (Orth et al., 1986; Wilde et al., 1986) and orogenic causes is lacking. It is true that the global climatic gradient decreased, but not precisely at the Ordovician-Silurian boundary. Levels of provincialism decreased at this time (Wang Yu et al., 1984, correct Boucot's, 1975a, earlier misconception of widespread Llandoveryan cosmopolitanism), but did not approach the high level cosmopolitanism of the Late Devonian or Triassic.

Communities: The rich communities of the latest Ordovician were taxonomically impoverished by the extinction event, and the reef community complex of the Middle-Late Ordovician totally eliminated. The surviving earlier Silurian communities are fractions of their former, Ordovician, selves. There is widespread, although not total, community reorganization. In this regard, the terminal Ordovician event is similar to what happened in the tropical-subtropical world following the end Cretaceous event, as well as following the mid-Late Devonian event. It is worth commenting that at the end of Ecologic-Evolutionary Unit V, within the late Llandovery, there is a marked increase in numbers of taxa/community group owing to the dispersal of so many taxa from the Uralian-Cordilleran Region into the North Atlantic Region (Wang Yu et al., 1984).

MID-LATE DEVONIAN (FRASNIAN-FAMENNIAN) (Fig. 1): Beginning with McLaren's (1970) Presidential Address to the Paleontological Society, and followed by his subsequent Presidential Address to the Geological Society of America (1983), great attention has been devoted to the mid-Late Devonian extinction event (e.g., Walliser, 1986). McLaren emphasized the geologically instantaneous nature of the event. It is now clear that this was one of the three major extinction events which affected the level bottom shelf benthos during the Phanerozoic. (However, the extinction at the end of the Permian was the greatest.) Many units at the class to ordinal level and below were terminated at this time. Recent work suggests, however, that not all aspects of this extinction were geologically instantaneous (Becker, 1986; Stearn, 1987), but rather extended over a period of as much as a million years. Copper (1986) reviews the later Devonian record of the atrypcean brachiopods to arrive at a similar conclusion, although suggesting an even longer, more extended time interval. However, Copper's interpretation suffers from the absence of the necessary benthic community data that might have allowed us to decide whether the extinctions he reported are potential artifacts based on collecting failures (samples too small to recover uncommon taxa), or collecting failures based on local absence of particular community types for particularly stenotopic atrypid genera. Information about this question of time interval duration during which extinction occurs is still very preliminary. Sorauf and Pedder (1986), following up on Pedder (1982), emphasize that most of the shelf depth rugosan corals terminated at this time, but that many of the offshelf, shelf margin-upper bathyal equivalent corals continued on relatively unscathed; this is more evidence for decoupling; their data indicates a relatively rapid event insofar as rugosans are concerned. It is clear

that this particular extinction was not followed immediately by an adaptive radiation affecting the level bottom benthos, a character shared with both the earliest Silurian-post-Late Ordovician and Permian extinction events, although a few groups did radiate near the very beginning of the Silurian (including such things as the stricklandiids and eospiriferids).

Enough is known about pelagic organisms during the Late Devonian to make it clear that, although the ammonites were greatly affected by the mid-Late Devonian extinction event, they subsequently underwent several Famennian (Late Devonian) adaptive radiations (House, 1985; Korn, 1986), unlike the shelf benthos. The marine fish, on the other hand, were not too greatly affected by the mid-Late Devonian extinction event, but did undergo a major terminal extinction event at the end of the Famennian, in contrast to the shelf benthos (Harland et al. 1967; Hansen, written comm., 1985).

The reef community complex and its taxa were totally terminated in the mid-Late Devonian extinction event (McLaren, 1970).

Causation: A cause for the mid-Late Devonian extinction event is obscure. The Late Devonian was biogeographically very cosmopolitan, had a very low global climatic gradient, was relatively but not completely anorogenic, and was a time of moderately high global transgression. No good evidence has been found for an extra-terrestrial cause (McGhee et al., 1984; McGhee et al., 1986a, b; Donovan, 1987b; McLaren, 1985; Geldsetzer et al., 1987).

Communities: The bulk of the Silurian-Devonian benthic, level bottom community groups terminated at this extinction boundary. Only remnants of some of them straggled through the Famennian, prior to the massive adaptive radiation affecting the level bottom benthic world at the opening of the Carboniferous. Famennian level bottom benthic faunas and communities can be described in one word--impoverished.

END OF THE PERMIAN (Fig. 1): The beginning of Ecologic-Evolutionary Unit VIII, the Carboniferous, was marked by a major adaptive radiation affecting level bottom shelf benthos, and by major community reorganization. Within the Carboniferous a minor extinction event took place at the Mississippian-Pennsylvanian (NOT the Early Carboniferous-Late Carboniferous!) boundary (Ramsbottom et al., 1982), but there was no event at the Pennsylvanian-Permian boundary. Sepkoski's, 1986, generic data indicating minor extinction events at both the Mississippian-Pennsylvanian and Pennsylvanian-Permian boundaries I regard as coincidence in the first and artifact in the second case, owing to the all too common tendency for taxonomists to change generic names at Period boundaries; remember that the "placement" of the Pennsylvanian-Permian boundary was a difficult question that was finally "decided" by a committee (see Mudge and Yochelson, 1962, for references, and a mass of stratigraphic range data). The community evidence at the Pennsylvanian-Permian boundary strongly indicates the absence of an extinction event, as everyone knows who has ever collected fossils adjacent to the boundary in Kansas and Nebraska with their supremely repetitive series of

cyclothem community types in environments ranging from the nonmarine to the deeper shelf. The situation on the Russian Platform at the same horizon is little different for either stratigraphic ranges of varied taxa or for community types. The absence of a similar generic level, artifactual "extinction" event at the Silurian-Devonian boundary may reflect the relatively recent redefinition of that boundary as contrasted with the Pennsylvanian-Permian boundary.

The greatest Phanerozoic extinction event took place at the end of the Permian (Newell, 1967, 1973). Class after class was eliminated, together with most orders, superfamilies, and lower taxa. This event was an order of magnitude greater than any other, including the next two greatest at the end of the Ordovician and in the mid-Late Devonian, at every taxonomic level from the Class on down. This extinction was not immediately followed by an adaptive radiation affecting the level bottom shelf benthos; a major adaptive radiation did take place near the beginning of the Middle Triassic. It is fascinating evolutionarily, as well as biogeographically, to attempt to understand where group after group of organisms underwent the high taxonomic level changes during the Early Triassic that must have occurred in order to explain the presence of distinctly different orders of the same classes in the Permian and Middle Triassic, with no Early Triassic representation known (Boucot and Gray, 1978, for a summary). It is interesting to emphasize that the pelagic ammonoids, just as after the mid-Late Devonian extinction, did radiate in the Early Triassic (i.e., another example of decoupling of the pelagic from the benthic).

However, even with this greatest of all extinction events, the evidence suggests that the actual extinctions were not instantaneous or simultaneous in all taxa (Newell, 1967; Teichert, 1968, 1985; Ager, ms.), because there is good evidence for many benthic taxa lingering on for a very brief interval into the earliest Triassic (the Permian-Triassic transition in the marine environment is best preserved in South China). Additionally, there are a few taxa, such as the gastropods (Batten, 1985) and nautiloids (Teichert, 1985) which are characterized by having many taxa that passed through the Permian-Triassic, only to become extinct near the end of the Triassic. Newell (1973) emphasized the apparently stepwise decline in later Permian diversity (this decline now needs to be further examined in an ecostratigraphic manner in order to see if any parts can be ascribed to inadequate sampling).

Causation: Reams of paper have been devoted to trying to establish a cause for this extinction event which wiped out the reef community complex and its taxa in toto, most of the level bottom taxa, and the bulk of the pelagic organisms. However, when all is said and done, most of the phenomenon has not been explained. A great regression, possibly the greatest in the Phanerozoic, does correlate very well with the extinction event (Newell, 1967), but alone is inadequate to explain the event, because vast shoreline regions and shallow depans are always present (unless one wishes to totally eliminate the oceans); it is the bulk of the epicontinental seas that are eliminated during major regressions, not the continental shelves (although, the latter may be narrowed). Not all Phanerozoic regressions correlate by

any means with extinctions (consider the lack of any global extinction during the Quaternary with its many regressive events), and some actually correlate with increases in taxic diversity (e.g., the later Silurian and earlier Devonian). A Permian lowering of the global climatic gradient did take place, but most of the lowering was completed by the middle of the period, many millions of years before the extinction event. Orogeny was moderate at the very end of the Period. A marked change took place from the high provincialism of the later Permian to the very cosmopolitan Early Triassic. That, however, again can explain only a part of the extinction, even combined with the lower global climatic gradient. Boucot and Gray (1978) have commented critically on some of the more extravagant suggestions for causality. We clearly still lack the ability to explain this event satisfactorily. Clark et al. (1986) provide evidence for discounting an iridium anomaly at the boundary.

Communities: The complex and varied level bottom community groups of the Permo-Carboniferous were abruptly terminated at the end of the Permian, together with the reef community complex, sponge complexes, and pelmatozoan plus bryozoan complexes. The level bottom benthic communities of the succeeding Early Triassic were the fewest in number and taxonomically the most impoverished of the entire Phanerozoic.

END OF THE TRIASSIC (Fig. 1): The extinction event at the end of the Triassic has only recently begun to receive the attention its non-cephalopod portion deserves, although biostratigraphers have been well aware of this event since before the middle of the last century. The event witnessed the end of many molluscan groups (Hallam, 1981; Teichert, 1986), as well as such groups as the conulariids (Babcock and Feldmann, 1986) and the conodonts (Clark et al., 1986). The latter two may not, however, have been strictly benthic, although a demersal, epibenthic possibility for some is reasonable. The bryozoans (Schafer and Fois-Erickson, 1986), ostracodes (Whatley, 1986, in press), brachiopods (Ager, ms.), cephalopods (Teichert, 1985), bivalves (Hallam, 1981), gastropods (Batten, 1985), and many other groups suffered massive extinctions at the ordinal, superfamily, and family levels. Much of the information, unfortunately, has not yet been synthesized. The Upper Triassic reef community complex terminated at this time.

In many ways the Triassic as a whole is distinct from the Paleozoic and the Mesozoic in terms of its level bottom biota--it belongs to neither, although possibly having more affinity with the Mesozoic than with the Paleozoic.

Causation: This was a time of marked global regression, although no more marked than during the mid-Early Devonian, a time for which no evidence of a major extinction event exists. Global climatic gradients remained low prior to and following the event. The interval is not notably orogenic.

Communities: The Triassic level bottom community groups came to an end at this time, with the later Jurassic-Cretaceous units being totally different in their organization and including many new, higher

level taxa--this is not just a question of family and lower level extinctions. This almost total community extinction and subsequent reorganization is comparable in extent to the geologically abrupt events following the Early Ordovician and Permian extinctions, as well as that beginning in the earliest Carboniferous. End Triassic and earliest Jurassic communities have not been formally described as such, but there is a rich literature, beginning in the 19th Century, that deals with this major biofacies change.

END OF THE CRETACEOUS (Fig. 1): The modern marine level bottom benthic fauna and communities really began with the Jurassic. This was the time interval when the planktonic globigerine Foraminifera appeared; diatoms were shortly to appear in the record, together with post-Paleozoic larger Foraminifera; in addition the first prominent regular and irregular echinoids, the first modern crustaceans in abundance (the crabs and lobsters of this world), most of the modern superfamilies, and many of the families of bivalves and gastropods were to appear, as well as some demersal fishes such as the batoids.

This "modern" biota was greatly affected, particularly the tropical-subtropical part, by the end Cretaceous extinction event. Many important groups (see Kauffman, 1984, 1986, for incisive summaries) terminated, but many others continued. Insofar as the marine level bottom benthic world was concerned, the terminal Cretaceous event was much less important than the terminal Permian, terminal Ordovician, and terminal mid-Late Devonian events. Kauffman emphasized that higher latitude, cooler climate, marine faunas were not as severely affected as the tropical-subtropical realms, where the reef community complexes, for example, terminated totally (Newell, 1971; Sheehan, 1985).

Causation: I will not belabor the end Cretaceous event, because so many others contributing to this volume, far better qualified than I, have worked at the task. However, it is clear from the work of others (Walliser, 1986, for example) that we still have no well agreed-upon explanation for the end Cretaceous extinction event, although a heightened global climatic gradient appears to be the most pleasing at the moment (see Officer et al., 1987, for a persuasive permutation; Patrusky, 1987, for an incisive review of the overall questions; and Jaeger, 1986, for a forceful, well documented evaluation).

Communities: The terminal Cretaceous event was not followed by a thorough reorganization of the level bottom, benthic communities. However, it did see the disappearance of certain community types such as the outer shelf inoceramid types, level bottom rudistids, and certain gryphaeid dominated types. Rather it featured the surviving taxa remaining in more or less the same community groups. In this regard it was similar to the situation following the mid-Late Devonian extinction events; it was unlike the others.

MINOR EXTINCTION EVENTS

I have said nothing about the many minor extinction events. A

fair amount, however, has been published on the later Mesozoic (see Kauffman, 1984, 1986, for examples). Rather than trying to paraphrase any of these items, I discuss a mid-Devonian event that has recently come to light. I refer here to the Kacak or otomari event (Walliser, 1984; Chlupac and Kukal, 1986; House, 1985). This event was first recognized in Europe by means of taxonomic discontinuities affecting mainly the pelagic and planktonic ammonites and nowakiids. An explanation was difficult to determine. However, it had been known for a long time that a probable contemporary change from warm temperate Eastern Americas Realm faunas (Onondaga Group and older) in the earlier Middle Devonian to somewhat warmer water in the later Middle Devonian (Hamilton Group and younger) faunas had taken place. This change was used to explain the major change in such things as the coral and brachiopod faunas. Then, with the more recent discovery that the cool to cold climate Malvinokaffric Realm fauna became extinct at just about the same time, to be replaced by a possibly warmer water biota, even in the Parana Basin of Brazil, we suddenly had a good basis for inferring a geologically sudden lowering of the global climatic gradient. That sudden event involved the extinction of an entire high latitude, cool to cold water, highly endemic biota, together with the less pronounced extinction of warmer region taxa in a far more selective manner. This is a low level event compared with the major extinction events, but it is a definite extinction event. The Kacak Event is opposite in temperature sign to the North Atlantic and Arctic Ocean late Cenozoic, glacially moderated extinction of many taxa, which so reduced the North Atlantic and Arctic Oceans marine diversity that we see to the present day (Stanley, 1984), with the first case involving warming as contrasted to cooling in the second case. What is common to both is a relatively abrupt change in global climatic gradient. Doubtless many other such low level events wait to be better documented. Other minor events are known. For example, I have reviewed (Boucot, 1985) the evidence favoring still lower level, possibly very minor events at the Silurian-Devonian boundary, and within the Emsian part of the later Early Devonian. These last two events are so minor that they are recognizable only with the aid of the most susceptible groups of organisms (and remain undetected by Sepkoski, 1986), and only after a great deal of attention to many groups of unrelated organisms, to try to uncover trends having some real significance. There was a low level of community reorganization at the Silurian-Devonian boundary that correlates well with the minor extinction event and subsequent adaptive radiation also present at that boundary (Boucot, 1985). This minor event is most easily detected by paying careful attention to the obvious changes in overall community composition (Boucot, 1975a, Fig. 35; Boucot, 1982).

REEF AND OTHER NON-LEVEL BOTTOM COMMUNITY COMPLEXES

Throughout this paper I have mentioned briefly the occurrence of reef community complexes. They clearly appeared and disappeared through time (Newell, 1971; Boucot, 1983; Sheehan, 1985). It should be emphasized that the reef community complexes present in each distinct interval of reef presence are almost totally distinct from each other in a Darwinian sense, presumably having been derived independently from distinct level bottom taxa. The archaeocyathid-algal reefs

(Selg, 1986) of the Early Cambrian were followed by a lengthy interval containing no reef community complexes (the biohermal community complexes of the later Cambrian and Early Ordovician are not thought to have had a wave resistant organic framework). Then came the reef community complexes of the Middle and Late Ordovician, followed in turn by a reef-barren interval until the early part of the late Silurian (late Wenlockian). From the late Wenlockian on there was a coral-stromatoporoid reef community complex until the end of the Frasnian (There may be a reef barren interval between the Frasnian, latest Silurian, and the Pragian part of the Early Devonian, which separates the stromatoporoid-tabulate type reefs of the Silurian from the stromatoporoid-colonial tetracoral parts of the Devonian reef complex.). A reef community complex was absent from the Famennian (some algal complexes present), as well as the Mississippian (the Waulsortian mounds are community complexes but not true reef complexes), but a new one appeared in the Pennsylvanian and Permian. Reef community complexes were lacking in the Early Triassic, but reappeared in the later Triassic and terminal Triassic, although the details about timing are uncertain (see Boucot, 1983, for brief discussion). The Jurassic (Sheehan, 1985, Fig. 1, indicates reef absence in the lowest Jurassic which separates the Triassic type reefs from the younger types) and Cretaceous contained reef community complexes, but the Paleocene had almost none (they came back in force with the Eocene and then persist to the present). The lesson here is that the extinctions of the reef community complexes coincided with the major extinctions affecting the level bottom environments, but that the reinitiation of the reef community complexes (i.e., the adaptive radiations giving rise to the reef community complexes) commonly do not coincide with the initiation of the level bottom community groups--the reef complexes generally appear later in time.

We have no reliable summaries for the stratigraphic ranges of the many other, important, non-level bottom community complexes. One can predict, however, that they follow an initiation and extinction pattern similar to that for the reef community complex (i.e., extinctions in common with the level bottom world, but initiations commonly later than those of the level bottom community groups).

COMMUNITY COLLAPSE

In the section dealing with the mid-Late Devonian extinction event I mentioned evidence for an abrupt event noted by McLaren (beginning with his 1970 paper), and of evidence for more gradual extinction, taxon by taxon during some millions of years prior to the event emphasized by McLaren. How can one reconcile these data? I suspect that what gives rise to these apparently conflicting observations is the influence of a gradually increasing set of extinction influences that gradually eliminate the more stenotopic, more endemic, less abundant taxa earlier from the communities in which they existed, followed by ultimate community collapse (McLaren's event) in which the abundant, higher biomass, eurytopic, more cosmopolitan taxa are eliminated. Just why community collapse should occur suddenly in geologic time is uncertain. Possibly there are certain "keystone" taxa that when finally eliminated cause the whole

community structure to crash. If so, we have no understanding for the dynamics of the process, nor for which taxa might most likely fill the keystone role, nor whether taxic types regarded by modern day ecologists as keystone are what is involved here. We clearly need to collect additional data adequate for testing these possibilities not only near the mid-Late Devonian extinction event, but also at others, such as those within the Cretaceous discussed by Kauffman (1984, 1986) who has noted more gradual extinction phenomena prior to the Cenomanian-Turonian and Maastrichtian-Danian extinction events.

INITIATION OF ECOLOGIC-EVOLUTIONARY UNITS: COMMUNITY GENERATION

Sheehan (1985) suggested that each ecologic-evolutionary unit is characterised by an initial, geologically brief interval (I have suggested [1983] no more than a few million years) of adaptive radiation. He also views units V, VII, and IX (lower 2/3 Early Silurian, Famennian, Scythian) as such intervals, rather than as proper ecologic-evolutionary units. I am sympathetic to his suggestion that there were such early, geologically brief intervals of adaptive radiation and community group formation, but am unfamiliar with evidence suggesting that units V, VII, and IX have this character. We clearly need to gather data adequate to test his proposal. The largely North American Cambrian biomes have been described in a manner conforming to Sheehan's suggestion.

What is really being considered here is whether the generation of new community groups, ancestral to varied community groups, takes place over a few million years or so. If so, we currently lack the information to properly describe and understand the process. Carefully collected samples from the many ecologic-evolutionary unit boundaries will be needed to answer these questions.

DECOUPLING

I have used the term "decoupling" (1983) to refer to the fact that different parts of the global ecosystem undergo massive adaptive radiations at distinctly different times. This fact makes it unlikely that extraterrestrial influences have had a very profound effect in initiating most adaptive radiations. The non-coincidence in time of many of these major marine adaptive radiations with those occurring at different times in the nonmarine environment is involved here, as well as distinctly separate parts of the marine (for example, shelf and bathyal) and nonmarine environments. For example, the paleobotanical time terms Palaeophytic, Mesophytic, and Cenophytic refer, of course, to the beginnings of the Paleozoic-type vascular flora in the Paleozoic, to the following flora in the later, but not latest, Permian, and to the angiosperm-dominated flora beginning in the mid-Early Cretaceous. These three time intervals (Middle Ordovician-later Permian; later Permian-earlier Cretaceous; earlier Cretaceous-present) do not correspond very well with any major events in the marine realm. The earliest, Palaeophytic phase of the higher land plants invasions occurs in the Middle Ordovician (Gray, 1985), followed in the later Llandoveryan, by the appearance of the vascular plants (Gray, 1985),

followed in turn by woody plants near the Silurian-Devonian boundary. Gray (in press) emphasizes that there is no hint in the spore record of the higher land plants for any extinction event at or near the Ordovician-Silurian boundary, i.e., a fine example of decoupling of the marine from the nonmarine. However, Richardson and McGregor (1986) point out that the major, late Paleozoic change in spore floras occurs at about the Frasnian-Famennian boundary, i.e., an exception to the apparent non-coincidence in time of major terrestrial and marine events. The well documented rise of the angiosperms also accords with an accompanying insect radiation, as well as the initiation of the placental, presumably insectivorous mammals, but no first rank, major adaptive radiation in the marine environment. The poor correlation in time between major extinctions and adaptive radiations in the marine and nonmarine environments is what really provides the basis for avoiding extraterrestrial factors as heavily involved in either process. The adaptive radiations of the reef community complex have already been reviewed briefly, and as stated do not accord very well with major adaptive radiations in the level bottom realm. If we knew more about the other marine community complexes in terms of their initial adaptive radiations we might have still more evidence of this kind with which to emphasize large scale decoupling. There are, of course, any number of lower level decoupling phenomena, such as the probable rise of grasslands in the Eocene of South America as contrasted with their much later origins in North America. Comments have also been made about the decoupling in time for several elements of the pelagic as contrasted with the level bottom environment, such as ammonites vs. benthos during the Famennian.

Others: The radiations of the marine reptiles in the Mesozoic are notable, as is the initial radiation of marine mammals in the Eocene. The rise to importance of the diatoms in the mid-Mesozoic is still another example.

Note that the cited vertebrate examples are very decoupled from the marine, level bottom story, and provide still more evidence for a poor correlation between extra-terrestrial events and such phenomena.

SUMMARY & RANKINGS

Extinctions: 1) The Lower Cambrian, and possibly the Ediacarian, are first, at the Subclass to Phylum levels, whereas the Permian is first, at the Phylum through species levels; 2) The end Ordovician and mid-Late Devonian are second, at the Class or Ordinal through species levels; 3) The end Triassic is third, at the Class through species levels; 4) The end Cretaceous is fourth, at the Ordinal through species levels; 5) The end Cambrian, and earlier, post-Early Cambrian biomes, are fifth, together with the end Early Ordovician, at the Family through species levels, among events reviewed here.

Adaptive Radiations: The beginning Early Cambrian, and possibly beginning Ediacarian, are first, at the Subclass to Phylum levels; 2) The beginning Middle Ordovician (larger than the others at the ordinal level (Sepkoski and Sheehan, 1983), beginning Carboniferous, beginning Middle Triassic, and beginning Jurassic are second, at the Ordinal

through Familial levels; 3) the beginning Middle Cambrian, through the beginning Early Ordovician are third, at the Familial level.

Community Reorganizations: 1) First in magnitude are the Ediacarian and Early Cambrian; 2) followed by the Middle Ordovician, Early Carboniferous, Middle Triassic, and Jurassic; 3) followed by the Middle Cambrian through Early Ordovician (including the biomes), and Early Silurian; 4) followed by the Famennian, Early Triassic, and Cenozoic.

Dispersal: A major dispersal event occurs between the C2-C3 parts of the late Llandoveryan (later Early Silurian).

CAUSATION

We have little understanding of the cause or causes for either extinctions or adaptive radiations. The gradual aspect of some extinctions suggests that instantaneous extraterrestrial events are unlikely to have been prime causes. However, extraterrestrial events manifesting themselves over a lengthy time interval, if responsible in large part for major climatic shifts, or for the change in position of major water masses might be involved (although it would probably be most difficult to recognize such extraterrestrial factors unless they happen to show undoubted periodicity over a statistically very significant part of the Phanerozoic. As our understanding of paleogeography and paleoceanography improves we may be able to recognize the coming and going of important "gateways" in the marine world that are involved with surface current circulation patterns, and possibly in turn with climatic changes. However, the relatively instantaneous community collapse, major biomass events, might have involved instantaneous physical events of one type or another, if unconnected with the prior, gradual type extinction of the more stenotopic taxa.

Meyerhoff (written comm., 1987) points that out the later Ediacarian-Early Cambrian, Late Silurian-Frasnian, and later Permian-Carnian highs in evaporite deposition and preservation, suggesting that these highs might be related to changes in seawater concentration and composition, which produced (at least in part) the extinctions. Holser (oral comm., 1987) suggests that the overall changes in seawater concentration brought about by these evaporite highs was probably not more than about 3-4 parts per mil. Relying on the importance of selenium as a poison in the terrestrial ecosystem (Trelease and Beath, 1949) Meyerhoff (written comm., 1987) suggests that minor changes in selenium concentrations in the oceans, since selenium substitutes for sulfur, paralleling changes in seawater concentration, might have been the critical factor in the major extinctions, although other elements might also have contributed.

Wilde and Berry (1984; see also Berry and Wilde, 1978) propose destabilization of oceanic density structure as another potential cause of major extinctions. Their suggestion is worthy of careful, further investigation, particularly in terms of the "anoxic events" suggested for certain time intervals in the deep oceans.

QUESTIONS.

The following basic questions are raised by the data:

1) Why do the major extinctions appear to affect the taxa of many unrelated major groups during a geologically very brief interval (up to a few million years)? Is it merely a symptom of collapse affecting major parts of the ecosystem that had fairly obligate, coevolved relations, or is something else involved, such as the more or less coincidental exceeding of the physical tolerances of varied, unrelated taxa, with coevolution not being involved to any serious extent?

Why, immediately prior to the extinction horizon, do the more abundant, higher biomass taxa (those emphasized by McLaren, this volume) belonging to varied, unrelated groups contemporaneously become extinct? Keep in mind that these abundant, higher biomass taxa are relatively few in number.

2) Why do the major adaptive radiations affecting taxa belonging to many unrelated, major taxa occur at about the same time over a geologically very brief interval (up to a few million years)? Is this a symptom of geologically almost instantaneous, developing coevolution, or is it merely a time coincident reaction to newly appearing physical parameters to which the taxa of these unrelated major groups happen to be sensitive?

3) Why do the major adaptive radiations invariably occur at some time following major extinction events? Does this indicate the presence of vacant niches, or are other factors involved?

4) Why after certain of the major extinction events (end of the Ordovician, end of the Frasnian, mid-Late Devonian, end of the Permian) are there geologically lengthy intervals during which there is no evidence for extensive adaptive radiations in the level bottom environment, as contrasted with the other major extinction events? Is there an environmental "lack" involved in a physical sense, or is this merely a stochastic phenomenon? In the same sense, why do most generations of the reef community complexes, presumably from level bottom antecedents, occur significantly later in geologic time than the adaptive radiations that affected the co-occurring level bottom biota? Is this, too, merely a stochastic phenomenon, or are there unrecognized factors involved?

5) Why is there such a melange, in terms of extinction magnitudes and adaptive radiation magnitudes, immediately before and after the major extinction-adaptive radiations? Is this adequate evidence to indicate that extinctions and adaptive radiations are unrelated to each other in a causal fashion? Does this situation provide any evidence about whether or not competition is involved in any of the major extinction events?

6) Why do some taxonomic groups persist through major extinction events, why do some community types persist through major extinction

events, are there specific morphologies that are more resistant to extinction, are there certain communities that are more resistant to extinction, with the same questions being asked for adaptive radiations, or is all of this evidence for varied stochastic processes?

7) Summing up, it is obvious that the mechanism(s) controlling both extinctions and adaptive radiations are poorly understood at this time. Hopefully, population biologists will eventually direct their attention to this puzzling area. Until we have a suitably biological explanation for these phenomena our understanding of organic evolution will be deficient insofar as these phenomena are concerned.

CONCLUSIONS

It is clear from this brief summary that no two major terminal extinction events affecting the widespread level bottom environment are identical. By "identical" I mean: (1) whether or not community structure was greatly changed, (2) which taxonomic levels were most affected, and (3) which major taxa were most affected. In view of this variety of extinction types, it seems unlikely that the cause or causes of any two are the same. Teichert (1968) arrived at essentially the same conclusion.

The overall conclusions made here need to be carefully reviewed with quantitative data obtained after the stratigraphic range data have been properly selected by removing thoroughly unreliable data, and appropriately weighting the remaining data. The selection and weighting process needs to consider the various aspects of sampling such as changing levels of global provincialism, size of individual fossil collections, and the taphonomic biases implicit in the widely differing preservational characteristics of varied fossil groups. After this has been carried out these compilations should provide a far more realistic account of the distinctive nature of the extinctions and adaptive radiations insofar as their purely numerical characteristics are concerned. But, their community characteristics must also be taken into account if we are to have any real hope of understanding these enigmatic events by means of paleontologic data.

One could take the view that the reason for the apparently differing natures shown by many of the extinction and adaptive radiation events is due to the unique taxa involved in each one. In other words, one would not expect similar reactions from trilobite-dominated events as contrasted with brachiopod- or coral-dominated events. There is certainly a possibility that distinct taxa will react in distinctive manners to the same forcing factors, but I suspect that there is much more to the matter than the mere nature of the taxa involved; i.e., it is more likely that varying mixes of physical factors have been responsible for the unique flavor of each event rather than that the unique taxic compositions have been the dominant control.

The basic reason why both extinctions and adaptive radiations are far more easily recognized on an ecostratigraphic basis than by

merely counting taxa, is as follows. The ecostratigraphic method pays careful attention to changing abundances, large biomass changes, of individual taxa within each community group (biofacies of the geologist, narrowly construed). The ecostratigraphic method brings out the fact that rare genera and their species are commonly unrepresented in the all too common small samples on which so much of our past work has been based. One must keep in mind (Boucot, 1986) that a very large percentage of most families contain only one or a few genera, and are commonly very provincial. The ecostratigraphic method, therefore, takes advantage of both taxic presence and absence (fully understanding that many, possibly the majority of absences, probably reflect sampling deficiencies) and relative abundances of all taxa. The other approach pays attention only to known, reported taxic ranges, and makes no attempt to weight the samples properly in view of what is knowable about community evolution or changing biogeography's effect on diversity. It is little wonder that the ecostratigraphic approach has proved far more sensitive in detecting both extinctions and adaptive radiations, particularly with the minor events, just as in an analogous manner attempts to sort out individual fossil collections by means of similarity indices are most effective when abundances are considered in addition to taxic presences and absences. Its merely a question of employing the most penetrating statistical approach, which in this instance happens to be the ecostratigraphic. We need to emphasize that organic evolution is not a smooth flowing river, as Darwin's work would suggest, but that it has been a stream interrupted by some major waterfalls; the leading adaptive radiations and extinctions preserved in the fossil record, as pointed out for us by d'Orbigny long ago.

It is worth noting (Boucot, 1983) that the major Phanerozoic community reorganizations on a global scale, excluding regional phenomena such as affected the Arctic and North Atlantic Oceans during the Quaternary and Pliocene, occur either immediately following major extinction events and subsequent adaptive radiations, immediately following second and lower rank extinction events followed by adaptive radiations of varying rank, or in a single instance (Ecologic-Evolutionary Unit V, Boucot, 1983) following a major dispersal event (a few other, smaller dispersal events are also immediately followed by community reorganizations, such as that affecting the well known later Middle Devonian Hamilton Group faunas of eastern North America in which many Rhenish-Bohemian Region organisms dispersed into and mixed with descendants of preexisting Appalachia Subprovince taxa).

The differing levels of community reorganization are clearly just another facet of the quantum evolution phenomena involved in the production of new families and higher taxa. Note that the major community reorganizations are invariably involved with the production of new families and higher taxa. In other words, the communities to which taxa belong are just one more facet of their taxonomy, although a statistical property rather than a morphological, cytologic, biochemical, or behavioral character.

An ecologically meaningful measure of extinction and adaptive radiation might be compiled by making a comparison between genera/family/community group for specific ecologic-evolutionary units

as contrasted with the changes in the numbers of genera/family/community group following specific extinctions and adaptive radiations. When compilations are prepared that begin to ask specific questions having ecologic-evolutionary significance we will be in a much better position to take advantage of the compiling possibilities.

It is also clear that we have far to go in collecting adequate paleontologic and stratigraphic data of a community and biogeographic type adequate even to find out just what are the major problems facing us. This conclusion merely repeats that published recently by Teichert (1986)! It is the conclusion favored by experienced paleontologists everywhere.

Undoubtedly, many surprises lie ahead!

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LEVEL BOTTOM COMMUNITIES

Ecological-Evolutionary Units	Time Intervals	Major* Extinctions	Major* Adaptive Radiations	Major* Community Reorganizations	Major* Dispersal Event
	Ediacaran	E1	A1	C1	
I	L ϵ	E1	A1	C1	
II	M-U ϵ	E5	A3	C3	
III	LO	E5	A3	C3	
IV	M-UO	E2	A2	C2	
V	$\frac{2}{3}$ LS			C3	
VI	$\frac{1}{3}$ LS- $\frac{1}{2}$ UD	E2		C4	D1
VII	$\frac{1}{2}$ UD			C4	
VIII	C+P	E1	A2	C2	
IX	L Tr			C4	
X	M-UTr	E3	A2	C2	
XI	J+K	E4	A2	C2	
XII	Cenozoic			C4	

* Ranks indicated, high to low, as follows: E1-E5, A1-A3, C1-C4, D1

Figure 1. The Ecologic-Evolutionary Units of the Phanerozoic (from Boucot, 1983). The abbreviations (E=major extinctions; numerals same as in "Summary & Rankings"; A=major adaptive radiations; numerals same as in "Summary & Rankings"; C=major community reorganizations; numerals same as in "Summary & Rankings"; D=major dispersal event) refer to material discussed in the text.

III JORNADAS DE PALEONTOLOGIA
PALEONTOLOGIA Y EVOLUCION: FENOMENOS DE EXTINCION

CHANGES IN BACKGROUND EXTINCTION RATE AS A FUNCTION OF CHANGING TAXON AGE DISTRIBUTION

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ABSTRACT: Changing taxon age distributions of fossil marine genera appear to control large-scale changes in background extinction rate through the Phanerozoic. Taxon age is defined as the length of time from the base of the stage in which a taxon originated to the top of the stage in question. Extinction rates are higher, on average, for genera with smaller taxon ages than for genera with larger taxon ages. The decline in susceptibility to extinction as a taxon becomes older may be a consequence of increased species richness within older genera, or increases in geographic area or adaptive space exploited by the constituent species of a genus. Large-scale changes in background extinction rate through the Phanerozoic can be modelled as a function of changing taxon age distribution. In periods where there is a large proportion of young genera, higher overall extinction rates prevail; however, as older genera increase their proportions of the total population, overall extinction rates decline. Differences in the taxon age distribution between genera becoming extinct in mass and background times are marked, but appear to be a consequence of sampling right-skewed age distributions.

III JORNADAS DE PALEONTOLOGIA

PALEONTOLOGIA Y EVOLUCION: FENOMENOS DE EXTINCION

FENOMENOS DE EXTINCION Y ACONTECIMIENTOS INUSUALES EN EL LIMITE DOGGER-MALM DE LA CORDILLERA IBERICA (ARAGON, ESPAÑA).

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RESUMEN: Los análisis realizados recientemente muestran la alta complejidad de los procesos causantes de la formación de los niveles en los que se localiza el límite Dogger-Malm (G. Meléndez *et al.*, 1982; W. Brochwicz-Lewinski *et al.*, 1984a,b, 1985, 1986; M. Zolenski *et al.*, 1985). El registro de anomalías en PGE y de un alto contenido en plagioclasas y en cuarzo de impacto hace posible considerar la siguiente secuencia de fenómenos: 1) Caída de uno o varios cuerpos cósmicos, causantes de una intensa generación de ondas-P, y como consecuencia, 2) una fase de movimiento de bloques; 3) grandes olas de tipo Tsunami, que dan lugar a la formación de "conglomerados", reconocidos en materiales de esta edad, desde España hasta el Mar Caspio; 4) actividad volcánica e hidrotermal, y desarrollo de estromatolitos de origen hidrotermal, y 5) caída de polvo volcánico y de material resultante de la ablación y desintegración del cuerpo cósmico (y del impacto). En el marco de este análisis, el impacto es considerado como un mecanismo impulsor, o "accionador" de los distintos procesos. Otro posible modelo alternativo, una fase tectónica de movimiento de bloques de gran intensidad pero de corta duración, no explicaría el alto contenido registrado en productos resultantes de la ablación ni tampoco el cuarzo de impacto ni las plagioclasas. Las extinciones faunísticas que han podido ser detectadas son de menor importancia en comparación con las registradas en los restantes límites estratigráficos expuestos en el modelo de Raup y Sepkoski (1984). En el caso de los Ammonites se han puesto de manifiesto variaciones del espectro faunístico al nivel de subfamilia, pero no en aquellos grupos considerados como propios de aguas profundas (Oppeliidos; Phyllo- y Litocerátidos). Los cambios reconocidos podrían ser interpretados como resultado de la extinción de las llamadas "faunas atrapadas" ("Perched faunas", Johnson 1974, 1984), como consecuencia de cambios ambientales relacionados con el impacto antes mencionado y sus efectos posteriores (especialmente, modificaciones drásticas en la composición química y la turbulencia de las aguas). Es preciso tener en cuenta, sin embargo, que en estos materiales se registran evidencias de procesos de removilización, con intensidad decreciente, hasta el comienzo del Oxfordiense medio y que la estimación de los fenómenos de extinción ha podido ser menor que la real debido a errores en las dataciones de los materiales.

ABSTRACT: There is growing evidence for a complex nature of processes responsible for deposition of M/U Jurassic boundary beds (G. Meléndez *et al.*, 1982, W. Brochwicz-Lewinski *et al.*, 1984a,b, 1985, 1986; M. Zolenski *et al.*, 1985). The record of PGE anomaly and rich material of possible shock quartz and plagioclases makes possible assuming the following sequence of events: 1) fall of large cosmic body(ies), giving rise to very strong P-wave and, therefore, 2) a phase of block movements, 3) tsunami-like waves which formed "conglomerates" traced from Spain to Caspian Sea, 4) volcanic and hydrothermal activity and origin of hydrotherm-related stromatolites, and 5) fall of volcanic dust as well as material from ablation and disintegration of cosmic body(ies) and ejecta. In this approach the impact is treated as a trigger mechanism. An alternative model -a very strong but short- lasting phase of block movements and volcanic activity fails to explain the wealth of ablation products and the possible shock quartz and plagioclases. The extinctions appear rather minor in comparison with those traced at the remaining boundaries in the D. Raup and J. Sepkoski (1984) scheme. In the case of ammonites, there are evidenced changes up to the subfamily rank but not in the fauna regarded as deep-water (oppeliids, phyllo- and lytoceratids). The changes may be explained as extinctions of "perched faunas" (J. Johnson, 1974, 1984) in result of environmental changes related to the impact and its after-effects (especially drastic changes in water chemistry and turbulence). However, there is growing evidence for redeposition continuing with decreasing intensity till early Mid Oxfordian and that the scale of extinctions was here underestimated because of errors in datings.

III JORNADAS DE PALEONTOLOGIA

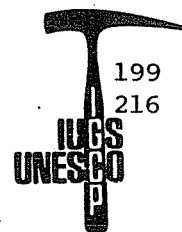
PALEONTOLOGIA Y EVOLUCION: FENOMENOS DE EXTINCION

DISTRIBUTION AND ECOLOGY OF BENTHIC FORAMINIFERA IN THE SANTOÑA ESTUARY, SPAIN

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ABSTRACT: The living and dead assemblages in the Santoña estuary were studied seasonally in order to determine the distribution and abundance of the benthic foraminifera in this area. Samples were collected from winter 1983 to summer 1985 to document the seasonal variation of the faunas and various ecological factors in the intertidal zone. Salinity is thought to be the main control of the living assemblages and two different foraminiferal biofacies characterising the upper and lower areas have been defined. Ammonia beccarii and Haynesina germanica are the most dominant forms throughout the estuary, with Miliammina fusca as co-dominant in the upper estuary and Quinqueloculina seminulum as co-dominant in the lower estuary. The dominant living species are also dominant in the dead assemblages but in the latter the agglutinated indigenous component is much more abundant. This compositional difference is thought to be caused by production rates and change in the environmental conditions in the estuary. The living and dead assemblages have been analysed and compared using the Fisher α diversity index, triangular plot of wall types and similarity index.



III JORNADAS DE PALEONTOLOGIA

PALEONTOLOGIA Y EVOLUCION: FENOMENOS DE EXTINCION

PALEONTOLOGY OF THE CRETACEOUS-TERTIARY BOUNDARY IN THE NORTHEASTERN APENNINES, ITALY.

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ABSTRACT: In the Umbro-marchean area (Northeastern Apennines, Italy) a 0.5-3 cm thick clay interbed occurs at the Cretaceous-Tertiary (K/T) boundary between the highest Cretaceous and the lowest Tertiary limestones beds. These limestones, which are homogenized by extensive bioturbation and burrowing (prevailing Planolites, Zoophycos and Chondrites), have a matrix of coccoliths and coccolith fragments, and a rich assemblage of almost exclusively planktonic foraminifera. The foraminiferal microfauna below the K/T boundary clay layer belongs to the A bathomphalus mayaroensis Zone. The lowest Tertiary sediments belong to the Globigerina eugubina Zone. Microfaunas from the K/T boundary clay layer are represented almost exclusively by fairly well-preserved agglutinated foraminifera. The assemblages are dominated by Spiroplectamina spp., Ataxophragmiidae and Astro-rhizidae. The agglutinated foraminifera are associated with fish teeth and scattered bed-preserved calcareous benthic foraminifera. In the K/T clay layer, fairly well-preserved uppermost Cretaceous and lowermost Tertiary planktonic foraminifera exceptionally occur. Their presence is related to a mild vertical mixing resulting from bioturbation and burrowing at the K/T transition. Detailed investigations suggest an essentially not-residual origin of the K/T boundary agglutinated foraminifera assemblages. No significant difference exists between the characters of such assemblages and those of the main underlying and overlying clay interbeds. The agglutinated foraminifera appear to survive the events which took place at the K/T boundary.

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PALEONTOLOGIA Y EVOLUCION: FENOMENOS DE EXTINCION

FOSILES EN NAVARRA

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RESUMEN: Este cartel forma parte de las actividades didácticas promovidas por el Museo de Paleontología de Zaragoza, para iniciar a los alumnos de Enseñanza Media en el estudio de la Paleontología y divulgar el conocimiento de los fósiles. Se ha elaborado siguiendo los mismos criterios didácticos utilizados en el cartel "Fósiles en Aragón" presentado en las II Jornadas de Paleontología. El cartel consta de:

- Una columna geocronológica en la que se representan Eras y Períodos con dataciones absolutas. Al lado aparecen fotografiados los fósiles más significativos, de cada período, en Navarra.
- Un mapa geocronológico de Navarra.

La columna geocronológica permite a los alumnos observar:

- Que el registro fósil en Navarra comienza a ser abundante a partir del Silúrico, estando bien representado en todos los demás períodos. Hay que exceptuar el Pérmico y el Triásico más difíciles de diferenciar y datados, fundamentalmente, con fósiles vegetales.
- Que la microfauna está muy bien representada en la región, existiendo incluso un género (Navarella) dedicado a Navarra.
- Formas conocidas por ellos de fósiles invertebrados, vertebrados y vegetales.

El mapa geocronológico les ayuda a reconocer las zonas geográficas donde se localizan estos fósiles.

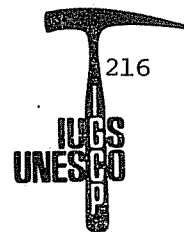
ABSTRACT: This poster is part of the scheme devised by the Museum of Paleontology of Zaragoza addressed to the Secondary School to initiate the students into Paleontology and to extend the study fossils. It has been designed following the same pedagogical principles that inspired the design of the poster "Fossils in Aragón" presented at the II Jornadas de Paleontología. The poster includes:

- A geochronological column in which Eras and Periods are shown in absolute figures, plus photos of the most significant fossils for each period in Navarra.
- A geological map of Navarra.

The geochronological column allows the students to notice:

- That the fossil record in Navarra seems to be significant at the Silurian Period, having a wide presence of all the other periods, with the exception of the Permian and Triassic periods which are more difficult to differentiate and are dated by means of vegetable fossils.
- That the microfauna record is very abundant in the region and there is even a genus dedicated to Navarra (Navarella).
- Fossils of invertebrates, vertebrates and vegetables already familiar to them.

The geochronological map helps them to recognize the geographical areas where these fossils can be found.



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PALEONTOLOGIA Y EVOLUCION: FENOMENOS DE EXTINCION

FUNCTIONAL MORPHOLOGY AND EXTINCTION OF SILICOFLAGELLATE GENERA

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ABSTRACT: Mobility is one of characteristics of silicoflagellates thanks to their flagellum. Their skeletons are an adaptation to two basic needs: resistance to sinking and ability to move around. To avoid sinking they have a basal surface as big as possible. As to the second need, their shapes enable them a horizontal mobility (streamlined basal ring and low apical window) or a vertical mobility (slanted basal spines and high apical window". According to their functional morphology we can distinguish the following groups. planar support (Mesocena, Paradictyocha, Septamesocena); mixed support (Dictyocha, Distephanopsis, Distephanus, Vallacerta); horizontal mobility (Naviculopsis, Deflandryocha) and vertical mobility (Cannopilus, Paracannopilus, Lyracula, Cornua). The analysis of the different morphologies in the Western Mediterranean since the Oligocene to the present time has led the author to the following conclusions: Since the Upper Oligocene to the Middle Miocene support shapes are dominant, though the other types exist and are more or less important. In the Middle Miocene a dramatic reduction of morphologies takes place, horizontal mobility and them vertical mobility disappear and only support shapes are left. A further major change takes place in the transition from Messinian to Pliocene when planar support shapes disappear and only mixed support shapes remain to the present time.

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PALEONTOLOGIA Y EVOLUCION: FENOMENOS DE EXTINCION

INVENTARIO DE LAS COLECCIONES DE PALEONTOLOGIA DEL MUSEU DE GEOLOGIA DE BARCELONA PARA SU INFORMATIZACION

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RESUMEN: Desde su fundación en 1878 hasta la actualidad, el Museu de Geologia de Barcelona ha ido ampliando sus grandes fondos paleontológicos. Aunque en su tiempo se catalogaron diversas de las colecciones que los forman (Baron-Pisani, Almera, Vidal, etc.) se trata aún hoy de trabajos inéditos. La sección de Paleontología del MGB inició a fines de 1986 el inventario general de dichos fondos para su posterior procesamiento por medios informáticos como paso previo a la publicación de catálogos. Esta informatización marcará un cambio significativo en la puesta al día de la información que tanto el público interesado como los especialistas solicitan cada vez más a menudo, ofreciendo servicios más eficientes y rápidos e impulsando nuevos trabajos monográficos de investigación sobre las colecciones como los que ya se llevan a cabo actualmente.

ABSTRACT: Since its foundation in 1878 to our present days, the Museu de Geologia de Barcelona (MGB) has increased the number of its paleontological collections. In spite of having some catalogued material (the Baron-Pisani, Almera and Vidal collections, e.g.), they still remain unpublished. The Paleontology Section of the MGB begun at the end of 1986 the general inventory of the collections in order to carry out a computer data base as a necessary step previous to the catalogues publication. The introduction of computing facilities will result in a significant change by up-dating the information that both interested public and specialists require, offering efficient and quick services and promoting monographic research on the collections like those actually in progress.



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PALEONTOLOGIA Y EVOLUCION: FENOMENOS DE EXTINCION

THE FRASNIAN-FAMENNIAN EXTINCTION EVENT IN WESTERN CANADA AND WESTERN AUSTRALIA: SEDIMENTOLOGY AND GEOCHEMISTRY

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ABSTRACT: Abrupt sedimentological changes occur at the Frasnian-Famennian boundary of one carbonate shelf section (N.W.T., Canada) and two basinal sections (Alberta, Canada; Canning Basin, Australia) both of which are downslope of partly buried reef complexes. Despite their geographic separation, all sections show a similar Late Devonian tectono-sedimentary development; prominent carbonate platform environments during the latest Frasnian were succeeded by a minor regression prior to or during the Frasnian-Famennian event. At the carbonate platform site of Trout River, N.W.T., a microkarst surface formed during the regressive interval. Minor clayey material was trapped in this zone and buried by thick marine sands and silts. Anomalously high readings of the trace elements Cu, Pb, Ni, Co, As, Sb and Zn were recorded from the clayey zone. In the Canning Basin a monotonous succession of red, nodular, siliciclastic, peloid packstone is interrupted by an environmental change allowing temporary proliferation and preservation of stromatolites (Frutexites) trapping high amounts of iridium and the trace elements Cu, Pb, Ni, Co, As, La, Ce, Th, V, Pt and Au. At the Alberta locality thick basinal, bioturbated, calcareous shale and dolomitic siltstone are abruptly overlain by black, laminated, argillaceous mudstone with a basal sedimentary pyrite bed that yielded anomalously heavy sulphur isotopes. The isotope anomaly indicates a sudden influx of a euxinic water mass. The contemporaneous availability of anomalously high amounts of trace elements and of a euxinic water mass along a faunal extinction boundary at widely separated localities suggests a global response to an extraordinary triggering mechanism.

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PALEONTOLOGIA Y EVOLUCION: FENOMENOS DE EXTINCION

LA COLECCION VILLALTA DEL MUSEO DE GEOLOGIA DE BARCELONA: YACIMIENTOS.

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RESUMEN: La colección que el Dr. Villalta donara al Ayuntamiento de Barcelona en Abril de 1983 ha supuesto para el Museu de Geología de esta ciudad un enriquecimiento general de sus fondos. El Museu ha redistribuido la sección de Paleontología creando un espacio independiente donde alojarla, ordenarla, registrarla, documentarla y ponerla a disposición de los investigadores. Grosso modo, la parte hoy ingresada de la col. Villalta comprende: 1) La sección de vertebrados del Cuaternario depositada hasta su ingreso en el Museu en el Instituto Jaime Almera del C.S.I.C., más algunas piezas singulares de diferentes yacimientos, con un monto global de 9445 ejemplares, ya siglados, fichados y registrados. 2) La colección paleobotánica del Neógeno, Oligoceno y Carbonífero de Catalunya, con un total de 1126 ejemplares, siglados, fichados y registrados. 3) Un número indeterminado de invertebrados, donde a los recogidos por el propio Dr. Villalta hay que sumar la antigua colección de la Universidad de Barcelona y materiales de Tesis y trabajos de otros investigadores, como Royo, Solé Sabarís, Virgili, Julivert, etc. En período de catalogación, se han registrado ya 860 yacimientos de toda España, desde el Paleozoico al Pleistoceno.

ABSTRACT: The collection donated by Dr. Villalta to the Barcelona Council in April 1983 has supposed for the Museu de Geologia of this city a very important acquisition. The Museu has redistributed its Palaeontological section creating an independent space to hold, register and document this collection in order to make it available to palaeontologists. Generally speaking, the part of the Villalta collection placed now at the Museu represent: 1) The Quaternary vertebrates section formerly kept at the Instituto Jaime Almera of the C.S.I.C. plus some singular specimens coming from different localities, with a total amount of 9445 marked, catalogued and registered specimens. 2) The paleobotanical collection from the Neogene, Oligocene and Carboniferous of Catalunya, with an amount of 1126 specimens also marked, catalogued and registered. 3) An indeterminated number of invertebrates, comprising those personally collected by Dr. Villalta, the old collection of the Universitat de Barcelona and samples from Ph. D. Thesis and works of scientists like Royo, Solé i Sabarís, Virgili, Julivert and others. In a catalogation phase, 860 Spanish localities ranging from Paleozoic to Pleistocene have been registered.

A COMPOUND SCENARIO FOR THE END-CRETACEOUS MASS EXTINCTIONS

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Abstract: Two major controversies have arisen in research on the end-Cretaceous mass extinctions, concerning the extent to which they were sudden or gradual, and terrestrially or extraterrestrially induced. A review of recent work supports more or less gradual extinction for a number of terrestrial and marine groups such as dinosaurs and ammonites, but the spectacular crash of the calcareous plankton and correlative ecological disaster in land plants in part of the northern hemisphere suggests a short-term catastrophic event. With regard to extinction selectivity in the marine realm, tropical groups and suspension feeders dependent on phytoplankton were relatively vulnerable, while on the continents large terrestrial reptiles were more prone to extinction than their freshwater relatives, while plants in western North America and eastern Asia suffered more severely than elsewhere.

Chemical and physical signatures of the Cretaceous-Tertiary boundary, including iridium anomalies, shocked quartz, microspherules and carbon, oxygen and strontium isotopes, are discussed and the evidence for and against a bolide impact-induced or volcanic catastrophe is reviewed, with the conclusion that it is not yet decisive either way. Evidence for longer-term changes is also cited, with strontium-isotope data supporting that from stratigraphy in suggesting a significant fall in sea level shortly before the end of the Cretaceous. A large body of evidence also supports a latest Cretaceous fall in seawater and at temperature, but this has recently been

disputed for western North America on the basis of leaf studies. It is concluded that both longer term causes, intrinsic to this planet, and a final catastrophe either involving bolide impact or volcanism on a spectacular scale, or perhaps a combination of the two, are required to account for the pattern of end-Cretaceous extinctions.

INTRODUCTION

The great interest stimulated by the asteroid impact hypothesis of Alvarez et al. (1980), based on the discovery of an anomalous enrichment of iridium in the Cretaceous-Tertiary boundary clay, is reflected in a huge literature which cannot be adequately summarised here. For comprehensive literature citations the reader is referred to Silver and Schulz (1982), Van Valen (1984), Alvarez (1986), Jaeger (1986) and Officer et al. (1987). In this article these will be for the most part a concentration on more recent work; where there is no citation the material is thought to be sufficiently familiar not to require it, but in any case the above-listed references should provide appropriate sources.

Much of the literature deals with controversial matters. An early controversy concerned whether or not dinosaurs and calcareous plankton suffered mass extinction at exactly the same time, as demanded by the Alvarez hypothesis. It soon became established to general satisfaction that both terrestrial and marine extinction events took place during the same magnetic interval, 29 R, but there could still have been a difference in timing of up to about half a million years. Recently, however, Saito et al. (1986) claim to have recognised in Hokkaido a sudden change in pollen and spore composition precisely at the base of the Cretaceous-Tertiary boundary clay as determined by planktonic foraminifera. This is held to correspond to the horizon of the so-called fern spike in the Western Interior of North America, which coincides with an iridium-rich layer taken by palynologists on the basis of floral turnover as the Cretaceous-Tertiary boundary in terrestrial sequences (Tschady et al. 1984). Acceptance of the Japanese workers' findings would mean that the marine and continental Cretaceous-Tertiary boundaries are indeed precisely coincident in time.

Two other major controversies persist. Many palaeontologists have challenged the Alvarez assumption of a geologically instantaneous mass extinction event, and argued for gradual changes extending from at least several thousand to as much as a few million years, most probably bound up with changes of sea level and/or climate, the most plausible events causing significant environmental change on a global scale over prolonged periods of time. Secondly, to account for the iridium anomaly and other distinctive features of the Cretaceous-Tertiary boundary layer, volcanism on a catastrophic scale has been invoked as an alternative to bolide impact. In the ensuing account an attempt is made to evaluate the evidence for and against these conflicting views and a scenario is presented in outline that invokes a multiplicity of interacting factors.

THE PATTERN OF BIOTIC CHANGE THROUGH THE LATEST CRETACEOUS

Two of the most important questions that must be addressed initially concern (1) the extent to which the extinctions were gradual or sudden and (2) extinction selectivity. In other words, were extinction rates for particular groups of organisms already increasing before the final demise, or was there no hint of change before a catastrophic event at the very end of the period? To what extent can a differential effect be discerned in the vulnerability to extinction of different groups? Answers to these questions will obviously have a critical bearing on which environmental scenario is favoured.

Before these questions are addressed the problem of sampling quality must be noted. Thus Signor and Lipps (1982) point out that if there is a progressive decline in sampling quality approaching an extinction boundary then even a razor-sharp, 'instantaneous' extinction event will appear as a progressive decline smeared out in time. (On the other hand even a minor erosional hiatus, if not spotted, can serve to enhance the apparent

sharpness of the extinction event). The sampling problem becomes particularly acute with large organisms, which are rarer than small organisms in accordance with the so-called Biomass Law. Thus in a terrestrial sequence without adequate palynological control should the Cretaceous-Tertiary boundary be drawn at the horizon of the highest dinosaur? Sampling considerations suggest that an error of up to several metres of section should be incorporated in the estimate.

Another consideration that should be borne in mind is that taxon counts alone are insufficient to give an adequate assessment of an extinction event. Thus if a particular group has gradually been reduced from many to merely one species before its final disappearance, a simple plot of species number against time will suggest a progressive decline, with the extinction of the last species being a trivial event calling for no special explanation. But if that last species was present in huge numbers of individuals until the last, then a phenomenon of potentially great significance would be missed by simply recording taxon number. The fairly recent disappearance of the Passenger Pigeon from North America might be considered a case in point. Therefore culling of the literature for records of the stratigraphic distribution of species or higher taxa, while undoubtedly a valuable and necessary exercise, must be supplemented by careful observation of the stratigraphic distribution of numbers of individuals.

Extinction - sudden or gradual?

Attention will be concentrated on some of the most discussed groups of organisms that suffered extinction, and on research that takes due note of the sampling problems noted above. For many familiar groups of organisms that became extinct by the end of the Cretaceous, such as the reptilian plesiosaurs, ichthyosaurs, mosasaurs and pterosaurs, and various marine

benthic invertebrates, there are either severe sampling problems or the available data are insufficient to allow any generalisation.

Calcareous plankton. Without question the most striking mass extinction event at the Cretaceous-Tertiary boundary was that affecting the planktonic foraminifera and coccolithophorids in the oceanic realm (Thierstein 1981, 1982). This is clearly expressed both in the drastic reduction in numbers of individuals and taxon diversity. Thus it is easy to locate the boundary at a classic section such as Gubbio, Italy by the sudden disappearance of numerous forams which are just discernible with the naked eye. Perch-Nielsen (1986) estimates that the taxonomic turnover at the boundary of nanoplankton (mainly coccolithophorids) is at least an order of magnitude higher than during the preceding Cretaceous. To a considerable extent the widespread occurrence of a boundary clay can be attributed to the sudden loss of the calcareous component of the bottom sediment as a consequence of mass extinction.

Detailed examination of the unusually thick and complete section across the boundary at El Kef, Tunisia, reveals however that the plankton extinction event cannot be attributed to a 'geological instant'. Planktonic forams and coccolithophorids exhibit a different extinction - recovery pattern. Whereas both groups are considerably reduced at the level of the iridium anomaly, the nanoplankton experienced their main extinction well into the Tertiary, probably several thousand years later (Smit and Romein 1985). According to D'Hondt and Keller (1985) many species of planktonic forams disappeared 20 cm below the base of the boundary clay at El Kef, and these authors argue for a progressive, stepwise extinction of this group during the latest Maastrichtian. Lamolda (1987) reaches a similar conclusion for sections in the Basque Country of Spain, including Zumaya. According to Lamolda the loss of forams below the boundary cannot plausibly

be attributed to dissolution effects, as in some deep sea cores, because the Maastrichtian deposits are more calcareous than the overlying Danian.

Marine molluses. It has long been recognised that some of the most familiar Mesozoic groups such as ammonites, belemnites, and inoceramid and rudist bivalves became extinct at or shortly before the end of the Cretaceous. Because of their greater individual size, and also possible facies restrictions, these groups pose more of a sampling problem for precise stratigraphic analysis than the calcareous plankton, and the number of well exposed, mollusc-bearing, biostratigraphically well controlled and complete sections across the Maastrichtian - Danian boundary is very restricted. It is therefore not possible to make pronouncements with the same degree of confidence as for the plankton but there are a number of clear pointers to some general conclusions.

The apparently complete section that has received the most attention is that at Zumaya, northern Spain (Ward et al. 1986, Wiedmann 1986). Ammonite diversity and numbers decreased more or less gradually through the course of the Maastrichtian; no new groups appear in the late Maastrichtian. Despite intensive search in suitable facies, no ammonites have been found in the top 13 m, corresponding to a time interval of approximately 130 thousand years. Thus the ammonite might have gone extinct well before the end of the Cretaceous. Although ammonites persist to the top of the Cretaceous at the well known locality of Stevns Klint, Denmark, there is a dissolution hiatus at the level of the Fish Clay (Ekdale and Bromley 1984). At Mons Klint nearby, where there is no such feature, the last ammonites are found a short distance below the boundary.

The other molluscan groups were apparently all in decline before the end of the Cretaceous (Dhondt 1986, Christensen 1976, Kauffman 1984). Thus true inoceramids went extinct at the end of the early Maastrichtian, with

only one related genus of doubtful affinities, Tenuiptera, persisting until the end of the stage, while rudists underwent a drastic reduction in numbers and diversity early in the late Maastrichtian.

Dinosaurs. Although they attract the greatest popular interest dinosaurs are one of the least satisfactory groups for this kind of study, because of the paucity of suitable stratal sections and the comparative scarcity of fossil material. Virtually all the conclusions that have been drawn about the final dinosaur extinction episode derive from a few sections in western North America. For all we know, the group might well have gone extinct in other parts of the world before the end of the Cretaceous, or even locally have persisted into the Palaeocene. At any event too much has been made of the end-Cretaceous dinosaur mass extinction as a unique event. In fact, as Padian and Clemens (1985) point out, the dinosaur generic turnover rate was exceptionally high throughout the group's history, and the most unusual feature of the end-Cretaceous event was the failure of a new replaceive group of dinosaurs to emerge. The implication of the high generic turnover rate is that dinosaurs were always relatively vulnerable to extinction throughout their long history, and that no environmental event of exceptional magnitude need necessarily be invoked.

Whereas Russell (1979) maintains that the dinosaurs were cut short in their prime, with the group exhibiting no decline from a high late Cretaceous diversity level at the end of the period, some detailed work reported on recently suggests otherwise. Carpenter and Breithaupt (1986) studied the latest occurrence of nodosaurid ankylosaurs in Wyoming and Montana, using the relative abundance of teeth as a good measure of species abundance, and inferred a real decrease in population levels during the late Maastrichtian, with the group going extinct well before the end of the stage. That this pattern is likely to be true of dinosaurs in general is

suggested by the more comprehensive work of Sloan et al. (1986). According to these authors, who take into account the discovery of articulated bones to eliminate the possibility of reworking, dinosaur extinction in Wyoming, Montana and Alberta was a gradual affair, beginning about 7 million years before the end of the Cretaceous and accelerating rapidly in the last 0.3 million years. This decline up the succession cannot apparently be dismissed as an artifact; there is more outcrop available for examination in the top 30 m of the Cretaceous in the Montana section than an equivalent thickness of strata below, where more dinosaur remains have been found. The rapid reduction through time of both diversity and individual abundance is attributed to a combination of environmental deterioration and more tentatively to competition from immigrant ungulate mammals. Sloan et al. also make the more controversial claim (see discussion in Science 234, 1170) that a dinosaur 'genera' (best interpreted as species) persisted into the early Palaeocene in Montana, with only 4 disappearing at the end of the Maastrichtian. The fossil teeth on which this claim is based occur in doubted Palaeocene strata, above the local iridium anomaly and correlated palynological change, but in stream channel sediments which raise the possibility of derivation by reworking from Maastrichtian strata. Sloan et al. discount this on the grounds that (a) the teeth bear no signs of abrasion and (b) dinosaurs are less common than mammals in the Maastrichtian sediments through which the channel is cut, yet no mammals have been found with dinosaurs in the channel deposits.

Terrestrial plants. For this group as well as the dinosaurs, one has to depend on North American data for the type of detailed information required. What can be called the conventional view, as reviewed by Hickey (1984), is that, while the rate of floral turnover increased in the latest Cretaceous, with a decline in angiosperm diversity, there was no catastrophic end-Cretaceous extinction event. This view has recently been challenged by

Wolfe and Upchurch (1986) on the basis of detailed leaf studies over an extensive region in the Western Interior from New Mexico to Alberta. They see no evidence of any major floral change through the Maastrichtian, but record a sharp and dramatic change at the Cretaceous-Tertiary boundary, with mesothermal evergreen vegetation suffering major extinction in the northern High Plains region. An episode of significant ecological disruption at the boundary, which consistently occurs coincident with an iridium anomaly, had earlier been recognised from palynological data, which indicated a drastic decline of angiosperms and gymnosperms at the expense of ferns - the so-called fern spike (Tschudy et al. 1984). A comparable event has been recorded for Japan by Saito et al. (1986). That this was more an ecological disturbance than a major extinction event is indicated by the reappearance of many taxa in the early Palaeocene, indicating that refugia must have existed, and the disruption to plant life was only temporary (Tschudy and Tschudy 1986).

Extinction selectivity

Within the marine plankton, dinoflagellates were evidently little affected by the end-Cretaceous extinction events, in marked contrast to the calcareous plankton, and the same applies to benthic as opposed to planktonic forams. Whereas, according to Thierstein (1982) the generic extinction was 92% for planktonic forams, 85% for radiolaria and 73% for coccoliths, it was only 23% for diatoms (Kitchell et al. 1986). Kitchell et al. relate this low rate of extinction compared with other elements of the plankton to a life history cycle adapted locally to surviving stress by forming non-planktonic resting spores. The same could well apply to the dinoflagellates. With regard to the macrobenthos, study of the section along the Brazos River, Texas suggests that suspension feeders, most notably epifaunal bivalves, were relatively vulnerable to extinction (Sheehan and Hansen 1986).

It has been stated that on the continents animals over 25 kg in weight were the most extinction - vulnerable (Russell 1979) but it should be noted that some dinosaur taxa were quite small and that, although nearly all end-Cretaceous mammals were small in size, the marsupials were much more severely affected than the placentals (Padian and Clemens 1985). Freshwater vertebrates such as crocodiles, turtles and champsosaurs survived with little change, as evidently did the birds; while of course the fossil record of this last group is relatively poor it has improved greatly in recent years and the inference is probably soundly based (Mr. Howgate, personal communication).

Because of the existence of seeds, spores, pollen and rhizome systems, terrestrial plants should be more resistant in the long term to severe environmental disturbance than many animal groups (Knoll 1984) and the pollen data reported by Tschudy and Tschudy (1986) appear to bear this out, as indicating rapid recovery of angiosperms following a short-term ecological disaster. Nevertheless there was a high rate of extinction in the Aquillapollenites Province of western North America and eastern Siberia, with angiosperms being more vulnerable than conifers in mid to high latitudes. Floral turnover in the Normapolles Province of eastern North America and Europe was less pronounced and in the southern hemisphere little or no change has been recorded across the Cretaceous-Tertiary boundary (Collinson 1986).

A number of general conclusions have been drawn on the basis of comparison of various groups. By studying evolutionary patterns among late Cretaceous bivalves and gastropods Jablonski (1986a) argues that the end Cretaceous extinctions involved more than an intensification of normal 'background' extinction. Factors that enhanced survivorship during normal times, such as planktotrophic larval developments, broad geographic species

range and high species richness, were ineffectual during the mass extinction phase, but broad geographic range of an entire lineage, regardless of the ranges of its constituent species, evidently correlates with reduced vulnerability to extinction.

Stanley (1987) perceives a climatic theme, with tropical taxa in the marine realm being relatively vulnerable to extinction (cf. Kauffman (1984) for bivalves). Thus cool-adapted species of planktonic forams, with a simple globigerine shape, migrated to low latitudes within the last few thousand years of the Cretaceous, replacing warm-adapted species with ornate skeletons that suffered extinction (Gerstel et al. 1986). Similarly, gastropods that lived in cool northern waters in the late Cretaceous migrated to North Africa at the end of the Cretaceous, replacing tropical gastropods (Kollman 1979). It is of course well known that low latitude organisms such as reef corals and rudists have been relatively vulnerable to extinction, but it should be borne in mind before a simple temperature decline scenario is adopted, that tropical groups are generally stenotopic and hence potentially vulnerable to a variety of environmental disturbance. They are also more taxon-rich, and it remains to be demonstrated with quantitative rigour that there is a significant differential effect between low and high latitudes which involves proportion rather than absolute numbers of taxa that went extinct.

Sheehan and Hansen (1986) put forward a hypothesis of great generality embracing both marine and continental realms. They observe that the marine phytoplankton, because of its low biomass at a given time and short life history, is very vulnerable to environmental disturbance. A model is generated whereby organisms dependent on living plant material are more vulnerable than those that feed on detritus or scavenge for their food. The fauna of the Brazos River section supports the model, because suspension

feeders dependent on plankton were more affected by the end Cretaceous extinction than deposit feeders such as nuculanid bivalves, and carnivores. As regards the continents, it is argued that the herbivorous dinosaurs probably depended for their food on living plants, while placental mammals were probably insectivores. Freshwater ecosystems, however, are based fundamentally on land-derived detritus, which would have enabled the vertebrates to survive. The Sheehan and Hansen hypothesis is, of course, only relevant to the short-term catastrophic type of scenario presented by Alvarez et al. (1980) and not ~~the~~^{to} any longer-term events lasting thousands of years or more.

CHEMICAL AND PHYSICAL SIGNATURES OF THE CRETACEOUS-TERTIARY BOUNDARY

The evidence supporting the impact hypothesis has been eloquently reviewed recently by Alvarez pere et fils (L.W. Alvarez 1987, W. Alvarez 1986) and need not be gone into in detail here. The key discovery was made at the end of the 1970s. A clay layer at Gubbio, Italy, identified by micropalaeontologists as marking exactly the Cretaceous-Tertiary boundary, was found to be greatly enriched in the platinum-group trace element iridium, by a factor of 30 compared to the normal background. Subsequently an iridium anomaly, signified by a more or less pronounced 'spike', has been found at the boundary across the globe at over 75 localities, including a few in sections of continental sediments. The high iridium concentration, and that of other siderophile trace elements, is much too great for crustal rocks but matches that of chondritic meteorites. Concentration of micrometeorite background material at a time of exceptionally low sedimentation rate appears to be inadequate to account for the size and extent of the anomaly, though without much doubt condensation factors have played a role in controlling the level of iridium recorded locally (e.g. Ekdale and Bromley 1984). Similarly the fact that kerogen can

preferentially adsorb a variety of metallic elements or their compounds may help to explain the exceptionally high iridium level in the kerogen-rich Fish Clay at Stevns Klint, but there is no general correlation of the iridium anomaly with black shales, nor have iridium enrichments of comparable magnitude been recognised in organic-rich deposits of other ages. A possible concentration by marine organisms that were subsequently buried by bottom sediment fails to explain the existence of iridium anomalies in continental sections in North America.

Independent evidence supporting the Alvarez hypothesis is claimed on the basis of two discoveries in clay layers at the Cretaceous-Tertiary boundary. The first discovery, which seems to be impressive, is of so-called shocked quartz, with multiple laminar features held to be uniquely characteristic of impact events; it has been recorded at several localities in North America and Eurasia (Bohor et al. 1984, Izett and Pilonore 1985, Badjakov et al. 1986). The second discovery is of spherules in the general size range 100-1000 μm , composed of sanidine and other minerals, first recorded at Caravaca, southern Spain by Smit and Klaver (1981) and subsequently found at many other localities. These are believed by some workers including the above-named authors to be mineralogically altered examples of microtektites formed by the cooling of droplets of impact melt.

Much publicity has also been given to the discovery of soot in the organic fraction of the Fish Clay at the Cretaceous-Tertiary boundary in Denmark (Wolbach et al. 1985). The soot content is about four times higher than that of the clays above and below. On the assumption that the Alvarez hypothesis is correct, and that the boundary clay was deposited in less than a year, then the carbon flux during that year is $10^3 - 10^4$ times the normal value. This has led Wolbach et al. to propose the occurrence of wildfires on a spectacular scale, which would have had devastating environmental effects globally, comparable to a nuclear winter. If, however, the

sedimentation rate of the Fish Clay was similar to the clays above and below, and bearing in mind that it is relatively enriched in organic matter, there is nothing unusual about the presence of soot or charcoal, which is commonplace in the stratigraphic record, marking the persistent occurrence of forest fires on a modest scale. The Wolbach hypothesis depends implicitly on the assumption that the Alvarez hypothesis is correct, that the Cretaceous-Tertiary boundary clay is exclusively post-impact fallout of dust, and the soot data cannot therefore be cited as independent evidence in support (see discussion in Science 234, 261-4).

With regard to other chemical signatures at the Cretaceous-Tertiary boundary other than the iridium anomaly, the most striking is a strong and short-term negative excursion of ^{13}C in coccoliths and planktonic forams in deep-sea cores (fig. 1a), which is best explained in terms of a reduction in the ^{13}C gradient between surface and deep ocean waters such as would result from a drop in the global rate of photosynthesis over the ocean surface (Shackleton 1986). This is of course what one could predict from a mass extinction event in the phytoplankton. The calcareous plankton oxygen isotope record reveals no such dramatic change (fig. 1b), with several oscillations in ^{18}O directly above and below the boundary being almost as marked as the small rise of 0.5 immediately at the boundary (Shackleton 1986). Whether such short-term oscillations represent environmental signals as opposed to diagenetic noise has not yet been clearly established. The $^{87}\text{Sr}/^{86}\text{Sr}$ ratio increases from the late Cretaceous to the Recent in a regular way that promises well for stratigraphic correlation, but with a major interruption at the end of the Cretaceous, signified by a small but distinctive sharp rise followed by a restoration to the original level (fig. 1c; Koepnick et al. 1985; Hess et al. 1986, Elderfield 1986).

An analysis of the Cretaceous-Tertiary boundary clay at several localities revealed a different clay mineral composition in each, with no exotic mineralogy; all samples were typical of normal marine Cretaceous clay (Rampino and Reynolds 1983; cf. Preisinger et al. 1986).

COMPARISON OF THE IMPACT AND VOLCANIC HYPOTHESES FOR THE END
CRETACEOUS CATASTROPHE

Whatever the ultimate cause, there now seems to be little doubt that the Cretaceous period ended in a geologically short-term event or rapid succession of events of catastrophic magnitude and more or less global extent. Within the biosphere this event is recorded by mass extinction of the marine calcareous plankton and by an ecological disaster in at least much of the northern hemisphere among the more evolved land plants. Contemporary extinctions in animal life most probably reflect a devastating disturbance to primary food production and may therefore require no special explanation. Directly following the catastrophe, marine deposits record a short-term population explosion of the opportunistic phytoplankton genera Braarudosphaera and Thoracosphaera in the oceans (Thierstein 1981), and of ferns on at least two continents, followed by the gradual restoration of angiosperms along the lines of an ecological succession. The striking and globally widespread iridium anomaly, and associated occurrence of shocked quartz and microspherules, has not been matched at any other generally accepted mass extinction horizon and may yet prove to be unique to the Phanerozoic (Donovan 1987).

Given this array of evidence, there appear to be only two plausible causes that can be invoked to account for such a catastrophe, bolide impact or volcanicity on an exceptional scale. Rival hypotheses based on these alternatives give rise to quite similar environmental scenarios.

The impact scenario as first put forward by Alvarez et al. (1980) and subsequently modified somewhat (Alvarez 1987) is that a 10 km diameter bolide hit the earth, creating a crater about 150-200 km in diameter and expelling a huge quantity of pulverised rock. The earth was in consequence enveloped by an opaque blanket of dust, which for a period of months blotted out sunlight and thereby stopped photosynthesis, leading to the mass starvation of animal life. The dust eventually settled to form the Cretaceous-Tertiary boundary clay, laced with iridium-enriched material from the bolide remnants. Significant short-term temperature changes would have ensued, probably an initial drastic fall followed by a rise because of the greenhouse effect. Perhaps the most important killing mechanism would derive from the shock heating of the atmosphere by the expanding fireball. This would give rise to the production of huge amounts of nitrogen oxides in the atmosphere, leading to highly acidic rain. The acid rain would lower the pH of oceanic surface waters sufficient to dissolve calcareous material such as plankton skeletons.

The volcanic scenario proposed by Officer et al. (1987) differs in that the events in question extended over at least 10,000 years. It is known that flood basalt fissure eruptions that produce individual lava flows with volumes greater than 100 km^3 at very high mass eruption rates are capable of injecting large quantities of sulphate aerosols into the lower stratosphere, with potentially devastating atmospheric consequences (Stothers et al. 1986). Such volatile emissions on a large enough scale would lead to the production of immense amounts of acid rain, reduction in alkalinity and pH of the surface ocean, global atmospheric cooling and ozone layer depletion.

It is clear that the environmental consequences envisaged for either the bolide impact or the volcanic scenario are essentially similar, but with the latter being much more extended in time because no individual episode of volcanism could match the devastating effect of a large bolide impact. In

deciding, therefore, which is the better supported by evidence, it is of crucial importance to establish as precisely as possible the time spans signified by the horizon of abnormal iridium enrichment and correlative biotic changes. Because the time interval for either scenario falls well within the finest resolution available by conventional means of stratigraphic correlation or age determination, this is not a straightforward matter.

I give below a personal assessment of the evidence for and against the alternative scenarios, abbreviated to I (impact) and V (volcanic).

1. Iridium enrichment

I. The substantial enrichment of iridium (and other siderophile elements) in the Cretaceous-Tertiary boundary clay matches the composition of chondritic meteorites but not that of the earth's crustal rocks. The global distribution signifies an event of major significance and the intimate coincidence with mass extinction of the plankton is remarkable. Simple calculations based on iridium concentrations in the boundary clay lead to the inference of a bolide 10 km in diameter, whose impact with the earth would have deleterious consequences of the appropriate magnitude. Although much of the earth's mantle has a composition similar to that of chondritic meteorites, it is implausible to invoke a mantle source because of (a) the global extent and amount of iridium, (b) the iridium-enriched aerosol erupted recently at Kilauea was a light mantle differentiate. The iridium/platinum ratio of the Cretaceous-Tertiary boundary clay signifies, in contrast, no such differentiation (F. Asaro, personal communication).

V. The composition of the aerosol erupted at Kilauea, with an enormous enrichment of iridium compared to normal Kilauean lavas (Zoller et al.

1984) weakens the case for excluding a terrestrial source for the Cretaceous-Tertiary boundary clay iridium, especially as the ratios of iridium to arsenic and antimony of the boundary clay resemble those of the Kilauea eruption but differ significantly from those of meteorites (Officer and Drake 1985). Provided the appropriate mantle source could be tapped for an extended period of time, a global enrichment of iridium of the appropriate magnitude of the Cretaceous-Tertiary boundary could be produced.

2. Stratal distribution of iridium

V. A number of profiles of the Cretaceous-Tertiary boundary clay indicate that the zone of iridium enrichment often extends over a thickness of strata indicating, according to reasonable estimates of sedimentation rate, a time duration of at least several thousand and perhaps several tens of thousand years, which is inconsistent with the prediction of the impact hypothesis. In several cases multiple iridium enrichments have been recorded (Officer et al. 1987, Wiedemann 1986). It is implausible to invoke bioturbational smearing up and down the section, because such disturbance would substantially diminish the iridium anomaly. In addition, some classic sections such as Stevns Klint do not show bioturbation at the critical horizon.

I. Careful cm by cm sampling of Cretaceous-Tertiary boundary sections in the Gosau Basin of Austria shows a sharp rise to the maximum value of iridium, followed by a gradual diminution over a thicker portion of section back to normal values (Preisinger et al. 1986). Similar patterns have been discerned at Gubbio and Caravaca and can best be interpreted as due to iridium deposition due to impact, followed by redeposition over a longer time interval of iridium-enriched material from elsewhere.

3. Shocked quartz

I. The shocked quartz found at the Cretaceous-Tertiary boundary at a number of widely scattered localities in three continents has the highly distinctive features of impact deformation in the form of multiple sets of laminae. These have not been recognised in any volcanic rocks.

V. The recognition of shock features, many of which are subtle and present only in small grains, in volcanic rocks requires specialised skills and the subject has not hitherto been studied intensively. Shock features have now been recognised in plagioclase and biotite phenocrysts erupted from the Toba caldera, Sumatra (Carter et al. 1986). Shocked features in minerals are also known to occur in the Bishop's Tuff of California. It is admitted that, so far, no shocked quartz grains of the distinctive type described by Bohor et al. (1984) have been recognised, but even in the Cretaceous-Tertiary boundary clay only a small minority of the quartz grains fall into this category. Discovery of shocked quartz grains at horizons other than the boundary clay would weaken the case for associating them with an impact event that caused mass extinction. (See discussion between Carter et al. and Izett and Bohor, Geology 15, 90-92).

4. Microspherules

I. The microspherules found at the Cretaceous-Tertiary boundary in many localities around the world are most reasonably interpreted as the low temperature alteration products of droplets of impact melt.

V. A detailed examination of the Gubbio section reveals that, while there is indeed a concentration of microspherules containing K-feldspar or K-feldspar and glauconite, in the Cretaceous-Tertiary boundary clay,

they are not unique to this horizon, but extend over a stratigraphic range from Turonian to Palaeocene (Naslund et al. 1986), so that they cannot be regarded as unique to the Cretaceous-Tertiary boundary.

Spherules of the appropriate size range of clearly volcanic origin are known to occur, so the concentration in the boundary clay could signify a peak of volcanism at that time. Recent Danish work (Hansen et al. 1986) suggests that the spherules have nothing to do with either impact or volcanism, but are the result of diagenetic infill of prasinophyte algae.

5. The Cretaceous-Tertiary boundary clay

I. The boundary clay first studied at Gubbio and subsequently found in other parts of the world is direct evidence of the fallout of material of the earth-embracing dust cloud produced by the impact event. A detailed mineralogical study of the boundary clay at Stevns Klint shows the central part to be composed of pure smectite in contrast to the illite and mixed layer smectite/illite of the clays above and below. An impact melt rather than volcanic glass origin is supported by major element chemistry (Kastner et al. 1984).

V. A Cretaceous-Tertiary boundary clay is by no means found in all marine sections (Officer et al. 1987). Where such a clay occurs, the most obvious explanation for it is that it makes a concentration of non-calcareous material following mass extinction of the planktonic organisms that supplied the calcareous component of the sediment, aided perhaps in some cases by post-sedimentation dissolution. In a number of examples that have been studied there is nothing unusual about the clay mineral composition, which varies from locality to locality in a way suggesting control by regional palaeogeographic circumstances (Rampino and Reynolds 1983). With regard to the Stevns Klint boundary

clay, the mineral smectite is most easily formed by the alteration of volcanic ash. A layer of pure smectite in the midst of normal detrital clays is usually a clear indication of a bentonite. This argument was used to propose a volcanic origin for distinctive fuller's earth clays in the Jurassic and Cretaceous of Southern England (Hallam and Sellward 1968), an interpretation confirmed by the subsequent discovery of a diagnostic suite of minerals and relict glass shards (Jeans et al. 1977).

Kastner et al.'s argument contains a flaw. According to the impact scenario, the meteorite component would have comprised at most only 20% of the fallout dust and may be much less (Rampino and Reynolds 1983). Thus most of the boundary clay should be the alteration product of a mixture of earth rocks expelled from a huge crater; only a small fraction of this would have been melted on impact. Furthermore, no convincing evidence has been put forward that smectite is the normal product of impact melts. In the circumstances, citation of major element chemical data seems rather meaningless.

6. The site of the impact crater

I. It is disappointing rather than devastating to the impact hypothesis that no convincing crater of the appropriate age has yet been recognised. If the impact took place on a continent, perhaps it has subsequently been buried by sediment or destroyed by erosion. The buried Manson crater of Iowa seems to be of the right age to account for the occurrence of shocked quartz of sand grade in the U.S. Western Interior. It is statistically more probable, however, that impact took place somewhere in the oceans.

V. The Manson crater, with an estimated diameter of about 25 km, is far too small to be invoked for the devastating environmental scenario required by the impact hypothesis. There are plenty of records of dated craters extending back through the Phanerozoic. A continental crater as young as end-Cretaceous and of the large size required, is unlikely to have been destroyed by erosion or buried without trace. If the impact took place on the ocean floor, where did all the shocked quartz come from? The sediment of the deep ocean is largely calcareous or argillaceous, interrupted at some horizons in the Atlantic by layers of turbiditic quartz sand. Much of this rock is incompletely consolidated, and it is difficult to see how impact stresses could be transmitted through such sediment to impose shock deformation features on the quartz grains. Most of the expelled rock would in fact be quartz-free basalt. A possible way out of the dilemma posed is to invoke an impact site on the continental shelf, but this is statistically improbable because of the small area involved. Moreover it is highly unlikely that such a site would no longer be recognisable. An impact anywhere in the marine realm should have generated tsunamis on an enormous scale, which should have created significant disturbance to the sedimentary record across the Cretaceous-Tertiary boundary. Although slumping seems to have occurred in a few sections, this has not been tied to a Cretaceous-Tertiary boundary event.

7. Appropriate volcanism

V. There is evidence from various parts of the world of substantial volcanism at the end of the Cretaceous, the most striking example being the emplacement of the Deccan lavas of India. With a minimum estimated volume of 10^6 km^3 they are the largest continental flood basalt eruptions of the past 200 million years and the most recent determination of their date of eruption suggests that it all took place

within magnetic interval 29 R, with a duration of about 600 thousand years and embracing the Cretaceous-Tertiary boundary (Courtillet et al. 1986). It would be an astonishing coincidence if volcanicity on such an immense scale was totally independent of the Cretaceous-Tertiary boundary mass extinction event. Modelling calculations based on the volume of lavas and the injection of mantle-derived material into the atmosphere and stratosphere suggest that it is plausible to invoke the Deccan Traps to account for the end-Cretaceous catastrophic disruption to the biosphere (Officer et al. 1987).

I. It is implausible to invoke the Deccan Traps or any other localised volcanic source to account for the global distribution of iridium, on the basis of the small Kilauean gas eruption, and no other iridium-enriched volcanic rocks are known. No iridium-enriched layer has been found in sediments associated with the Deccan Traps. The presence of shocked quartz implies explosive volcanism if an impact origin is to be rejected, whereas the Deccan Traps are flood basalts.

8. The biotic response

I. From the initial work at Gubbio, where an intimate correlation was first demonstrated between the iridium anomaly and mass extinction of the calcareous plankton, a strong association of the two has been repeatedly demonstrated. Allowing for sampling and preservational problems it is highly likely that many animal groups went extinct at the same time. The work of Wolfe and Upchurch (1986) on angiosperm floras in North America points to a single geologically very short-lived disturbance event coincident with an iridium anomaly, which is more consistent with bolide impact than more prolonged volcanism.

V. When sections signifying an unusually high sedimentation rate are studied, such as El Kef, it can be demonstrated that the main planktonic foram and coccolith extinction phases were not coincident in time, but separated by up to a few thousand years, and the extinction rate among the forams was already increasing before the end of the Cretaceous. The impact scenario is too drastic to account for the selective nature of the end-Cretaceous extinctions, with many groups of organisms surviving into the Palaeocene with little or no change.

From the foregoing evaluation it should be apparent that both scenarios have their shortcomings as regards evidential support, and more research is required to resolve the issue decisively. Meanwhile the possibility must not be discounted that bolide impact triggered large-scale volcanism, though such a circumstance could confuse attempts to devise critical tests of clear-cut alternative hypotheses. Moreover, the Deccan Traps volcanism ^Y stated before the end of the Cretaceous (Courtillet and Cizowski 1987).

EVIDENCE FOR LONGER-TERM ENVIRONMENTAL CHANGES

Before the impact hypothesis was put forward it was customary to relate the end-Mesozoic extinctions to either fall of sea-level or climatic cooling, or a combination of the two, climate and sea-level being, with volcanism, the only earth-bound phenomena that could influence environment on a global scale. Their influence would be felt, however, over a longer period of time than the paroxysmal effects discussed in the previous section, ranging probably from hundreds of thousands to a few million years. Evidence for sea-level and climatic changes of this time span is reviewed below.

Sea-level change. It has been widely acknowledged since the last century that the end of the Cretaceous was marked by a significant global fall of sea level, followed by a rise in the Palaeocene. One important consequence

of this is that stratigraphic sections across the Cretaceous-Tertiary boundary in shallow marine facies are extremely rare; hiatuses of varying magnitude are virtually always present. However, precision about the amount and rate of sea-level change has been lacking, though the situation has improved in recent years.

Fig. 2 presents three different estimates of sea-level change in the latest Cretaceous. Sliter's curve (fig. 2a) is based on the amount of continental area covered by sea and is therefore very approximate; it also makes no distinction between different divisions within the stage and merely indicates a progressive Maastrichtian decline correlative with sea-level fall. Kauffman's curve (2b), though only a qualitative estimate, is more precise stratigraphically and is based on changes in sedimentary successions as well as areal changes; it indicates a late Maastrichtian sea-level rise followed by a fall to the end of the stage, after a mid Maastrichtian fall. The revised curve of the Exxon group (2c), based on seismic stratigraphy, offer even more stratigraphic precision. As with the Kauffman curve, a mid Maastrichtian fall is followed by an early late Maastrichtian rise, after which there is a rapid and pronounced fall immediately before the end of the stage. Thereafter there is an equally rapid rise, which more or less ceases across the Cretaceous-Tertiary boundary. All three curves, derived using different methods and of a different degree of precision, agree on a notable sea-level fall shortly before the end of the Cretaceous. The claim by Haq *et al.* (1987) that the minimum sea-level was reached not at but immediately before the end of the period is based on microfossil correlations that have not been published, so that the evidence in support cannot be assessed. The subject is sufficiently important to warrant independent investigation.

Stratigraphic data are sometimes criticised as being both imprecise and difficult to quantify in an illuminating way, so it is gratifying that

independent geochemical evidence can be cited that apparently bears on the question of sea-level change. As noted earlier, there is a clearly discernible positive excursion of the $^{87}\text{Sr}/^{86}\text{Sr}$ ratio across the Cretaceous-Tertiary boundary (fig. 1c), indicating an increase in continental influence of the sort recorded progressively through the Cenozoic to reach the present-day abnormally high level of 0.709. By far the likeliest reason for this Cenozoic change is the correlative fall of sea level, thereby increasing continental area and runoff (Koepnick et al. 1985). Applying the same reasoning to the end-Cretaceous event leads to the inference of a sea-level fall of a magnitude greater than for many millions of years previously, followed by a rapid rise to the earlier level.

While the strontium isotope data must record an event that lasted for a geologically significant period of time, rather than a mere 'instant', their stratigraphic precision and ratio scatter are inadequate at present to allow further inferences as regards duration. Some intriguing clay mineral data from Gubbio perhaps point the way to greater stratigraphic resolution. Johnsson and Reynolds (1986) report a large influx of kaolinite over a 3 m thick part of the section spanning the Cretaceous-Tertiary boundary, compared with the strata above and below, suggesting an environmental event lasting probably a few hundreds of thousands of years. The authors confess themselves somewhat mystified by this phenomenon, but note the well known fact that kaolinite tends to increase in abundance in nearshore facies, probably reflecting its coarse-grained nature and tendency to flocculate more readily than other clays. The simplest and most elegant explanation I can offer is that this kaolinite pulse in a pelagic facies section reflects the end-Cretaceous sea-level fall recorded independently by stratigraphic and geochemical data.

Jones et al. (1987) record facies evidence of a marine regression within the last 300,000 years of the Cretaceous, in a section near Bragg,

Alabama, and a correlative rise in the strontium isotope ratio, while an injection of sand and silt turbidites into the deep Atlantic off New Jersey, precisely at the Cretaceous-Tertiary boundary, is reported by Van Hinte et al. (1985a,b). The authors relate this event to an impact-induced tsunami, but it could just as well signify a marked fall of sea level.

Climatic change. The best record of oceanic temperatures comes from oxygen isotope data obtained from planktonic and benthic forams, principally in the Pacific (Savin 1982). Both surface and bottom waters apparently underwent a more or less steady post-Coniacian temperature decline which was arrested only at the end or immediately before the end of the Maastrichtian (fig. 3). A detailed analysis of Upper Maastrichtian carbon and oxygen isotope stratigraphy at Zumaya, Spain, using bulk sediment derived from the plankton, has been undertaken by Mount et al. (1986). They find that the 2 per mil negative shift in both ^{13}C and ^{18}O at the Cretaceous-Tertiary boundary is no greater than several preceding shifts in the Upper Maastrichtian. The disappearance of ammonites and inoceramids coincides with these earlier isotope excursions. The striking similarity of the ^{13}C and ^{18}O curves is held to imply a direct relationship between warm surface water temperature and decrease in primary productivity. The implication of a succession of El Nino-type warming episodes is thought to be consistent with a volcanic scenario, with injection of CO_2 in the hydrosphere and atmosphere leading to rise of oceanic CCD and greenhouse warming. Clearly such intriguing results need to be confirmed by comparable analysis of other stratigraphic sections, and a more positive demonstration that true oceanographic as opposed to diagenetic signals are being recorded.

If one accepts the arguments of Kauffman (1984) and Stanley (1987) concerning the relative extinction vulnerability of tropical marine

organisms, then there is independent evidence of climatic cooling towards the end of the Cretaceous.

There has also been a general ^sconsensus about a late Cretaceous decline of air temperatures, based on the record of terrestrial plants (Savin 1977, Hickey 1984) but this view has been challenged for the North American Western Interior by Wolfe and Upchurch (1986). From angiosperm leaf studies they find no evidence of climatic cooling through the late Maastrichtian (indeed, fig. 6 of Upchurch and Wolfe (in press) suggests the reverse) but infer a major long-term increase in precipitation starting at the Cretaceous-Tertiary boundary, following the brief episode of ecological disruption discussed earlier. Because such conflicting results have been obtained from the analysis of leaf margins (Hickey 1980, Wolfe and Upchurch 1986) there is doubt as to how to interpret them and the matter needs urgently to be resolved.

CONCLUSIONS

A substantial and rapid sea-level fall would severely restrict habitat area. Notwithstanding Stanley's (1987) reservations, and a causal relationship that has as yet been inadequately worked out, marine regression seems to provide the best correlation with mass extinction episodes throughout the Phanerozoic (Jablonski 1986b). Consider for example the ammonites; throughout their history, diversity peaks correlate with sea-level high stands and diversity troughs, leading in extreme cases to extinction or near extinction of the whole group, with sea-level low stands. Kennedy's graph (1977, fig. 33) suggests strongly that, regardless of any bolide-induced catastrophe, ammonites would have gone extinct by the end of the Cretaceous. Sea-level fall would, of course, increase continental habitat area, but seasonal temperature extremes would increase as the climate became more 'continental' and this might have been sufficient to

cause the extinction of large (probable) ectotherms with low population density, such as the dinosaurs. It appears likely, however, that climate was deteriorating towards the end of the Cretaceous, independent of tectonically-induced sea-level change. If, indeed, temperatures fell by a sufficient amount, small polar ice caps could have been established, that would induce rapid sea-level fall. Subsequent early Palaeocene climatic amelioration would cause these to disappear and the sea level to rise with comparable rapidity. So far no evidence has been discovered that such ice caps actually formed.

It seems clear, however, that a combination of sea-level and temperature fall is insufficient to account for the catastrophic end-Cretaceous plankton extinctions and short-lived ecological disaster among terrestrial plants, so that a final, paroxysmal, disturbance needs to be invoked in addition, due either to bolide impact or volcanicity on a spectacular scale rare in earth history. There has been a temptation for some supporters of the impact hypothesis to accept the phenomenon of stepwise extinction extending over a period of up to a million years or more, and explain it by the collision with the earth of a shower of comets that might leave no chemical signature (Alvarez 1986). It has now been argued, however, by a group of astronomers (Bailey *et al.* in press) that comet showers are not produced with either sufficient frequency or intensity by individual known bodies, whether stars or molecular clouds, to account for either periodic or episodic mass extinctions. One of the great strengths of the original Alvarez hypothesis was its testability. The comet shower hypothesis is weak because it seems impossible to falsify it by data from the stratigraphic record. Taking due note of the astronomers' scepticism, it appears to be a wiser strategy to adopt an extinction scenario derived from events intrinsic to this planet, perhaps with the exception of a single bolide impact coup de grâce to an already wilting biosphere.

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Figure Captions

1. Isotopic changes across the Cretaceous (K) - Tertiary (T) boundary,
 - a, carbon isotope data for bulk sediment in a number of DSDP sites.
Based on fig. 3 of Shackleton (1986).
 - b, oxygen isotope data for bulk sediment in a number of DSDP sites.
Based on fig. 3 of Shackleton (1986).
 - c, strontium isotope changes in seawater from the mid Cretaceous to the present. Based on fig. 6 of Elderfield (1986).
2. Changes of sea-level inferred for the two last stages of the Cretaceous,
 - a, estimate based on area of continent caused by sea, after Sliter 1976.
 - b, high and low stands of eustatic sea-level based on classic stratigraphic methods, after Kauffman 1979.
 - c, high and low stands of eustatic sea-level based on seismic stratigraphy, after Haq et al. 1987.
3. Estimated palaeotemperature curves for low latitude oceanic waters from the late Cretaceous to the present, based on oxygen isotope data from planktonic and benthic foraminifera. Based on Savin 1982, fig. 18.1.

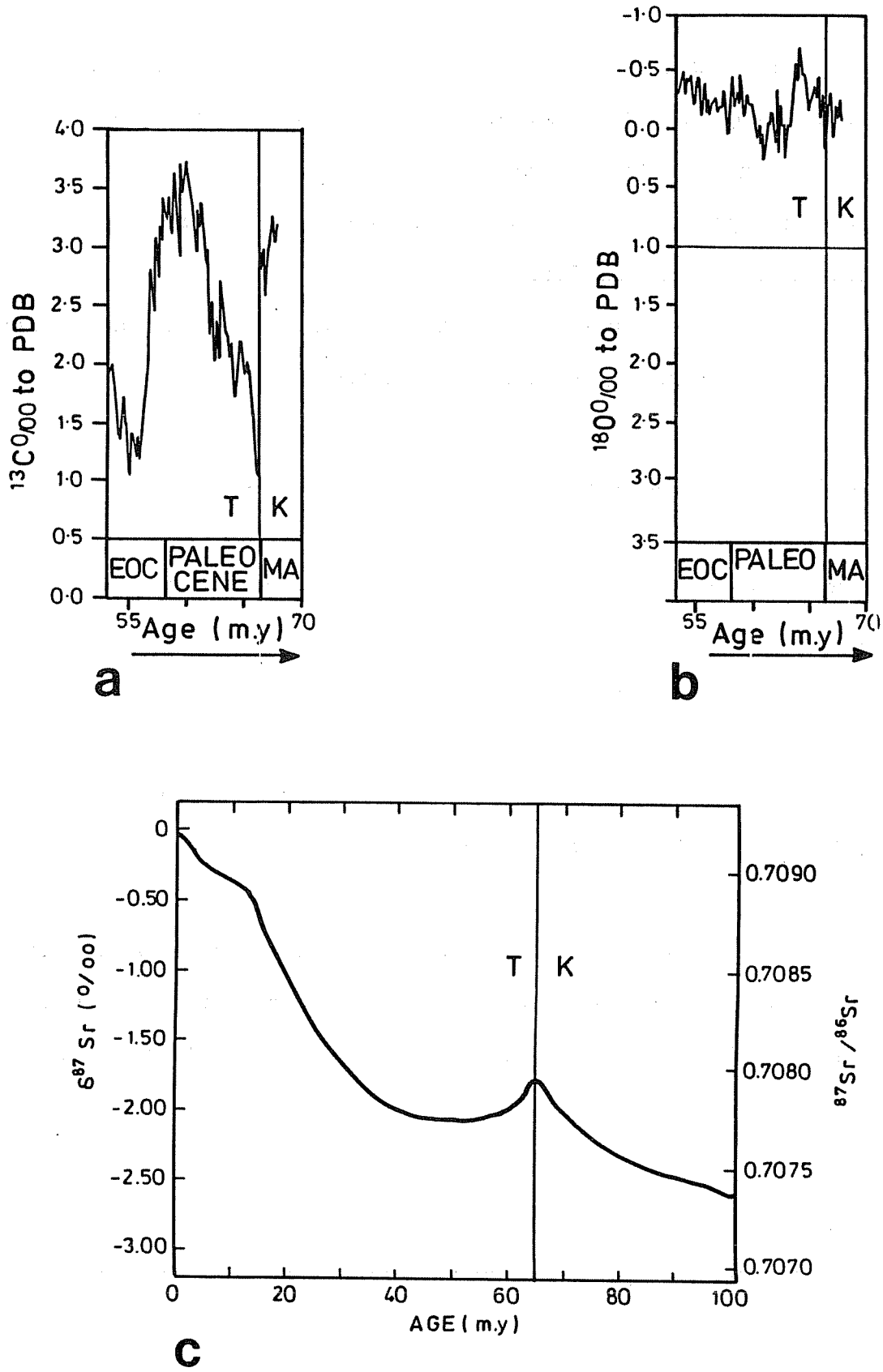
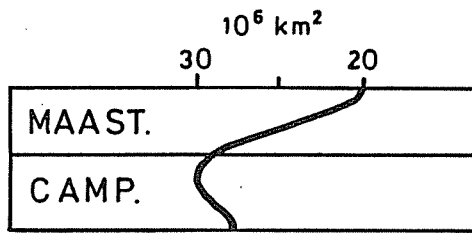


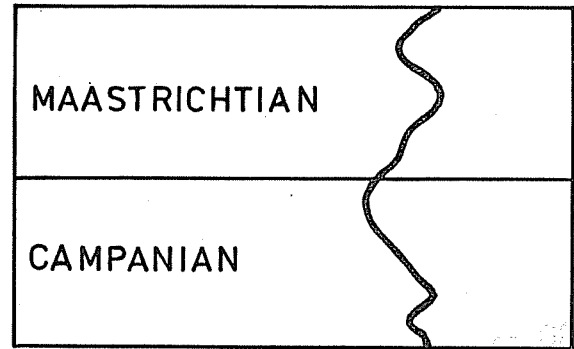
Figure 1.

HIGH
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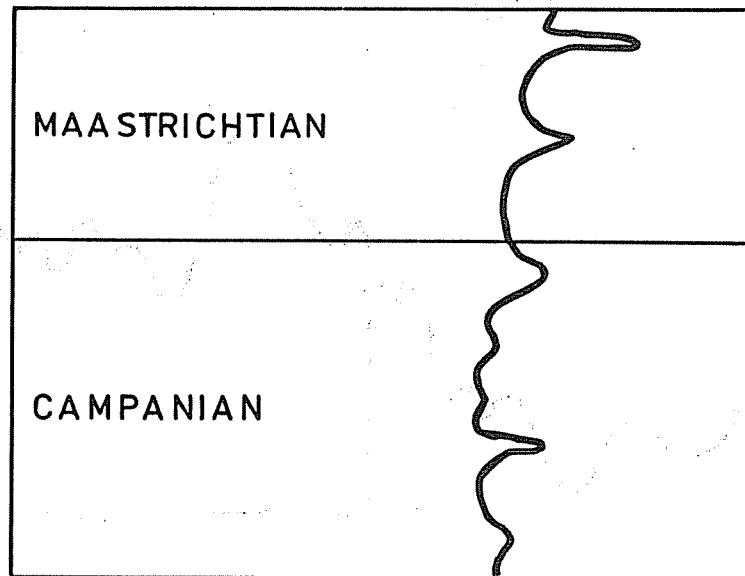
a



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c

Figure 2.

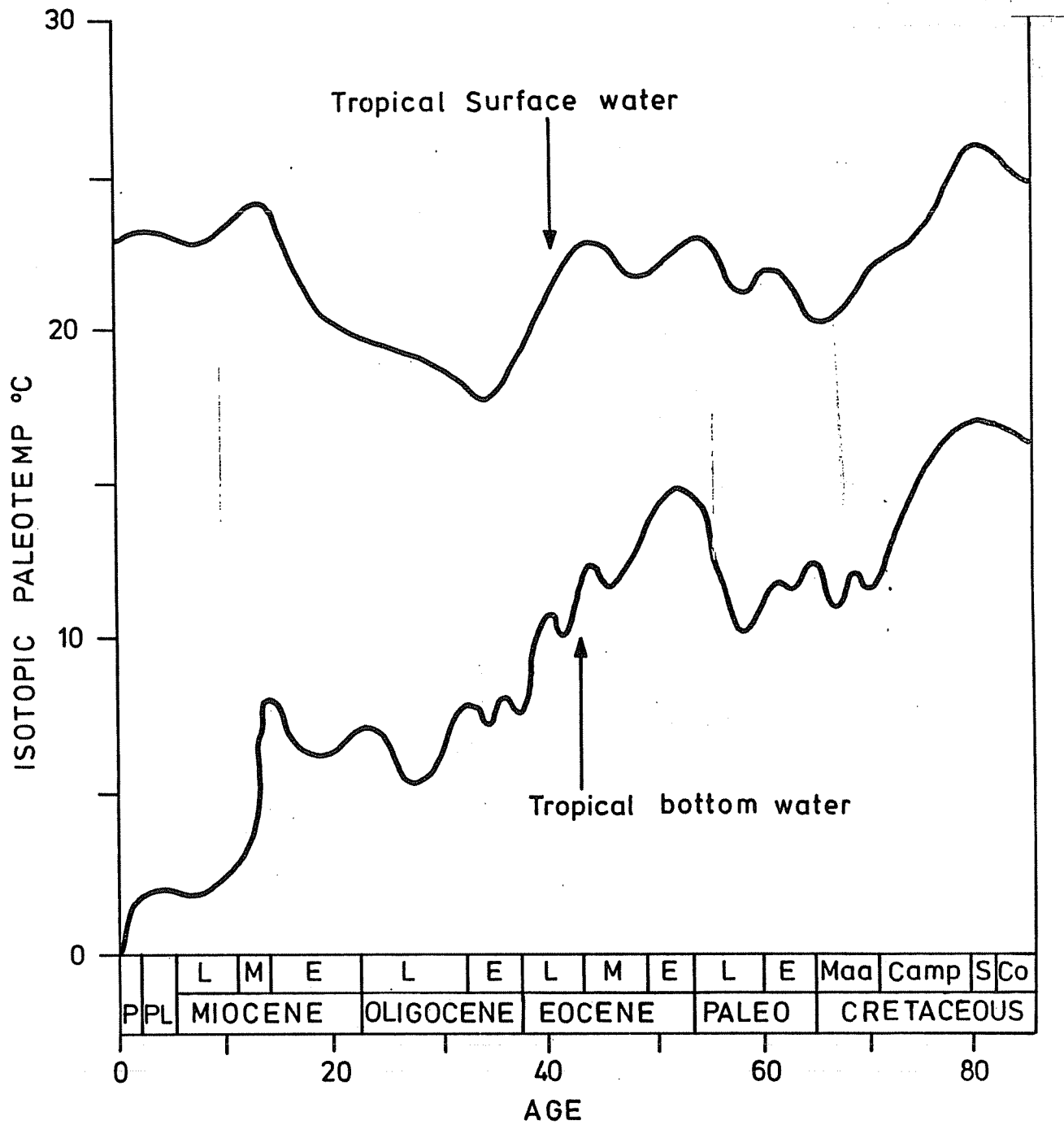


Figure 3.



III JORNADAS DE PALEONTOLOGIA
PALEONTOLOGIA Y EVOLUCION: FENOMENOS DE EXTINCION

HIGH-RESOLUTION TRACE ELEMENT CHEMISTRY ACROSS THE CRETACEOUS-TERTIARY BOUNDARY
IN DENMARK.

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ABSTRACT: Only two localities in Denmark are un-affected by tectonic disturbances of the K/T boundary clay. The one is situated on Stevns Klint and has earlier been reported (Hansen *et al.*, 1986) to have 185 ppb Ir as peak value. This is about 45 times the general estimated global value of around 4 ppb. The red bottom layer of the Fish Clay was pointed out as being a level of semi-filled burrows containing i.a. spherical algal remains filled with the mineral goethite (Hansen *et al.*, 1986a) earlier reported as microtectite-like spherules. Sampling was made *in situ* by aid of 3 mm diameter aluminum capsules, that were pressed directly into the soft deposit. Selected elements from this series is shown in Table 1. from these values it is obvious that the elements Ir and Cr are strongly correlated (actually a 7 star correlation). The remaining elements are correlated with Fe. These

Table 1. Elemental concentration in % of max value.

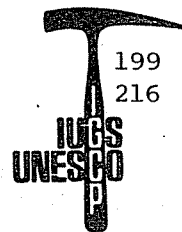
Sample level	Ir	Cr	Fe	Co	Zn	As	Sb	Au
in mm								
60	4	15	5	-	7	-	3	15
59	7	19	6	3	7	-	3	11
58.5	6	20	6	3	6	-	3	4
56.5	8	26	8	5	8	-	4	20
50.5	7	26	7	4	7	-	2	10
47	8	32	7	4	6	-	3	16
43	10	29	5	3	6	-	2	-
39	15	34	5	4	6	-	3	6
35.5	24	36	10	9	12	-	9	11
32	18	36	7	6	9	-	6	9
28	19	41	6	5	7	-	3	8
23.5	29	46	18	15	18	-	19	23
19.5	34	45	20	13	20	26	13	12
16.6	44	54	20	10	19	18	8	22
12.5	50	58	16	11	19	-	8	18
9.5	73	83	22	21	24	25	20	42
7.5	100	100	28	28	30	38	34	51
5.5	93	91	24	24	25	28	27	48
3.5	18	58	90	76	78	82	76	39
1.5	15	54	100	100	100	100	100	100
maximum	185	373	14	238	0.22	302	29.8	55
	ppb	ppm	%	ppm	%	ppm	ppm	ppb

are Co, Zn, As, Sb and Au. It can be concluded that the Ir-Cr peak is separated from the Fe-Co-Zn-As-Sb-Au peak by 6 mm. The two elemental peaks are not correlated but represent different events in the depositional history.

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Hansen, H.J., Gwozdz, R., Bromley, R.G., Rasmussen, K.L., Vogensen, R. & Rasmussen, K.R. 1986a: Cretaceous-Tertiary boundary spherules from Denmark, New Zealand and Spain. Bull. Geol. Soc. Denmark., 35, 75-82.



III JORNADAS DE PALEONTOLOGIA
PALEONTOLOGIA Y EVOLUCION: FENOMENOS DE EXTINCION

THE CRETACEOUS-TERTIARY BOUNDARY ON THE BRAZOS RIVER, TEXAS: STEPPED EXTINCTIONS
AND GIANT TSUNAMI OR STORM DEPOSITS.

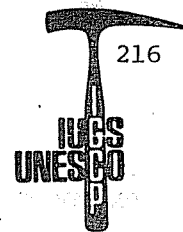
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ABSTRACT: The Brazos River in East Texas has some of the most complete and well-preserved Cretaceous-Tertiary (K/T) boundary sections in the world containing both aragonitic and calcitic macrofossils and microfossils. The Cretaceous sediments contain the latest Maastrichtian Micula prinsii nannofossil zone, and the Paleocene includes the typical nannofossil "disaster" sequence of Thoracosphaera and Braarudosphaera bigelowii. Paleocene sediments also include a complete planktonic foraminiferal sequence including Globigerina eugubina. The K-T boundary on the Brazos River occurs in magnetic zone 29r and it contains an iridium anomaly. There is at least one and possibly two abrupt molluscan extinctions that occur below the K-T boundary as defined by planktonic foraminifera. The uppermost extinction occurs about 0.5 m below the K-T boundary and involves a 75% loss of molluscan species within 15-20 cm of sediment. An impoverished molluscan fauna, dominated by deposit-feeders and carnivores, continues to the K-T boundary which is marked by the final Cretaceous planktonic foraminiferal extinctions, an iridium anomaly and 0.3-0.6 m thick sandstone beds. These beds, characterized by a brecciated and scoured clay base and upward-fining sandstone and clay layers with occasional hummocky cross-stratification, are unique in the section and probably represent tsunami or massive storm deposition. Ten to fifteen centimeters above this layer, there is another iridium anomaly associated with the nannofossil "disaster" species. These data suggest that the K-T mass extinction in the Brazos River region is stepwise, associated with one or more impact events and marked by several extraordinarily large tsunami or storm events reaching middle to outer shelf depths.



III JORNADAS DE PALEONTOLOGIA
PALEONTOLOGIA Y EVOLUCION: FENOMENOS DE EXTINCION

SELECTIVE EXTINCTION OF MARINE PLANKTON AT THE END OF THE MESOZOIC ERA: THE
MANGYSHLAK RECORD

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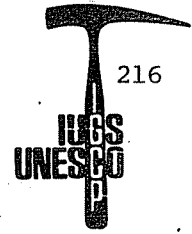
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ABSTRACT: Macro-micro-nanno fossils and stable isotopes were studied from a continuous sequence of latest Cretaceous and earliest Tertiary (K/T) shallow water marine carbonate deposits located on the Mangyshlak Peninsula, NE of the Caspian Sea. Fossil evidence indicates that the K/T boundary extinctions were selective, affecting 90% of the warm water calcareous phyto and zooplankton. Oxygen isotope analyses of bulk sediments indicate a sharp positive spike at the boundary, primarily attributed to a sudden and severe cooling of the surface mixed layer, immediately followed by warming. Benthonic fossils show only a modest positive shift, suggesting a less drastic temperature decline of the bottom water. Independent geologic evidence indicates that the K/T temperature decline was coeval with widespread and intense volcanic activity which reached a peak at the end of the Cretaceous Period. It is surmised that volatile emissions from volcanic eruptions caused or amplified the severe cold event and depressed surface water pH, inhibiting calcareous shell production. The increased acidity dissolved the calcareous shells and temporarily prohibited calcite nucleation, leading to the mass mortality of the warm-water calcareous plankton. The dissolution of CaCO_3 resulted in addition of bicarbonate to the ocean water which ultimately buffered its pH.



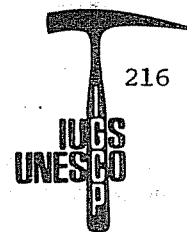
III JORNADAS DE PALEONTOLOGIA
PALEONTOLOGIA Y EVOLUCION: FENOMENOS DE EXTINCION

THE PLANKTONIC FORAMINIFERA OF THE EARLIEST TERTIARY AND THEIR ECOLOGIC INTERPRETATION

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ABSTRACT: The most complete sections showing the Cretaceous-Tertiary boundary are found in deep sea sediments of the Tethys (Italy, Northern Alps, NW and S-Spain, Northern Africa) and in profiles of the Deep Sea Drilling Project. The first two biozones (G. fringa and G. eugubina Zones) of Tertiary age are characterized by very small globigerinids, but specimens with well preserved surface structures were found in a few sections only. The surface structure of all these tiny globigerinids is a calcite crust, independent of other morphological differences. Specimens with the typical honeycom or regular reticulate surface structure do not appear before the G. pseudobulloides Zone (G. edita Subzone). During this zone an enlargement of the reticulation takes place. In recent planktonic foraminifera the formation of a calcite crust appears in some species during ontogeny and migration into deeper and thus colder water. Experiments undertaken with these species have shown a growing calcite crust when lowering the temperature during ontogeny. Species with different surface textures in early ontogeny may have the same calcite crust in later stages. The formation of a calcite crust on the globigerinids of the earliest Tertiary thus is probably not related with phylogeny but indicates a change of ecology at this time.



III. JORNADAS DE PALEONTOLOGIA
PALEONTOLOGIA Y EVOLUCION: FENOMENOS DE EXTINCION

ANALYSIS OF MID-PALEOZOIC EXTINCTIONS

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ABSTRACT: International studies encouraged by the working groups of the Commission of Stratigraphy has provided a precise scale for the analysis of mid-Palaeozoic extinction and diversification events. The Devonian, for example, is currently divisible into some 55 conodont and 45 ammonoid faunal divisions. Some ways in which this precision can be used to investigate evolutionary processes will be outlined and this helps to separate specific causations for events. Some generalisations have already emerged.

- 1.- Despite its acclaim, the so-called Frasnian/Famennian boundary extinctions are similar in style, if not degree, to several others in the mid-Paleozoic.
- 2.- Most extinction events, when well-documented, seem to take place over a significant period of time in a way unlikely to be caused by bolide events.
- 3.- Many extinction events correlate with transgressive/regressive events seen in sedimentation changes. These suggest intra-terrestrial causes.
- 4.- Some extinction events show clear association with anoxia and probable times of ocean upwelling which seems related to tectonic break-up.
- 5.- Ammonoid extinction events appeared to show successive stages of decline, minimum diversity, initiation of novelty, and new diversification. This suggests models for innovation in evolution.

The time for wild speculation is over. The time for detailed analysis of the actual record has arrived. The tools are available. But are there dedicated scientists prepared to do the work?.



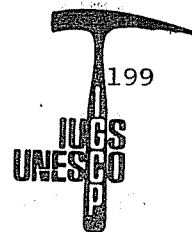
III JORNADAS DE PALEONTOLOGIA
PALEONTOLOGIA Y EVOLUCION: FENOMENOS DE EXTINCION

EVENT CONTROLLED EVOLUTION AND EXTINCTION OF THE PERMIAN FUSULINACEAN FAUNAS OF THAILAND

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ABSTRACT: The evolution and extinction of the Permian fusulinacean faunas of Thailand is controlled by events. The first event occurred in the upper Lower Permian and is characterized by the disappearance of the Arctic-Tethyan elements. This event can be correlated with the closure of the Urals and a worldwide regression. The most important event happened during the lower Upper Permian (Midian). It is characterized by the extinction of approximately 90% of the fusulinaceans. This bioevent is controlled by the closure of the Paleotethys in China and Thailand, which again led to a worldwide regression and ultimately to the greatest extinction event in the Phanerozoic history of the Earth. If the described scenario is correct then it can be concluded that the evolution and extinction of the fusulinaceans during Permian times is closely related to major falls of the eustatic sea level caused by Late Variscan orogenies which led to the final assembly of the Permo-Triassic Pangaea.



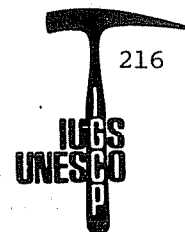
III JORNADAS DE PALEONTOLOGIA
PALEONTOLOGIA Y EVOLUCION: FENOMENOS DE EXTINCION

SHOCK-METAMORPHOSED MINERALS IN CRETACEOUS-TERTIARY BOUNDARY SEDIMENTS PROVIDE MINERALOGIC CONSTRAINT ON BOUNDARY IMPACT SITE.

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ABSTRACT: The Cretaceous-Tertiary boundary interval in western North America consists of two kaolinitic claystone units that form a distinctive couplet. The lower one is a 2 cm thick bed called the "K-T boundary claystone". The upper one is a 5 mm thick layer called the "K-T boundary impact layer". The impact layer contains composite grains (lithic fragments) of quartzite, metaquartzite, chert, and granite-like mixtures of quartz, oligoclase, and microcline in addition to single optical units of quartz, oligoclase, and microcline. About 30 percent of the grains (except chert) contain as many as nine intersecting sets per grain of planar lamellae clearly of shock-metamorphic origin. Moreover, primary volcanic minerals typical of silicic pyroclastic rocks are not present in the impact layer. These two observations make a pyroclastic origin for the shock-metamorphosed minerals highly unlikely. The larger size (0.64 mm) and greater abundance of shocked mineral grains at western North American K-T boundary sites relative to elsewhere in the world provide compelling physical evidence that asteroid (or comet) postulated by Alvarez et al. (Science, v. 208, p. 1095) struck quartz-rich crustal rocks in North America at the end of Cretaceous time.



III JORNADAS DE PALEONTOLOGIA

PALEONTOLOGIA Y EVOLUCION: FENOMENOS DE EXTINCION

CLIMATIC OSCILATIONS AND LATE DEVONIAN EVENTS

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ABSTRACT: Late Devonian, especially Famennian, events and the role of the climatic oscillations in the evolution of carbonate sedimentation as well as in the evolution and extinction of calcareous foraminifera and other faunistic groups are discussed. The diachronic nature of foraminiferal extinctions, the paleogeographical differences and the importance of the employed time and spatial scale are manifested.

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THE DYNAMICS OF MARINE STEPWISE MASS EXTINCTION

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ABSTRACT

Mass extinction is characterized by the loss of 50 - 90+ percent of genetically and ecologically diverse species within 1-3 My intervals. Three conflicting theories exist: (1) Graded Mass Extinction; (2) Stepwise Mass Extinction; and (3) Catastrophic Mass Extinction. These can only be adequately tested with high-resolution (cm-scale) stratigraphic data spanning the entire mass extinction interval and adjacent strata. Such data are presently available only for the Eocene-Oligocene (E-O), Cretaceous-Tertiary (K-T) and Cenomanian-Turonian (C-T) extinctions. In general, prevalent uniformitarian stratigraphic philosophy and use of the modern Earth/Life system as a model for the Phanerozoic has hindered the search for, and expectations of, high-resolution stratigraphic data critical to mass extinction research. The modern Earth/Life "model" predicts highly variable, environmentally and biologically resilient systems and a dominance of localized (autocyclic) over regional to global (allocyclic) stratigraphic response to large-scale, predictable or perturbational forcing mechanisms. Yet, present environmental systems are not typical of 90+ percent of Phanerozoic history, which was characterized by more stable and delicately balanced environmental/ecological systems, with no permanent polar ice, much higher sealevel, warmer and more equable, maritime-dominated climates, little seasonality, and much broader temperature and habitat gradients. Phanerozoic marine species were largely adapted to widespread warm stable environments, and were predominantly stenotopic and stenothermal. Delicately perched, non-resilient Phanerozoic Earth/life systems were

capable of rapid, widespread response to abrupt environmental fluctuations, including mass extinction. A stratigraphic and biological record dominated by near-isochronous to short-term depositional events is predicted by dominant Phanerozoic environments. Testing of the three mass extinction hypotheses with the best high-resolution data available (C-T, K-T, E-O boundary intervals) demonstrates the following phenomena in common: (1) All are stepwise extinctions, graded ecologically from stenotopic (first) to eurytopic groups, and from Tropical to Temperate taxa, over 1-3.5 My intervals. Steps are abrupt (100 Ky or less) to catastrophic; background extinction rates and patterns separate them. (2) All steps of each mass extinction are contained within an interval of extraordinarily large (2-5 times background), rapid fluctuations in atmospheric/oceanic temperature and chemistry, as depicted from geochemical profiles. These exceeded the adaptive ranges and evolutionary response rates of many marine taxa, causing steps of extinction at major fluctuations. (3) Each interval has diverse evidence for one or more comet/asteroid impacts ("storms") on Earth, clustered around the extinction. Most well-defined impact events are directly associated with major marine geochemical excursions and mass extinction steps. A mass extinction theory based on these case histories suggests that initial impacts by comets/asteroids within a storm are in the sea, causing large-scale disruption of temperature, chemistry, stratification, and circulation dynamics within the marine system, and initiating long-term dynamic feedback processes represented by large-scale geochemical fluctuations. Many fluctuations were too large and rapid for survival by narrowly adapted, predominantly stenotopic, stenothermal marine taxa; stepwise extinction resulted. Additional impacts exaggerated the oceanic/climatic perturbations, and reset the extinction clock.

INTRODUCTION

Mass extinction is characterized by the loss of more than half of the ecologically and genetically diverse species on Earth within a very short interval of geological time (50-95% species loss in 1.0-3.5 My in well-documented examples). Rates and ecological patterns of species loss during mass extinctions are distinct from those of background extinction (Jablonski, 1986); taxa with predictably long species life, based on population size, dispersal mechanisms, dispersion and breadth of adaptive range, commonly die out at the same time as those with predictably short species lifespans during mass extinction.

The fact of mass extinction lies in the more than century-old, careful stratigraphic documentation of the fossil record by systematic paleontologists and biostratigraphers who have consistently noted narrow stratigraphic intervals of marked biological change that exceed the predictions of normal environmental/habitat changes. Many of these events lie within uniform facies precluding their interpretation as responses to rapid environmental change. These data have been the bases for statistical documentation of the timing and magnitude of mass extinction events, and their relationship to background extinction, by Raup and Sepkoski (1984, 1986); from these analyses has evolved the hypothesis of a 26.2 My periodicity of mass extinction events. Subsequently, estimates by diverse authors on mass extinction cyclicity have ranged from 26-33 My.

Three existing hypotheses of mass extinction (Kauffman, 1986) are shown in Figure 1; these are much debated. Historically, systematic paleontologists and ecologists have favored an hypothesis of **GRADED MASS EXTINCTION** (Kauffman, 1984, 1986) - an acceleration of background rates of extinction

reflecting acceleration of biological stress brought on by relatively rapid Earthbound environmental changes (i.e. rapid thermal, chemical, climatic, oceanographic and/or sedimentologic fluctuations). Rapid climate changes associated with intervals of intense volcanism, major glaciation or greenhousing; eustatic sealevel fall, large-scale regression of epicontinental seas and associated loss or rapid modification of ecospace etc., are typical mechanisms for extinction cited by those favoring the graded mass extinction hypothesis. The great ecological range of the modern global biota, and the inference that ancient biotas were similarly resilient (a uniformitarian argument which is subject to strong criticism), is further cited as favoring graded mass extinction theory. Ideally, extinction is ecologically graded in this hypothesis from (first) ecological specialists (stenotopic taxa) to (finally) ecological generalists (eurytopic taxa), and from taxa in more exposed habitats to those in more protected habitats.

STEPWISE MASS EXTINCTION (Kauffman, 1984a, b; 1986; Kauffman and Hansen, 1985; Keller, 1986) is a new hypothesis suggesting that mass extinction proceeds through a series of discrete steps, each a near-simultaneous ("catastrophic") to short-term (100 Ky or less) interval of highly accelerated extinction rates, between which extinction rates return to background levels. Cumulatively, these steps may span up to 3.5 My or more. Only a portion of the global biota is affected by each step, and the steps show a general ecological gradient through time. Early steps in a marine system mainly affect Tropical-Subtropical and/or otherwise stenotopic shallow water taxa (e.g. reef ecosystems); intermediate steps affect warm water plankton and shallow water, moderately stenotopic taxa; and later steps mainly affect more Temperate, deeper water, and/or more eurytopic taxa. The data presented in favor of stepwise mass extinction theory are

the extinction patterns documented for the three global biotic crises with the most detailed stratigraphic resolution - the middle Cretaceous Cenomanian-Turonian (C-T), the Cretaceous-Tertiary (K-T), and the Eocene-Oligocene (E-O) mass extinctions (see review in Kauffman, 1986). Mechanisms cited for stepwise mass extinctions include multiple meteorite/comet impacts and/or extraordinarily rapid, large-scale shifts in climatic and oceanic parameters (temperature, chemistry, circulation patterns, etc.).

CATASTROPHIC MASS EXTINCTION theory (Alvarez, et al, 1980) proposes that world-wide extinction of ecologically and genetically diverse taxa occurs simultaneously, within days, months, or tens of years at the most, as a result of some catastrophic perturbation to the global ecosystem. No ecological or evolutionary gradient exists. The most common cited causes today are large and/or multiple extraterrestrial impacts by meteorites and comets (Alvarez et al, 1980, 1984; Hut et al, 1987, in press) and deep-seated explosive volcanism (Officer & Drake, 1985; Officer et al, 1987 and references cited therein). Both hypotheses have the potential for development of dense atmospheric debris/ash/smoke clouds, rapid global cooling (antigreenhousing) and warming (greenhousing) pulses, consumption of the ozone layer and the subsequent potential for increased radiation, and chemical poisoning from fallout (acid rain, etc). The effects of very close supernovae, close-passing stars, solar explosions, or other extra-terrestrial phenomena are more remote possible causes cited in the literature. The large meteorite impact(s) proposed for the K-T (Alvarez et al, 1980, 1984) and late Devonian (Frasnian-Famennian) mass extinction boundaries (McLaren, 1985) are the most cited examples of catastrophic processes.

THE DATA BASE: QUALITY AND CONSTRAINTS

Detailed data suitable for the testing of these three hypotheses are lacking for nearly all mass extinction events cited by Raup and Sepkoski (1984, 1986). Only data for the C-T, K-T, and E-O events are partially adequate for this purpose (Kauffman, 1986). Similar data are being developed for several other mass extinctions (Devonian, Permo-Triassic, mid-Jurassic, Jurassic-Cretaceous, and Miocene extinctions) but are not yet available.

The problem with most published data on biotic and environmental changes through mass extinction intervals is its scale of resolution. If, on the average, fine-grained strata of distal shelf and basinal marine facies (those preserving the most complete and continuous fossil record) represent 1,000 years in 1-2 cm of rock on the average, then sampling resolution to test conflicting mass extinction theories must be at the cm-scale instead of the more normal 10 cm (5-10 Ky) to 1 m (50-100 Ky) scales of sampling for fossil biotas across mass extinction intervals. The reasons are obvious: (1) If catastrophic mass extinctions occur, the evidence for them will be contained within 1-2 cm of fine-grained rock, at the most; but in most cases we don't yet know where, if at all, such events occur in a given rock column; we must test for them cm by cm; (2) the same argument as (1) can be made for stepwise mass extinction, where individual steps, in theory, will be contained within 1 to 100 cm of strata; (3) the proof of graded mass extinction lies in the precise documentation of the last and first occurrences of taxa, again at the cm-scale; (4) our search for causes, whether catastrophic, short-term, or graded over millions of years, also requires cm-scale physical and geochemical analyses of strata spanning a mass extinction interval. Even graded mass extinction may be driven by

short-term events. Thus, all hypotheses for mass extinction require cm scale collecting of data for adequate testing.

A second failing of much existing data pertaining to mass extinctions is the extent of stratigraphic coverage. Most available biological and environmental extinction data are focused around the 1-2 meters on either side of the paleontologically designated main extinction boundaries (usually stage boundaries). This, in effect, is a test for only a single step or catastrophe. However, the Raup-Sepkoski data (1984, 1986) initially defining mass extinction events are only resolved to the stage level (6-8 My on the average) and do not pinpoint thin stratigraphic intervals or horizons, nor stage boundaries. It is further significant that most extinction events carefully documented for the C-T and E-O "boundaries", and certain important K-T extinctions, actually took place below these explicit stage boundaries. Experience with the well-documented extinctions of the C-T, K-T, and E-O boundary intervals (summarized in Kauffman, 1986) all suggest that cm-scale sampling must span 3 My to adequately test various mass extinction hypotheses. Significantly, Hut (in Hut et al, 1987 in press) independently calculated that a single comet shower derived from perturbation of the Oort Comet Cloud (a primary candidate for impact-related mass extinctions) would cause an increase in the rate of Earth impacts over a 3 My time span, and that crater ages clustered around mass extinction intervals (Grieve, 1982; Alvarez & Muller, 1984) also span a few million years.

Thus, new multiple impact hypotheses, as well as new data detailing patterns of extinction within the more broadly defined Raup-Sepkoski mass extinction events, all support the concept that these biotic crises can span up to 3.5 My intervals. This, in turn, dictates the stratigraphic interval to be sampled at the cm-scale in testing mass extinction hypotheses.

STRATIGRAPHIC AND ENVIRONMENTAL CONCEPTS

Fine-scale sampling of paleontological, chemical and physical data for mass extinction intervals has also been seriously hampered by prevalent stratigraphic philosophies derived from Uniformitarianism. Uniformitarian concepts in biology and geology, including the stratigraphic sciences, are still largely based on the modern Earth-Life system model which, when compared to that characterizing the bulk of geological time, is ecologically atypical, environmentally more variable and resilient, generally cooler, and still strongly influenced by the Pleistocene Ice Age and remnant polar glaciation. Process models based on today's environmentally variable, unstable Earth predict a dominance of localized autocyclic forcing and response in shaping the stratigraphic and paleontologic record. They do not predict, nor encourage the search for short-term, event-stratigraphic/biologic phenomena of regional and global extent; such short-term phenomena would predictably be developed in response to widespread Earthbound and extraterrestrial allocyclic processes, to major point perturbations such as meteorite impacts, and/or to rapid large scale shifts in Earth environments, all acting on an environmentally more uniform, stable, and less resilient Earth-Life system.

Approximately 90% of the Phanerozoic was not like today's glacially influenced Earth environment and ecosystem. Instead, it was characterized by a lack of permanent polar ice, by significantly higher eustatic sea level (Haq, et al, 1987) covering up to 85% of the globe, and as a result, by predominantly warm, equable, widespread maritime climates, low seasonality, more sluggish, stratified, oxygen-deficient oceans and by extensive epicontinental seas. Such environmental regimes had much broader thermal gradients and more widely distributed Tropical-Temperate climate zones, more

extensive and continuous watermasses, and as a result, more widespread and temporally stable marine and terrestrial environments or habitats than today. These were predictably less variable than today's environments, and thus more delicately perched on the Earth's surface and more sensitive to even small-scale cyclic changes or perturbations (e.g. Milankovitch climate cycles, giant storm events, extraterrestrial impacts, etc).

In these typically sensitive, broadly equable Phanerozoic environmental systems, and especially in shallow epicontinental and shelf seas and the upper part of the oceanic water column, regional to global allocyclic forcing of sedimentary and biological phenomena should have been more important, even dominant, in shaping the stratigraphic record. Through most of the stratigraphic record we should thus expect that short-term event deposits and abrupt biotic changes will be common, readily observed, and useful in refined regional correlation as chronostratigraphic (isochronous to short-term) units. The emergence of high-resolution event stratigraphy, and detailed studies in event stratification (e.g. Einsele & Seilacher, 1982; Kauffman, 1986, 1987) reflect the realization that short-term deposits and biological events are much more predominant in ancient strata than predicted from the modern Earth system by uniformitarian philosophy.

It is thus no accident that the search for and development of cm-scale, high-resolution stratigraphic data within mass extinction intervals has been contemporaneous with the rapid rise of high-resolution event stratigraphy as a modern tool of regional and global correlation. Mass mortalities, mass extinction steps and catastrophes; explosive volcanism; impact-related deposits and their geochemical signals; and rapid, large-scale geochemical fluctuations in the ocean-climate system commonly associated with mass extinction intervals (Kauffman, 1986) are also common and important compo-

nents of high-resolution chronostratigraphy. Regional to global, punctational and allocyclically forced events were thus very common in the Phanerozoic, and may reflect, in part, causal mechanisms for mass extinction. High-resolution event stratigraphy has now extensively documented unusual chemical, physical and biological events associated with well-studied mass extinction intervals (Kauffman, 1986).

It is equally important to mass extinction theory to consider probable biological response to the maritime-dominated environments that characterized the Phanerozoic (i.e. broadly distributed, predominantly warm climate/ocean zones; low, diffuse thermal gradients from equator to pole; low seasonality; higher eustatic sea level resulting in broad marine connections between oceans and across land masses). Characteristic Phanerozoic global biotas adapted to a world characterized by much more widespread, stable habitats with relatively more predictable, narrower year to year environmental fluctuations than found today over most of the Earth. Stenotopic, stenothermal taxa would therefore have dominated most ecosystems after long time-stable intervals of evolution, and these would have been "extinction-prone" in the face of the extraordinarily large-scale, unpredicted, rapid environmental perturbations that characterized most well-documented mass extinction events, as determined by geochemical and paleoecological analysis (Kauffman, 1984a, b; 1986). Rapid to catastrophic mass extinction events among ecologically diverse taxa would clearly be much more probable in such a Phanerozoic world than they would be today, and could be caused by relatively smaller-scale perturbations than those that would result in widespread mortality among the modern biota. In other words, catastrophic and stepwise extinction theories find logical support in the predictions of predominantly more stable, delicately balanced

environments associated with warmer, more equable climates and higher global sea level.

It comes as no surprise, therefore, to learn through high-resolution stratigraphic analysis of the three best-studied extinction boundaries (C-T, K-T, E-O) of the Phanerozoic, that these intervals are characterized by short-term to near-catastrophic stepwise extinction events. These are, further, ecologically graded in a general way, with the loss of Tropical taxa first, to Temperate, more eurytopic taxa last. In each of these mass extinctions, individual extinction steps can be clearly related to widespread, large-scale, geochemically and physically defined perturbations imposed on broadly equable, warm, maritime-dominated global environments. No examples of graded mass extinction emerged from this research. A summary of each of these mass extinction intervals is given below, with references to detailed data sources. Kauffman (1986) has most recently summarized these events.

CASE HISTORIES FOR STEPWISE MASS EXTINCTION

Cenomanian-Turonian (C-T) Mass Extinction (Fig. 2) - Raup and Sepkoski (1984, 1986) documented the C-T boundary interval, long regarded as one of the biologically best-defined stage boundaries of the Mesozoic, as a moderate-scale mass extinction within their 26.2 My extinction cycle. Koch (1977, 1980) and Kauffman (1984) first collated North American Interior data for this boundary interval and noted that it consisted of a series of short-term extinction events associated with major marine biogeographic changes and environmental perturbations of unusual magnitude and character (e.g., a global oceanic anoxic event: rapid changes in temperature and marine chemistry, etc.) occurring at an unusual time - near peak eustatic highstand, global climate amelioration, and normalization of marine

epicontinental environments. Jefferies (1963) had documented similar biotic patterns in England and France within this interval.

Subsequently Pratt (1985) and Zelt (1985) did highly detailed geochemical analyses across the boundary interval in North America, defining extraordinarily large, rapid (50-150 Ky) stable isotope (O^{18} , C^{13}) perturbations, Corg fluctuations, and Uranium-Thorium fluctuations over a 1.5-2 My interval which also encompassed the C-T mass extinction. Collectively, these data reflect dynamic changes in temperature (2-5° C estimated), and salinity (normalization followed by an unusual 0.2 My freshening event crossing the C-T boundary in North America) in shallow seas, and global changes in the marine carbon cycle associated with an oceanic anoxic event (OAE), the Bonarelli Event.

Predictably, the magnitude of these changes and their rapid shifts, within 50-150 Ky intervals similar in scale to Milankovitch climate cyclicity (possibly an independent catalyst acting on an environmentally stressed global system), should have exceeded the adaptive ranges of many "extinction prone" marine taxa that had become adapted to broadly equable, widespread warm marine environments associated with eustatic highstand. Subsequently, high-resolution stratigraphic sampling and geochemical analysis across the 2-3 My boundary interval by Dr. Carl Orth (Orth et al, 1987, in press) has revealed two moderate size and possibly three minor, thin iridium enrichment intervals just below the C-T boundary at Pueblo, Colorado (Fig. 2); each correlates closely with one of the extinction steps comprising the C-T mass extinction event (Elder, 1986; Elder & Kirkland, 1986; Kauffman, 1986). These suggest one or more extraterrestrial impacts associated with the stage boundary interval, as do two broadly dated impact craters (Grieve, 1982; Alvarez & Muller, 1984) near the boundary. Major

regional volcanic ash layers occur within the C-T extinction and stage boundary interval (Fig. 2) but have no correlation to either extinction steps or iridium enrichment horizons; in fact, these ashes yield lower than background iridium levels (Orth et al, 1987, in press). Volcanism seems to have had no direct relationship to mass extinction or C-T boundary events in North America. Within this well-studied, 1.5-2 My interval of extraordinary perturbations in temperature and marine chemistry, Elder (1986; Elder & Kirkland, 1986; and in Kauffman, 1986) has carefully documented the extinction history of Mollusca in the Western Interior of North America through high-resolution stratigraphic analysis and event correlation of faunas from 10 widely spaced boundary sections (Fig. 2). These have subsequently been integrated with equally detailed physical and geochemical data. Elder's data (1986) show 6-7 major, abrupt mollusc extinction steps spanning the C-T boundary interval in North America, with low background levels between them (Fig. 2). Eicher and Diner (1985) and Leckie (1985) documented, for North America, a major abrupt planktonic foraminifer extinction (Rotalipora extinction) between Elder's steps 1a and 1b (Fig. 2). Nearly all extinction steps lie below or at the C-T stage boundary, within the interval of initiation and peak development of $\delta^{18}O$, C^{13} and Corg fluctuations, and of iridium enrichment.

Integration of all physical, chemical, and biological data across the C-T boundary interval suggests the following series of events: (1) Initiation of major stable isotope disruption at about 94.25 My, just prior to initial iridium enrichment and the first molluscan extinction step in the Western Interior of North America; the cause of this perturbation is unknown. Here or earlier in the Late Cenomanian, data on Tropical rudistid bivalve extinction recently compiled by the author and C.C. Johnson (in

manuscript) for all Caribbean Province species show a major extinction event for Tropical reef communities. (2) First step of North American (mainly subtropical) molluscan extinction, consisting of two discrete levels between which lies the major C-T planktonic foraminifer extinction level (Rotalipora extinction; Eicher & Diner, 1985; Leckie, 1985). The first of two major iridium enrichment layers and subsequent two minor Ir spikes (Orth et al, 1987, in press) are associated precisely with the lower step 1 molluscan extinction, the Rotalipora extinction, and the upper step 1 molluscan extinction of Elder (1986; Elder & Kirkland, 1986), as are major positive and negative excursions of the O^{18} and C^{13} isotope curves (Fig. 2), respectively. This interval also initiates the main part of the Bonarelli global oceanic anoxic event. A relationship between impact or another mechanism for iridium enrichment, major oceanic (stable isotope) temperature/chemistry disruptions, and ecologically selective stepwise extinction is implied. The most diverse Warm Temperate to Subtropical biotas of North America are broadly decimated at this time.

(3) Molluscan extinction step 2 (93.48 My) (Fig. 2) is associated precisely with a slight iridium enrichment level, barely above background levels, initiation of a major negative excursion of O^{18} , depicting the start of a regional desalination event (giant storm or monsoon interval?) in the Western Interior Seaway of North America, and the earliest phases of the global C^{13} positive excursion recording a major change in the marine carbon cycle. (4) Molluscan extinction step 3 (93.45 My), the largest of the sequence, is precisely correlated with the last and strongest iridium spike of Orth et al (1987, in press), and near maximum development of the North American desalination event and the global Bonarelli OAE; (5) extinction step 4 follows a series of minor steps and background

patterns at 93.4 My and lies just below the C-T Stage boundary during peak development of the main global Bonarelli OAE, the North American desalination event, and the positive global C^{13} excursion; (6) Extinction step 5, of moderate proportions, lies at the C-T boundary (93.3 My) and is characterized by final loss of warm water Cenomanian ecological generalists and the last phases of the major C^{13} and O^{18} isotopic excursions marking the end of the main Bonarelli global OAE and the North American desalination Event, respectively. Peak eustatic highstand and the final wave of immigration of Subtropical molluscan taxa into the Western Interior of North America follows this step. (7) extinction step 6 (92.8 My) (Fig. 2) is the last major sharp step, affecting mainly Subtropical and Warm Temperate molluscs, and correlates with the last abrupt positive O^{18} excursion, and final low-level phases of the Bonarelli OAE before return to stable background levels. (8) Extinction step 7 is spread out over 91-91.2 My and marks the last isolated stable isotope excursion of the C-T boundary sequence as well as the final demise of surviving Tropical/Subtropical to Warm Temperate molluscan faunas in the Western Interior Seaway of North America, immediately following eustatic highstand.

Major features of the C-T mass extinction, as defined by high-resolution stratigraphic data in North America and the Caribbean, are as follows: at least eight major, abrupt to subcatastrophic, ecologically graded extinction steps, starting with decimation of Tropical Caribbean reef communities and terminating with extinction of remaining Warm Temperate and Subtropical Mollusca, comprise the mass extinction; low background rates separate these steps. An unusual interval of extraordinarily large, rapid temperature and marine chemistry changes encompasses at least the first seven extinction steps (the main C-T boundary interval) including a global anoxic

event, a positive global C^{13} (carbon cycle) excursion, and a regional desalination event marked by a very negative O^{18} excursion in the North American Interior Seaway. Two major iridium enrichment horizons separated by three minor enrichment levels were discovered by Dr. Carl Orth in one Colorado section (Orth et al, 1987, in press); each of the five Ir levels precisely correlates with an extinction step (1-3 and the main plankton extinction between molluscan steps 1a and 1b, Fig. 2), and exaggeration of the stable isotope disruption curves, suggesting direct cause and effect. Two known impact crater ages roughly correlate with the C-T boundary interval, as do some large, but not unusual, explosive volcanic events in North America (none of which bear significant iridium or are correlative with extinction steps). The mass extinction interval spans 2.5-3 My or possibly more (depending upon the exact age of the Tropical reef extinction event), with the main events spanning 1.5 My around (mainly below) the C-T boundary in North America. The C-T boundary mass extinction is potentially the most completely known and best preserved of all Phanerozoic biotic crises.

Cretaceous-Tertiary (K-T) Mass Extinction (Fig. 3). - The K-T biotic crisis is the most intensively studied mass extinction. Yet the marine record of it is very sparse, especially in regard to macrofaunas, and completely preserved in only a few continuous boundary sections worldwide. This reflects widespread epicontinental erosion associated with terminal Cretaceous eustatic drawdown (Haq, et al, 1987). Reviews of existing data and pertinent references have recently been provided by Kauffman (1984a, 1986), based on the detailed work of many paleontologists. Figure 3 summarizes these events as follows; most data suggest a stepwise mass extinction pattern.

(1) The mass extinction event initiates (Step 1) with global demise of Tropical reef ecosystems and the most diverse Tropical to Warm Temperate

benthic community elements, near the Early-Late Maastrichtian boundary (Fig. 3; 67.5-67.75 My). The exact timing and duration of this step worldwide is difficult to define from scattered carbonate platform sequences. In Jamaica it lies in the basal part of the A. mayaroensis planktonic foraminifer biozone and occurs within a few meters of rock within a continuous carbonate platform sequence. (2) A second abrupt extinction step (2; Fig. 3) occurs in the middle Late Maastrichtian, about 66.5 My, and is marked by loss of the last scattered paucispecific rudistid frameworks, by depletion of diverse mollusc-echinoderm-dominated, Tropical-Subtropical benthic communities, and by final extinction of major lineages of the Inoceramidae - the dominant Temperate Cretaceous bivalves. A major interval of extraordinarily large, stable isotope excursions reflecting rapid marine temperature and chemistry fluctuations begins at this point. (3) Just prior to the K-T boundary ($\pm 100-150$ Ky), some calcareous plankton data (e.g. Thierstein, 1981) suggest a major short-term depletion in populations, especially among specialized Tropical-Subtropical groups, followed by recovery to near-normal levels. Initiation of significant species losses among remaining Tropical-Subtropical shelf molluscs (Hansen et al, 1984; Kauffman & Hansen, in ms.) and North Temperate brachiopods (Surlyk & Johansen, 1984), Bryozoa (Birkelund & Hakansson, 1982) and Mollusca (Alvarez et al, 1984, fig. 4); (also see papers in Birkelund & Bromley, 1979, etc.), and a giant storm/tsunami event in the Caribbean and Gulf of Mexico (Hansen & Kauffman, 1986) generally correspond to this level (Step 3; Fig. 3), the data for which are still being precisely correlated to determine the duration and magnitude of this extinction step (Hansen & Kauffman, in ms.).

(4) The K-T boundary extinction (Step 4; Fig. 3) is the major catastrophe of this sequence, broadly decimating remaining Tropical- Subtropical

groups of corals, larger foraminifera, molluscs and echinoderms, Temperate mollusc, brachiopod and bryozoan species, and the great bulk of calcareous plankton and Radiolaria at or near a peak in their evolutionary diversification. This extinction event affected groups of diverse evolutionary and ecological character simultaneously, and with decimation of a large portion of the oceanic plankton, must have caused a significant disruption or temporary collapse of the marine food chain. Of equal importance, this event also marks extinction of the last remaining ecological generalists among once-dominant Cretaceous groups such as marine and flying reptiles, ammonites, belemnites, rudistids and inoceramid bivalves (papers in Birkelund & Bromley, 1979; Christensen & Birkelund, 1979; review and references in Kauffman, 1984a, 1986; Alvarez et al, 1984). This event coincides with diverse evidence for a major bolide impact on Earth (papers in Silver & Schultz, 1982), including large-scale iridium enrichment (Alvarez et al, 1980), shock-metamorphic mineral grains (Bohor et al, 1984), a global smectitic boundary clay, and microtektite-sized and shaped, mineralized spheres (Montanari et al, 1983). This event is further marked by the most profound δ^{18} and C^{13} isotopic (temperature, carbon cycle) excursions of the K-T extinction interval (e.g. Boersma, 1984; Perch-Nielsen, et al, 1982), depicting rapid cooling (antigreenhousing) followed by rapid warming (greenhousing?) (Perch-Nielsen et al, 1982, Fig. 8). (5) A series of very abrupt extinction steps among North Temperate bryozoans and brachiopods are suggested by published Danish data (Birkelund & Hakansson, 1982; Surlyk & Johansen, 1984) during the 200-250 Ky following the K-T boundary (steps 5-13, Fig. 3) within uniform carbonate shelf facies containing abundant bryozoan mounds. But it is not yet known to what degree these "events" reflect sampling intervals or real extinction.

In the Gulf Coast region of North America (Hansen and Kauffman, in prep.) this same interval includes the final abrupt extinction of Cretaceous-style nannoplankton and eurytopic molluscan generalists, and possibly 1-2 Lower Paleocene iridium spikes suggesting additional impacts (Ganapathy et al, 1981; Hansen et al, 1984). Details and regional correlation of these events between Denmark and the Gulf Coast are still under investigation so that no definitive global sequencing is now possible. This series of extinctions is totally contained within the last half of a global interval of stable isotope disruption (e.g. Perch-Nielsen et al, 1982; Fig. 8).

In summary (Fig. 3), the K-T boundary interval is characterized by 4-13 discrete steps of highly accelerated to catastrophic extinction, ecologically graded from Tropical reef ecosystems (first), through Warm Temperate-Subtropical plankton and benthic macrofaunas (near K-T boundary), and terminates with decimation of outer shelf Temperate macrofaunas. All but the earliest steps lie within a zone of extraordinary climatic and oceanic perturbations as indicated by rapid, large-scale stable isotope fluctuations and a giant storm or tsunami bed in the Caribbean Province. One or more levels of iridium enrichment, etc, depict extraterrestrial impacting during this mass extinction interval of 2.75 - 3 My.

Eocene-Oligocene (E-O) Mass Extinction (Fig. 4). - Though less detailed data are available for this boundary than for the C-T and K-T events, very similar relationships exist. Thor Hansen (1987, in press) has studied molluscan extinction patterns of the Gulf Coast of North America (summary in Kauffman, 1986, Fig. 18) and Keller (1986) provided a very detailed data for the global record of planktonic foraminifer extinction and microtektite stratigraphy. A stepwise pattern of mass extinction predominates, and is

summarized on Figure 4, and in Hut et al (1987, in press) over a 3.5 My or less interval (Keller, 1986). The species-level extinction consists of four major steps; Keller (1986) has shown additional levels of severe population depletion during the Late Eocene.

(1) Step 1 (41-42 My) occurs at the top of the Middle Eocene G. lehneri foraminifer zone; it abruptly eliminates 4 of 13 planktonic foraminifer species and causes severe population decline in others. No molluscan extinction, microtektites or stable isotope disruptions are recorded for this level; (2) Step 2 (39 My) is a major extinction and/or population crisis of planktonic foraminifera (Keller, 1986), eliminating 6 of 15 species, and of molluscs; Hansen reports 89% loss of existing gastropod species and 84% loss of bivalve species among 385 molluscan taxa; this is coincident with the foraminifer extinction and initiation of a major positive excursion in the O^{18} isotope record at the Middle-Late Eocene boundary. (3) Step 3 (37.75 My) is the most dramatic event of the sequence (Fig. 4), and is marked by loss of 6 of 13 planktonic foraminifer species, great population depletion of others (Keller, 1986), and loss of 72% and 63% of existing gastropod and bivalve species ($N = 273$) respectively. This is associated with the lowest widespread microtektite layer and a strong negative O^{18} isotope excursion. Two microtektite layers succeed this level but are not associated with major extinctions; they do mark major foraminifer population changes (Keller, 1986). (4) The final extinction step (4) occurs just below and/or at the E-O boundary associated with the largest negative O^{18} excursion at the interval; 3 of 15 planktonic foraminifer species and 89% (bivalve) to 97% (gastropod) of the 86 extant Upper Eocene molluscan species become extinct near this level over a ± 100 Ky interval.

In summary, E-O mass extinction is comprised of four major steps, three of which are abrupt; one of these is directly associated with a microtektite layer reflecting impact. Major population decrease in surviving warm water foraminifer species is associated with each extinction step and with some intervening intervals. At least the last three extinction steps are contained within an interval of large-scale, rapid, stable isotope fluctuations; at least three levels of microtektites and 2-3 impact crater ages (Grieve, 1982; Alvarez & Muller, 1984) are contained within the interval. In a general way, both Foraminifera and Mollusca show ecological grading in successive extinction steps, from a greater effect on stenotopic warm water taxa early, to elimination of more Temperate or eurytopic taxa later in the extinction.

CONCLUSIONS

The three best documented mass extinction events (C-T, K-T, E-O) of the Phanerozoic share several things in common. They are all stepwise in nature over 3-4 My intervals. Each step is characterized by highly accelerated to catastrophic loss of discrete, ecologically compatible species sets. Background rates of extinction separate these steps and are of comparatively low level. In general, the steps are ecologically graded, initially affecting ecological specialists (stenotypes), especially among Tropical reef and platform communities, and ultimately affecting more eurytopic and more Temperate taxa through successive steps to the end of the mass extinction episode. An interval of exceptionally large-scale, rapid geochemical fluctuations envelopes most or all of each mass extinction interval; fluctuations significantly exceed background levels between mass extinctions and larger fluctuations in $\delta^{18}\text{O}$, $\delta^{13}\text{C}$, Corg etc, are commonly associated with

individual extinction steps. These fluctuations depict severe atmospheric, climatic, and/or oceanographic perturbations that probably exceeded the adaptive range and evolutionary rates of many taxa within very short time intervals. In the C-T boundary interval many stable isotope fluctuations are correlative with ± 40 -100 Ky Milankovitch climate cycles, which may have acted as an independent catalyst in driving or enhancing extraordinary fluctuations within perturbed ocean systems. Evidence for one or (commonly) more meteorite/comet impacts are associated with and selectively clustered around mass extinction intervals. These shared characteristics suggest the following hypothesis (Fig. 5) for mass extinction to be tested with additional high-resolution stratigraphic data at these and other extinction intervals.

During roughly periodic (26-33 My) Phanerozoic intervals of warm, equable, maritime-dominated climates and higher sea level, climate and ocean systems were more delicately balanced than today, and easily driven to widespread (regional to global) sedimentologic, oceanographic and biologic response by abrupt, large-scale, predictable events/cycles and/or by major perturbations. Marine biotas that evolved within this environmental setting had narrow adaptive ranges, especially for temperature fluctuations (stenotopic, stenothermal taxa) and were thus extinction-prone. Whether by random or periodic disturbance of the Oort Comet Cloud surrounding the solar system (Hut et al, 1987, in press), the Earth was episodically bombarded by comet and associated meteorite showers. Initial and most other impacts into the ocean were predictable during high sea level stand. Such objects would have sharply disrupted the atmosphere for a short time during entry, and would have rapidly disrupted oceanic stratification, thermal and chemical balance upon impact. Initial extraterrestrial disruptions of the ocean would, in

turn, have initiated a series of rapid temperature and chemical fluctuations that would have predictably exceeded the adaptive range of at least the most stenotopic taxa (Tropical shallow water species). Whereas rapid "healing" of the atmosphere within a few hundred years is predictable, modern ocean models suggest that such large-scale oceanic perturbations would lead to a longer-term series of dynamic fluctuations in temperature, water mass distribution and movement, density stratification and chemical cycling - intrinsic feedback processes seeking a new oceanic equilibrium. These could be enhanced or even independently driven, in part, by predictable cyclic Earthbound phenomena (e.g. Milankovitch climate cycles) or additional perturbations (e.g. subsequent impacts). Each additional large oceanic impact would reset the cycle of long-term oceanic feedback processes. Whether due to individual impacts or the long-term oceanic fluctuations following impact perturbations, each rapid change in ocean temperature and/or chemical cycling exceeded the adaptive ranges and evolutionary response rates of diverse taxa, driving a certain portion of the global biota to rapid extinction, and producing a stepwise pattern. Initial large rapid fluctuations in marine temperature and chemistry, working on an extinction-prone global biota characterized by narrow adaptive ranges, would naturally eliminate the most sensitive stenothermal/stenotopic taxa within the first set of perturbations. Subsequent extinction of more eurytopic Temperate taxa and surviving ecological generalists of once-dominant forms in later extinction steps might reflect the long-term effect of repeated environmental perturbations that eventually would deplete the species, by successive population crises, to numbers too low to guarantee survival under even normal environmental conditions. Within the stepwise extinction process (Fig. 5), large-scale impacts, and/or those producing suspended, long-term

debris clouds in the atmosphere through terrestrial impact, would logically account for catastrophic extinction steps of exceptional magnitude, as at the K-T boundary. This hypothesis best accommodates existing data on well-studied mass extinction intervals, but a great deal more data are needed, for different extinction events, to provide discriminating tests.

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FIGURES CAPTIONS

Kauffman

Figure 1.- Models of extinction patterns of taxa (vertical lines) within the framework of the three major theories for mass extinction. EX represents the level of either maximum taxonomic loss or of the extinction level of certain characteristic taxa (e.g. biostratigraphic indices). EX-1, EX-2, etc. define levels of stepwise extinction as components of a single mass extinction event (Kauffman, in manuscript).

Figure 2.- Composite plot of molluscan species ranges in the Western Interior United States having last occurrences in the Cenomanian-Turonian boundary interval. Data are plotted against the Western Interior standard reference section (left) at Rock Canyon Anticline near Pueblo, Colorado, and ^{13}C organic and ^{18}O carbonate versus PDB values from the same section (after Pratt 1985). Species ranges are a graphic composite of data from 10 widely scattered stratigraphic sections analyzed by Elder (in progress), and from published range data of Koch (1975, 1980), Cobban and Scott (1972) and Cobban (1985). Bios stratigraphic zones and subzones, in ascending order are: Vascoceras diartianum (V.d.) and Eumphaloceras septemseriatum (E.s.) subzones of the Sciponoceras gracile Biozone (SCIP); the Vascoceras gamai (V.g.), Neocardioceras juddi (N.j.), and Nigericeras scotti (N.s.) subzones of the Neocardioceras juddi Biozone (NEOCARD.); the Pseudaspidoceras flexuosum (p.f.) and Vascoceras birchbyi (V.b.) subzones of the Watinoceras Biozone; the Mammites nodosoides Biozone; and the Collignoniceras woollgari (C.w.) Biozone. Numbered horizontal lines of intervals mark the stepwise extinctions noted in the text. Approximately 14 additional, mostly infaunal taxa (not plotted) are known to range through the entire interval; and numerous other species are either too rare or their taxonomy is too poorly known to accurately determine their ranges. Rx= Rotalipora extinction event among planktonic foraminifera.

Figure 3.- Summary of stepwise extinction events (steps 1-12) transecting the Cretaceous-Tertiary mass extinction interval, with mainly Tropical-Subtropical generic data summarized below the K-T boundary (from many sources) and North Temperate (mainly Danish) species data summarized above the K-T boundary for well studied Bryozoa and Brachiopoda. This pattern reflects ecological grading and change in taxonomic magnitude of extinction events through time from more sensitive (stenotopic) Tropical toward more adaptive (eurytopic) Temperate biotas. Width of graphs below K-T boundary generally scaled to generic diversity in specific data sets; species ranges shown in black lines, terminating in arrows where range boundaries were not precisely defined. Note scale change at K-T boundary; the temporal scale vs. metric thickness of Paleocene strata is based on average rock accumulation rate of 5 cm per thousand years for the Danish chalk.

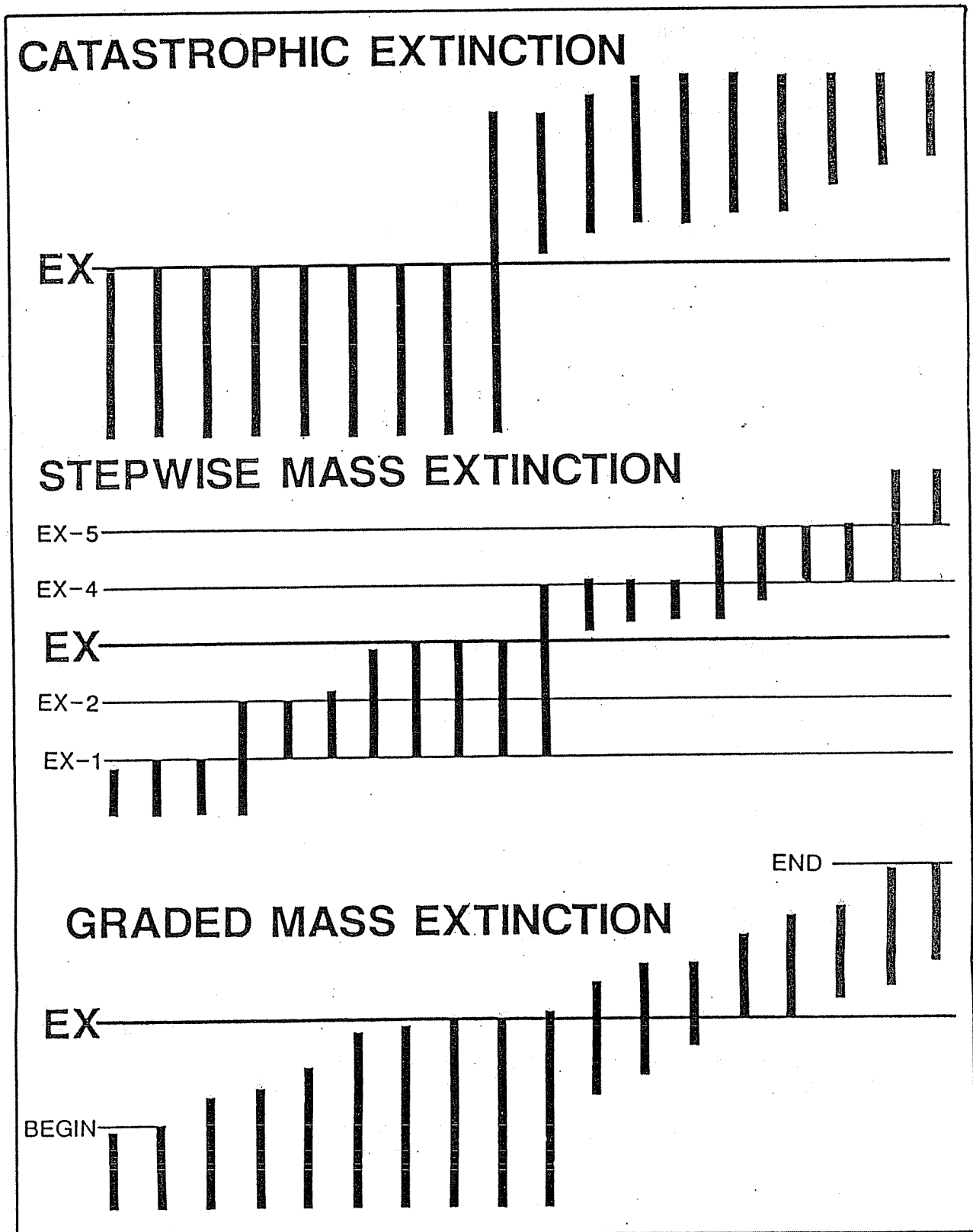


Figure 1.

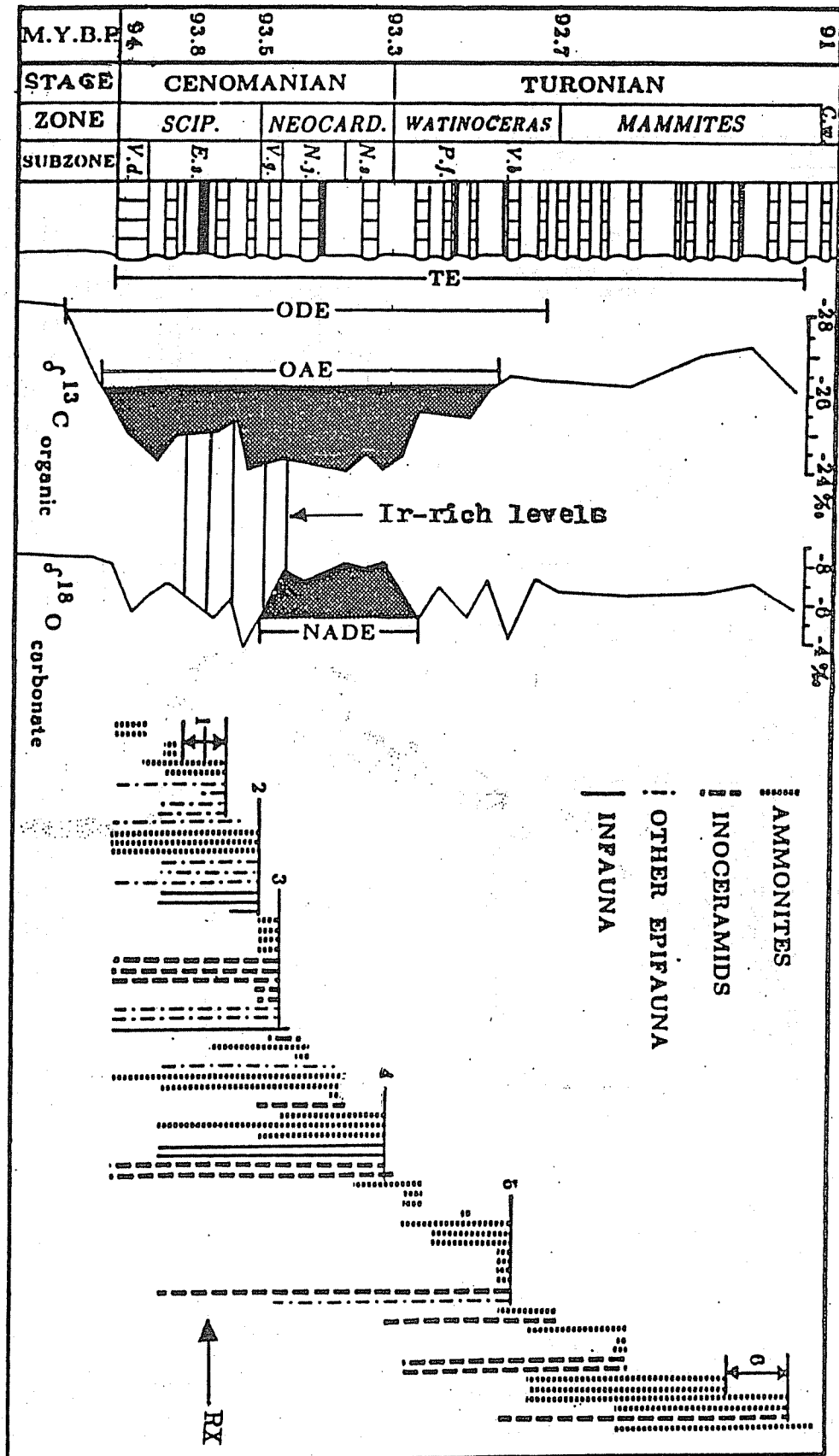


Figure 2.

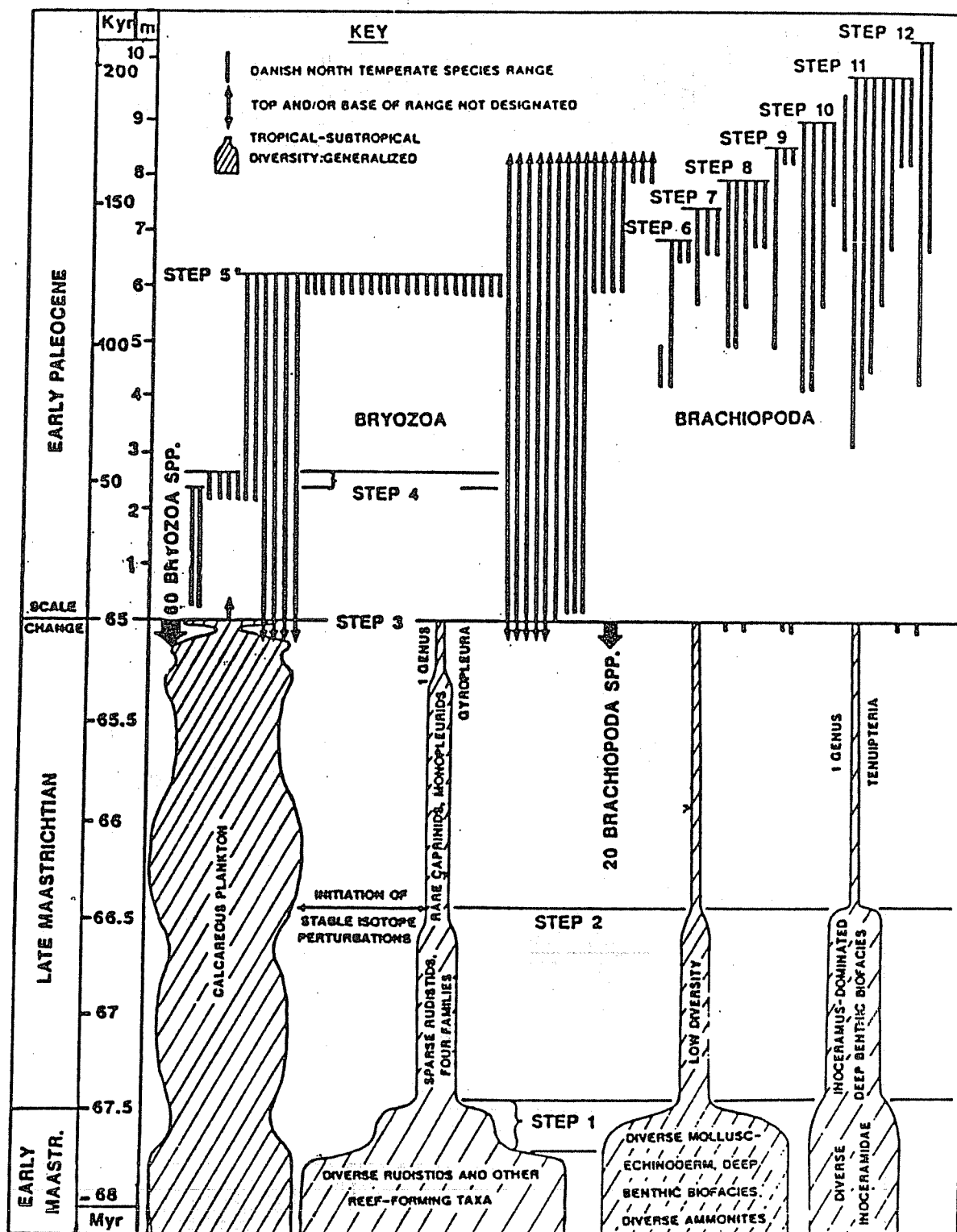


Figure 3.

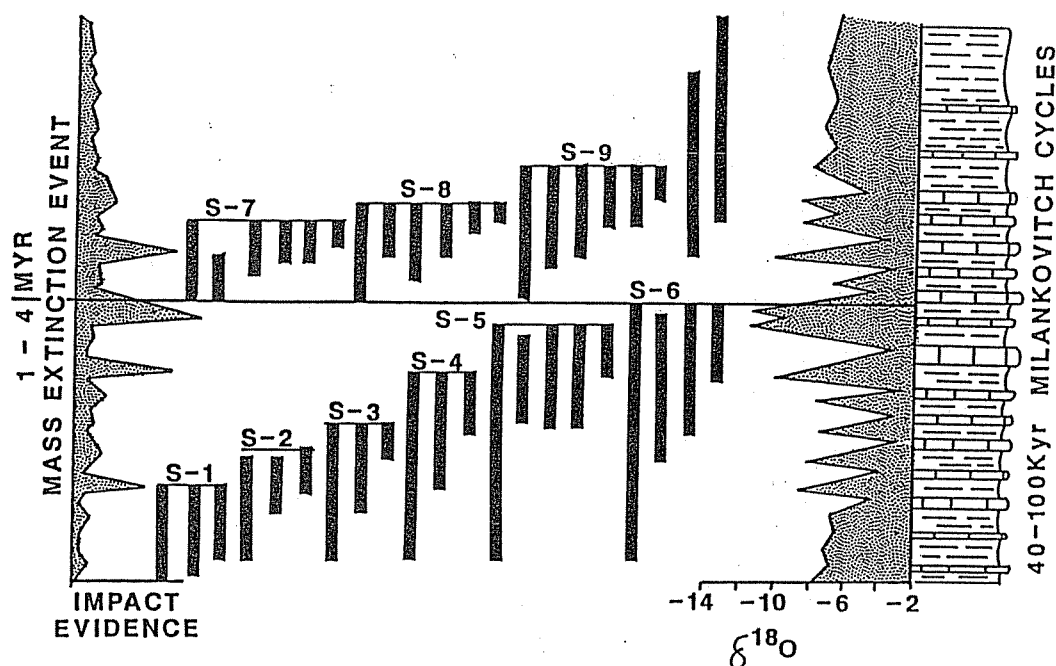
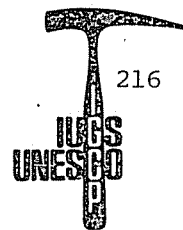


Figure 5. Summary model of environmental and biological dynamics proposed for the stepwise mass extinction theory. The 1-4 Ma mass extinction is contained within an interval of extraordinary stable isotope disruptions, many in concert with normal Milankovitch cycles (independent catalyst), and steps of extinction. Extraterrestrial impacts may initiate, and enhance the level of destabilization of the marine realm.



III JORNADAS DE PALEONTOLOGIA

PALEONTOLOGIA Y EVOLUCION: FENOMENOS DE EXTINCION

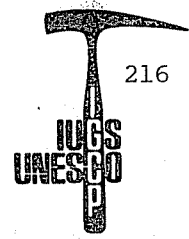
THE CRETACEOUS-TERTIARY BOUNDARY IN NORTHERN MEXICO

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ABSTRACT: Rapidly subsiding tectonic basins during the Cretaceous-Tertiary (K/T) boundary interval in northeastern Mexico contain thick siliciclastic-dominated boundary sequences without major disconformities. These contain westward-thinning, algal-dominated carbonate platform deposits of both Maastrichtian and Danian age. The K-T boundary sequence thins dramatically northward to the Texas-Mexico border. In siliciclastic sequences of the Parras Basin initial data indicate stepwise K-T extinctions among diverse molluscan biotas and the rise of Paleocene-style molluscs prior to the disappearance of Cretaceous vertebrates and ammonites. Extinction and origination events, from oldest to youngest, are: (1) Abrupt extinction of Exogyra; (2) short-term extinction of many elements of the Haustator bilira fauna, leaving a depauperate molluscan fauna dominated by trophic generalists; (3) abrupt extinction of most surviving Cretaceous molluscs associated with a regionally persistent chaotic sedimentary breccia/conglomerate (giant storm or tsunami bed?); (4) a "dead zone" with few fossils, several meters thick, contains ammonites, small surviving Cretaceous detritus-feeding bivalves, and the first small progenitor Paleocene-type molluscs; (5) expansion of the small Paleocene-style fauna with gradual disappearance of surviving Cretaceous generalists through several meters of proximal offshore/lower shoreface siliciclastics; (6) a middle shoreface sandstone contains large Paleogene-style bivalves resembling Cucullaea and Venericardia associated with entire ammonites and petrosaur bone, capped by a persistent bentonite bed, marking final extinction of Cretaceous taxa; (7) a persistent oyster bed containing a small inflated costate n. sp. overlies the ash and grades upsection into brackish water oyster beds and variegated fluvial deposits (peak regression) containing a major volcanic ash bed; (8) the new inflated oyster reappears in transgressive sandstones with a diverse Paleocene-style mollusc fauna; (9) a disconformity cuts this new transgressive marine unit and is overlain by algal carbonates containing typical Venericardia - Turritella - dominated middle Lower Paleocene molluscan faunas, marking a major extinction step. Eastward, in the La Popa Basin, similar siliciclastic sequences are inter-bedded with large carbonate ramps of Maastrichtian algal limestone; rudistid bivalves occur sparsely in the lower limestones, but disappear before the Exogyra extinction level; above this, steps of extinction and origination are similar to those in the Parras Basin, and the giant storm? bed lies within the upper La Popa limestone unit. Evolutionary hypotheses favoring derivation of new biotas from Tropical sources during mass extinction intervals, and stepwise extinction hypotheses, are supported by these observations.



BIOLOGICAL SELECTIVITY OF EXTINCTION

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Abstract. - Selective survival across major extinction event horizons is both a bothersome puzzle and an opportunity to delimit the biologically interesting question of causality. Heritable differences in characters may have predictable consequences in terms of differential species survival. Differences in magnitude and intensity of extinction are insufficient to distinguish background from mass extinction regimes. Biological adaptations may establish links of causality between abnormal times of mass extinction and normal times of background extinction. A current hypothesis, developed from a comparison of extinction patterns among Late Cretaceous molluscs, is that biological adaptations of organisms, effective during normal times of earth history, are ineffectual during times of crisis. A counter example is provided by data from high-latitude laminated marine sediments that preserve evidence of an actively exploited life-history strategy among Late Cretaceous phytoplankton. These data illustrate a causal dependency between a biological character selected for during times of background extinction and macroevolutionary survivorship during an unusual time of crisis.

PROGRESS AND THE SELECTIVITY OF EXTINCTION

What is the relationship between progress and the selectivity of mass extinction? The question can be rephrased, are the survivors of a mass extinction 'better' than the victims of the same mass extinction? It is trivially true that surviving a mass extinction event prolongs the expected time to extinction. In a review of fitness measures, Cooper (1984) showed that expected time to extinction is the fundamental measure of fitness, all other measures being derived from it. In this sense, survivors are more 'fit' (i.e. durable) than non-survivors. The issue, however, revolves around the question of whether or not directional trends in the history of life are powered by the selectivity associated with mass extinction bottlenecks. Heritable characters that enhanced survivability to one biotic crisis would predictably enhance the probability of survival to a recurrent perturbation.

The Darwinian theory rejects any innate tendency toward progress. Mass extinction has been portrayed as an extrinsic sorting process that nullifies extrinsically generated progressive trends (e.g. Gould 1985). It may (Gould and Calloway 1980). Or it may not. McKinney (1986) has recently argued that the directional trend of increased diversity among erect unilaminate bryozoan species represents not only an example of 'progressive evolution' but an example of a directional trend unaffected (or even enhanced) by mass extinctions.

The general question, ultimately, must escape an empirical resolution. The phenomenon does not fit into the mutually exclusive categories required of strong inference hypothesis testing. Examples of enhancement, ineffectiveness and neutrality are all expected by the theory. Evolutionary trends are not simple functions of time, but

interactive functions of time, character, and environment. As discussed below, extinction-resistance does not accumulate merely with age.

THE PROBLEM OF DISTINGUISHING BACKGROUND FROM MASS EXTINCTION

In what way(s) are mass extinctions, interpreted both as crises in the history of life and a potential motive force in evolution, distinguishable from background extinctions, interpreted as the inevitably normal fate of all species? The traditional means of differentiating these two extinction regimes has relied on relative differences in magnitude, but magnitude may be assessed using a variety of measures. In the mid-nineteenth century, Phillips (1860) showed that diversity declined abruptly at the close of both the Paleozoic and Mesozoic eras, framing the Mesozoic "within deadly brackets of time" (McPhee 1980). Raup and Sepkoski (1982) similarly identified principal mass extinction events over Phanerozoic time by relatively large and abrupt declines in standing (familial) diversity.

Diversity decline, as a metric of mass extinction, however, is ambiguous. The temporal trajectory of diversity must decline whenever extinction rate exceeds origination rate. The implication of equating mass extinction with diversity decline is that extinction rate rises during these intervals, but this is not the necessary case. A decline may occur with no change in extinction rate whenever there is a sufficiently large drop in origination rate. The number of originations generally has exceeded the number of extinctions on a per stage basis, as shown in Figure 1 which displays the relative rise and fall of originations and extinctions for the marine familial data of Raup and Sepkoski (1984).

Exceptions include the Late Permian and Late Cretaceous, confirming Philips' interpretation: here there are sharp rises in the number of extinctions, made more problematic, however, for the Late Cretaceous where the number of originations falls as abruptly. As a consequence of this ambiguity, most recent analyses of mass extinction have focused directly on the behavior of rate (or probability) of extinction.

The metric of extinction rate is also potentially equivocal as a means of differentiating times of background from times of mass extinction. Raup and Sepkoski (1982), Van Valen (1984) and Kitchell and Pena (1984) showed, using different analytical methods, that the Phanerozoic record of marine familial extinctions is characterized by an overall decline(s) in rate. The observed pattern of Phanerozoic marine familial extinctions expressed as probabilities of extinction per myr, normalized for standing diversity, is plotted in Figure 2. The observed (in dashed line) is compared to that predicted (in solid line) by a covariance analysis, such an analysis being appropriate to highly autocorrelated data (see Kitchell and Pena 1984). As is apparent, the absolute magnitude of some mass extinction events, such as the well-recognized Late Cretaceous crisis, is lower than the magnitude of some earlier background rates. The Late Cretaceous peak, however, is significantly above the predicted curve.

More recently, Raup and Sepkoski (1984) replaced absolute magnitude as a measure of extinction intensity with the criterion of reversal from an increase in extinction intensity to a decrease (see also Kitchell and Estabrook 1986). Such reversals, based on relative magnitude, define 'peaks' of extinction intensity. Some of the peaks have absolutely high levels of extinction intensity as well, but this is not a necessary criterion, as is evident in Figure 3. Peaks of local maxima vary in

number depending on whether reversal is the only criterion of recognition, or whether peaks are evaluated relative to either mean extinction rate over time or an a priori criterion of absolute magnitude.

Another approach has been to ask whether or not the distribution of magnitudes of extinction rate supports a separation of rates into two distinct regimes. Stigler (1987) found the distribution to support a continuum of extinction rates; mass extinctions represent the tail of a relatively smooth distribution. He reported that "we are not dealing with a single list of large catastrophes set off against a mundane background but with a gradual spectrum of extinction rates, from the mild to the more severe". Raup (1986) similarly concluded that there is a continuous range of variation. The dual classification of mass versus background extinction is not supported to date by the evidence of magnitude and intensity.

A PROPOSAL FOR DISTINGUISHING BACKGROUND FROM MASS EXTINCTION

The obvious problem with both absolute and relative magnitude as criteria that distinguish background from mass extinction regimes is that these criteria beg the question. Background extinction is expected to vary in intensity with time, and it would be a mistake to label the high end of aggregated but independent extinctions a mass extinction. Biotic crises in the history of life that attain mass extinction status must be (i) absolutely and (ii) relatively large in extent and intensity and (iii) the consequence of the same (or cascading) causal mechanism(s). The equivocal nature of magnitude may be better resolved by an additional criterion, that of selective extinction. Differential survival to closely

related causal factors, in conjunction with magnitude, better distinguishes mass extinction events from background extinction than any single measure of magnitude (Kitchell et al. 1986). A biotic crisis labeled a mass extinction should be supported by evidence of differential survival to a series of closely related causes whereas there is no such restriction on background extinction.

The phenomenon of selective survival necessarily involves the biological characters of organisms, expanding the study of mass extinction beyond measures of magnitude to the more informative measure of differential effect. Although most analyses of extinction report only a measure of the intensity of extinction, an account of the score between 'victim' and surviving taxa, the more relevant query is, What decided the score? The research focus is shifted from analyses of individuals toward analyses of classes, namely surviving and non-surviving taxa, the biological properties held in common within each, and the interactive effects of these in the context of a 'survival filter'.

A current opinion, however, is that "mass extinction is probably blind to the exquisite adaptations evolved for previous environments of normal times" (Gould 1984). This opinion reflects the hypothesis that evolutionary processes operate at levels ('tiers') arranged in a nested hierarchy (Gould 1985). Higher levels constrain the behavior of lower levels in nested hierarchies. Mass extinctions are described as occupying the highest tier status, thereby constraining macroevolutionary trends (at the second tier), both of which in turn constrain processes acting "at the ecological moment" of the first tier. Using this view of scale-dependent constraints, Gould (1984) has argued for "an irreducible randomness" to life's history. The examples that follow show - contrary to the prediction that mass extinctions are indifferent to biological adaptations

- that a biological trait may instead determine a pattern of differential survival. These biological traits operate in the framework of the ecological moment. Such examples show that biological characters (of the first tier) may play a role in second- and third-tier level processes. As a consequence, these biological adaptations establish links of causality between normal times of background extinction and times of mass extinction.

LINKS BETWEEN NORMAL (BACKGROUND) TIMES AND TIMES OF MASS EXTINCTION

Age Dependency: An Example

Extinction intensity varies over Phanerozoic time. Any hypothesis that extinction is random with respect to absolute time is rejected by the non-uniform pattern of extinction intensity as a function of geologic time. This pattern is a robust feature of the history of life. A means of examining this phenomenon is to follow the extinction-decay trajectories of species that originate simultaneously (true cohorts) or species that are simultaneously extant (pseudocohorts). Some periods of time are characterized by horizontal decay slopes, indicating no extinction within these cohorts whereas other periods of time are characterized by steep decay slopes, indicating increased extinction (e.g. for species, Figure 9, Hoffman and Kitchell 1984; for families, Figure 3, Raup 1986).

The pattern becomes increasingly more continuous when species within a taxonomic group and paleoenvironment are examined. Figure 4 illustrates the extinction-decay trajectories of species pseudocohorts for planktonic

foraminifera of the tropical Atlantic and Pacific. The arrow marks the time (11.3 myr BP) of a significant peak of extinction at the level of genus, recognized by Raup and Sepkoski (1986) from a compilation of 9250 extinct genera, and interpreted as a global disturbance. As is evident from the lack of a significant and simultaneous break in slope across cohorts at this time, these species are relatively insensitive to the perturbation.

Another way of analyzing the continuous versus pulsed hypotheses of background and mass extinction is to examine the pattern of first and last appearances, arranged in order of the time of each species' last record. All (extinct) species from the same data set used to construct Figure 4, as cohort trajectories, are shown in Figure 5 as individual cases. The overall right-hand margin is not linear, its upward slope indicating an increased probability of extinction as one approaches the Recent.

A character inherent in both survivorship and ordered data is age or duration time. Is extinction independent of the age of a taxon and, more specifically, are times of background and mass extinction similar or different with regard to this character? An interesting pattern of age-dependency emerged from a recent analysis of marine familial extinctions by Boyajian (1986). The supporting data are the differences in frequency distributions of duration times for taxa going extinct during mass extinctions (Figure 6C) compared to taxa going extinct during background extinctions (Figure 6D). During times of mass extinction, survival was more random with respect to age distributions than during background times. During background stages of time, the frequency distribution shifted toward young-aged families (Figure 6D). Such a selectivity difference was considered by Boyajian to be consistent with distinguishing between background and mass extinction regimes on the basis

of age-selectivity rather than magnitude alone.

It is informative to compare these family-level data with species-level data, on the frequency distributions of duration time. Figure 6A shows the distributions of duration times for extinct species of low- to mid-latitude Pacific planktonic foraminifera during the past 40 myr of background extinction time. The frequency distributions of duration times for extinct (stippled) and extant (open) species of tropical Atlantic and Pacific planktonic foraminifera over the same past 40 myr are shown in Figure 6B. Both distributions are similar in that frequency decreases with increasing duration. These distributions for species during background times, however, more closely resemble the familial distributions for mass extinctions.

Survival analyses of species-level extinction patterns are remarkable in the degree to which they are age-independent (e.g. Hoffman and Kitchell 1984; Kitchell and Hoffman, in press). Such independence is interpreted to represent the consequences of many, unpredictable stresses (associated with background extinction) such that age does not provide a margin of safety in the way that experience is a safeguard. One must not be misled, however, in drawing similar inferences at the family-level. The difference, of age-dependency within familial data and age-independency within species data, is consistent with the two consequences of 'age'. At the species level, increased age indicates increased persistence time. The fit of the species-level data to a Poisson process indicates a lack of memory in the system: experience does not accumulate. The element of surprise sometimes associated with the lack of a decrease in extinction probability among older species is tied to the expectation that longer persistence time means, on average, greater success in meeting an increasing number of challenges from a changing environment. The

biological traits of older species are more 'tested' and thereby more extinction-resistant, according to this reasoning. Extinction-resistance associated with increasing age of a family, however, is quite a different expectation. Here the intermediaries are species-richness and breadth of ecology and geographic range of constituent species; 'age' is a proxy measure. As a consequence, the finding of age-dependency lacks the element of surprise associated with age-independency of species. Such age-dependency of families is an intuitive prediction.

Geographic Range: An Example

Species age or duration time is not a character that belongs to an individual within the species; it is an aggregate character of the species (as individual). The same holds for geographic range of a species. Assuming *ceteris paribus*, a straight-forward prediction is that the probability of extinction will decrease with increasing geographic range. Not all environments are affected equally by the same catastrophe.

Such a positive relationship between evolutionary longevity and geographic range has been supported by studies of Early Tertiary volutid gastropods (e.g. Hansen 1978, 1980). Jablonski (1986) extended the question by asking whether geographic range was effective in aiding survivorship both preceding and during a mass extinction regime. Examining the distribution frequency of species longevities, he found that for both geographically widespread and geographically restricted molluscan species frequency decreases with increasing longevity. The modal values, however, are significantly different with widespread species having longer longevities, as predicted, during background time. During the Late Cretaceous mass extinction, endemic genera of both gastropods and bivalves

had a significantly higher extinction rate than widespread genera, again as expected. At the genus level, however, survival across the Late Cretaceous mass extinction horizon did not depend on the geographic range of constituent species.

Life History Strategy: An Example

What of heritable characters of organisms: to what extent may a biological, heritable trait of individual organisms causally influence a macroevolutionary pattern of selective survival? A current hypothesis, developed from a comparison of extinction patterns among Late Cretaceous molluscs, separated into two classes on the basis of larval development, is that the adaptation of larval development, effective during normal times preceding the Late Cretaceous mass extinction, is ineffectual during the time of crisis (Jablonski 1986). A counter example (Kitchell et al. 1986) of causal dependency between a biological character selected for during times of background extinction and macroevolutionary survivorship during an unusual time of crisis is provided by data of an actively exploited life-history strategy among Late Cretaceous phytoplankton.

One of the best known selective features of the close Cretaceous mass extinction is the high intensity of extinction of marine plankton groups. Among Late Cretaceous marine organisms, plankton experienced severe levels of extinction. But, among plankton groups, there was differential extinction. For coccolithophorids, radiolaria, and foraminifera, the generic extinction intensities exceed 70, 80, and 90%, respectively (Thierstein 1982). In sharp contrast, the current best estimate for diatoms is between 20-25% (Gombos, unpubl. ms, Harwood 1986). As Tappan (1982) noted, "of the phytoplankton, coccolithophore, diatom and

dinoflagellate pigment complexes are similar (all have chlorophyll a and c, and accessory photosynthetic pigments such as fucoxanthin), yet coccolithophores were nearly completely eliminated, dinoflagellates much less affected, and diatoms merely continued their rapid diversification across the boundary.~ This peculiarity is made even more puzzling in that suppression of photosynthesis, as a consequence of large dust loadings, is suggested by several lines of evidence (Alvarez et al. 1980, 1984, Smith and Kyte 1984, Wolbach et al. 1985) as the proximate cause of the Late Cretaceous crisis. Yet the plankton group least susceptible to extinction (the centric diatoms) are obligate photoautotrophs and thereby most susceptible to the putative mechanism. One line of evidence seems to contradict the other.

Why did diatoms fail to experience the Late Cretaceous boundary to the same extent as other plankton groups? Kitchell et al. (1986) recently reported that this dissimilarity may be a predictable consequence of a dissimilarity of life history strategies. A well-preserved assemblage of Late Cretaceous diatoms was recovered from a high-latitude site within the Arctic Ocean. Sections of the core are laminated. Macrosampling even the laminated sections of the core showed a high proportion of diatom resting spores within an assemblage of planktonic diatoms (Figure 7A).

Microsampling individual laminae revealed, however, that alternating layers are comprised of resting spores (without vegetative cells, Figure 7C) or vegetative cells (without resting spores, Figure 7B). The laminae provide evidence of an actively exploited biological adaptation, that of a meroplanktonic life history of alternating planktonic stages (the vegetative and sexual phases) and non-planktonic stages (the resting spore phase).

Studies of the ecological and physiological aspects of diatom resting

spores have led to an understanding of resting spores as a population-level 'survival strategy' (Fryxell 1983). The formation of resting spores is induced by locally unfavorable environmental conditions, including nutrient-depletion in oceanic upwelling systems. Paleoclimate modeling has shown that open-ocean upwelling would have been seasonally discontinuous at these high Arctic latitudes during the Late Cretaceous (Parrish and Curtis 1982, Barron 1985). The local environmental conditions, of nutrient depletion and high light levels, necessary for maintenance of a meroplanktonic life history today (Hargraves and French 1983), were met seasonally in this environment during the Late Cretaceous.

All diatom species, however, do not form resting spores. Consequently, both the presence of the character of spore-forming and its absence must be explained. In particular, families that evolved more recently than the Miocene, an approximate time of division between spore-forming and non-spore forming families (see Simonsen 1979), do not form resting spores. Instead, these families have the characteristic of forming a physiologically resting cell (Hargraves and French 1983). A comparison of these alternate strategies has shown that the more primitive trait entails both an increased energetic cost and a reduced number of potential cell divisions. Retention of the primitive trait in modern species within older genera has been given both a genetic and ecologic explanation: spore formation may be genetically linked to other indispensable aspects of cell metabolism; there may be selective advantages of retention of the strategy (Hargraves and French 1983); or unfavorable environmental conditions may be sufficiently frequent on an ecological time scale that many phytoplankton have retained the primitive life history strategy.

Equatorial upwelling, for example, is driven by the poleward

divergence of equatorial surface waters, a more continuous phenomenon. Correlative Maastrichtian diatom assemblages within the subtropics are conspicuously devoid of resting spores (Gresham 1985), confirming the modern-day observation that discontinuity of the favorableness of the photic zone is the probable causal factor linking the life history trait to the local environment.

The biological property of a meroplanktonic life history is an adaptation (Kitchell et al. 1986). As Sober (1984) has emphasized, the term is meant to imply (i) an historical process of selection for possessing this (heritable) trait and (ii) that the trait contributes to survival in the local environment. Resting spores contribute to adaptedness (Sober 1984) by providing a mechanism of survival during times when the conditions of the planktonic environment exceed either the physiological tolerances (Sandgren 1983) or competitive abilities (Garrison 1980) of the vegetative cells.

This adaptation resulted in what is termed 'effect macroevolution', an evolutionary process driven by upward causation from the ecological realm and the level of the individual organism to the macroevolutionary realm of differential survival and extinction. As Kitchell et al. (1986) concluded, "the adaptation of a meroplanktonic life cycle among populations of centric diatoms in the Late Cretaceous increased the probability of survivorship during normal times of local environmental deterioration, as it does today. This innovation of a meroplanktonic life history may have been differentially enhanced during the Late Cretaceous mass-extinction regime."

The chance interaction of this locally-adapted life-history trait and the close Cretaceous extinction mechanism(s) turn an otherwise enigmatic pattern of differential survival among marine plankton to a predictable

pattern. In so doing, the postulate that mass extinction is indifferent to organismal attributes is qualified. There is, in this example, a causal dependency between evolutionary survivorship during a time of global perturbation and a biological character selectively relevant in normal times. As a consequence, the differential selectivity of a mass extinction event has been reduced, in terms of explanation, to the organismal level of selection and aptation.

SUMMARY

Differential survival across major extinction boundaries is a means of understanding causality. Data on the differential magnitude of extinction are insufficient both to distinguish mass extinction from background extinction and to address the context-dependent relationship of cause and differential effect. In the case of Late Cretaceous phytoplankton, the interaction of a proximate ecological adaptation, selected for in a local environment, and the postulated extinction mechanism resulted in the fortuitous but macroevolutionary consequence of differential survival.

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FIGURE LEGENDS

FIGURE 1. The metric of extinction and origination is number occurring within each geologic stage. Originations are plotted in solid line and extinctions in dashed line. Data are from Raup and Sepkoski's (1984) compilation of marine family records.

FIGURE 2. The metric of extinction is the probability (i.e. normalized for standing diversity) of extinction per myr for the Phanerozoic stages of geologic time. The observed series is plotted in dashed line and the predicted series (see Kitchell and Pena 1984 for details of the analysis) in solid line. Data are from Raup and Sepkoski's (1984) compilation of marine family records.

FIGURE 3. The metric of extinction is percent extinction of marine families within each geologic stage. The criterion of reversal from an increase in percent extinction to a decrease in percent extinction identifies the peaks shown in shading. Modified from Raup and Sepkoski (1984).

FIGURE 4. The technique of plotting extinction-decay trajectories for simultaneously extant species (pseudocohorts) as a function of geologic time is used to identify periods of time when extinction intensity is high (slope steepens) relative to other periods of time, and to assess the degree of synchronicity of response across cohorts. The bold arrow identifies the 'peak' of extinction recognized as a global phenomenon in the analyses of Raup and Sepkoski (1984, 1986).

FIGURE 5. The pattern of species disappearance shown by ordering of species durations and times of first and last appearances by time of last appearance. Species are planktonic foraminifera in the tropical Pacific and Atlantic paleosystem; all known species are included if they are

present by the beginning of the Oligocene or appear subsequently.

FIGURE 6. Frequency distributions of species durations (A,B) compared to family durations (C,D). In A and B, the species are planktonic foraminifera; A represents the low- to mid-latitude species of the Pacific known from 111 DSDP sites; B represents the tropical species of the Pacific and Atlantic known from 116 DSDP sites; the shaded portions of histograms distinguish extinct species (with known durations) from extant (open histogram) species. C and D are the frequency distributions of ages of marine families becoming extinct during times of mass extinction (C) versus times of background extinction (D); redrawn from Boyajian (1986).

FIGURE 7. Smear-slide samples of material from Arctic core FI-437. A, from macrosampling across laminae showing mixed vegetative cells and resting spores of Late Cretaceous centric diatoms; B, from microscampling laminae rich in vegetative cells; C, from microsampling laminae rich in resting spores.

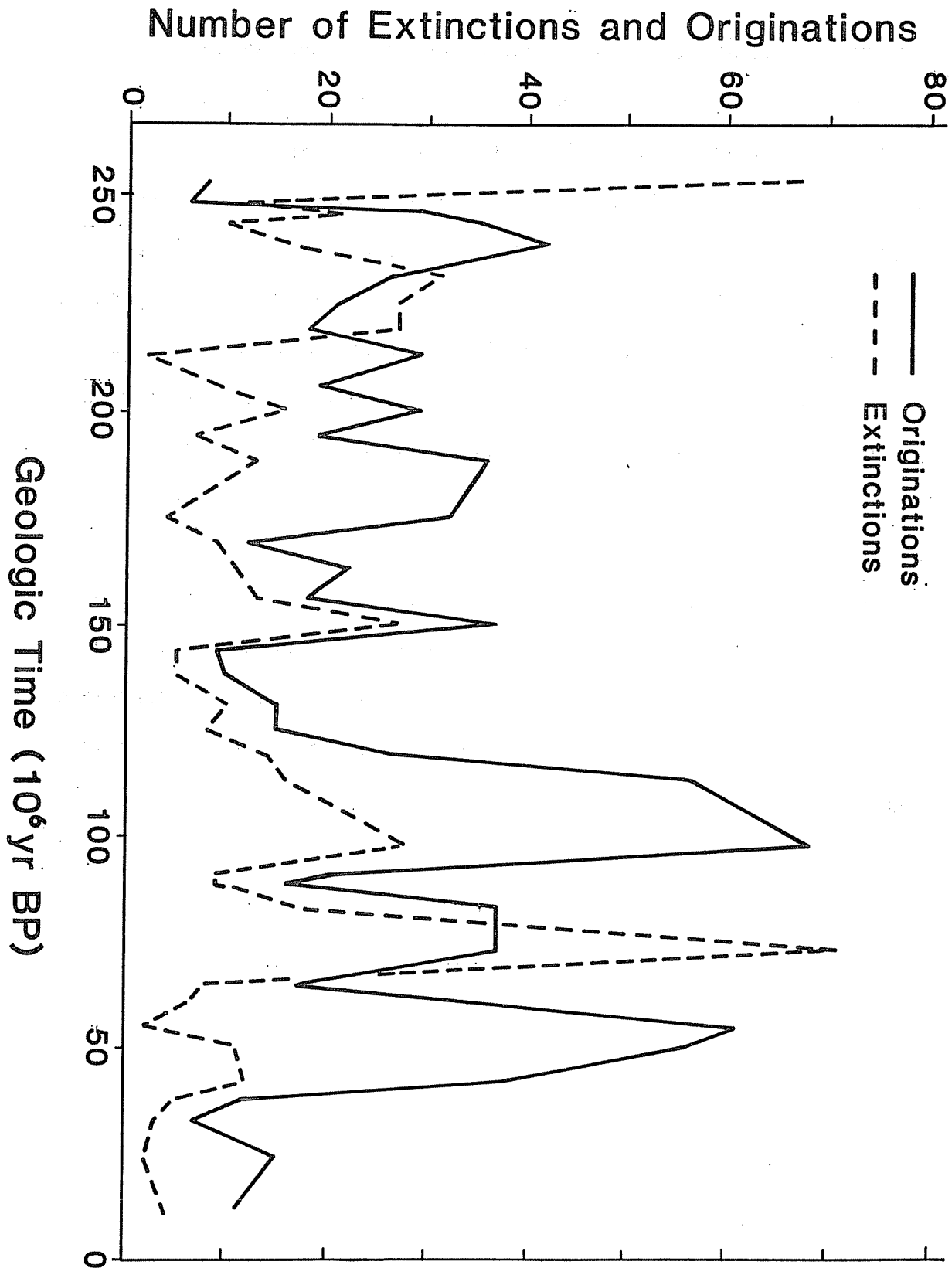


Figure 1.

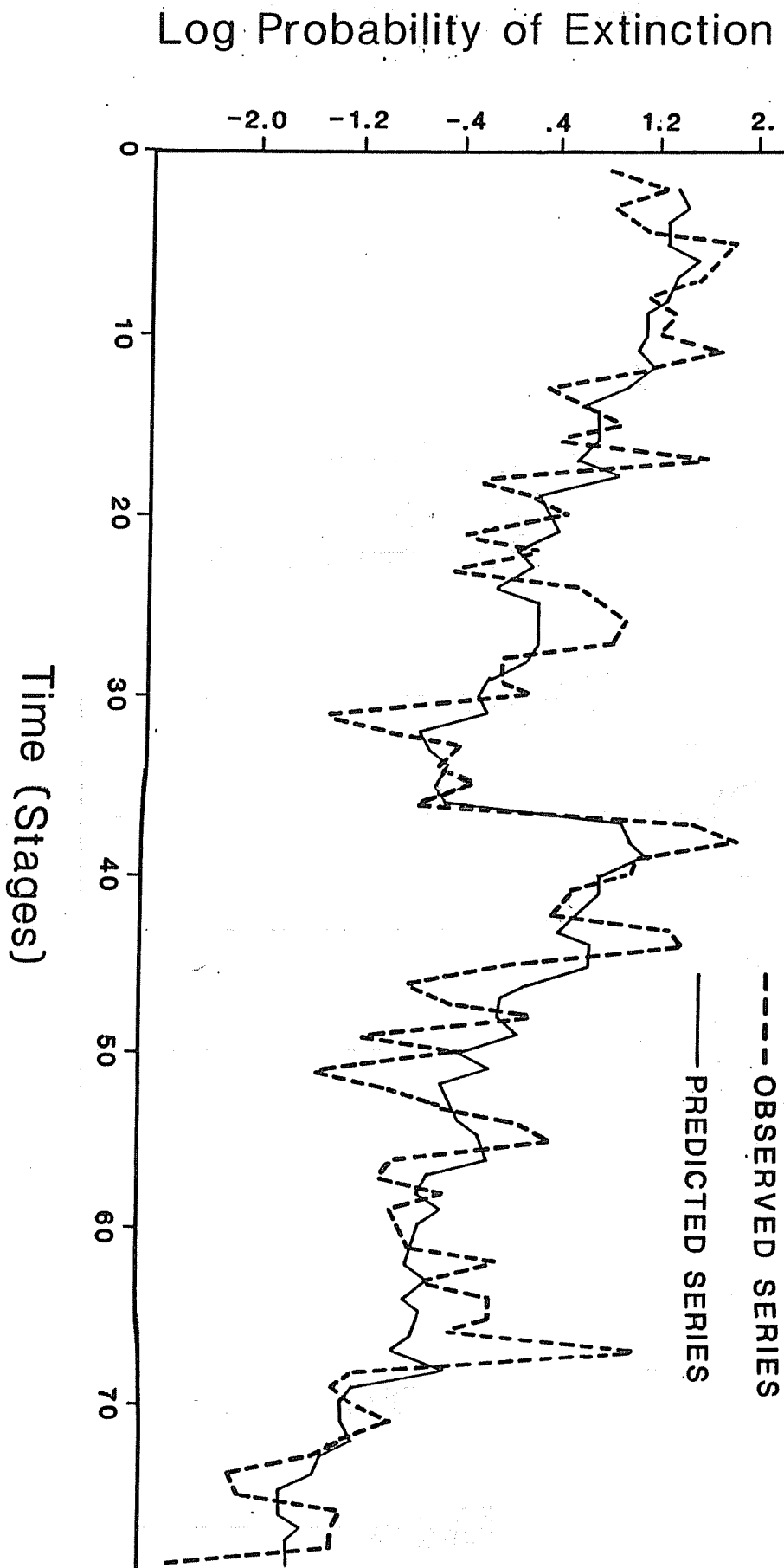


Figure 2.

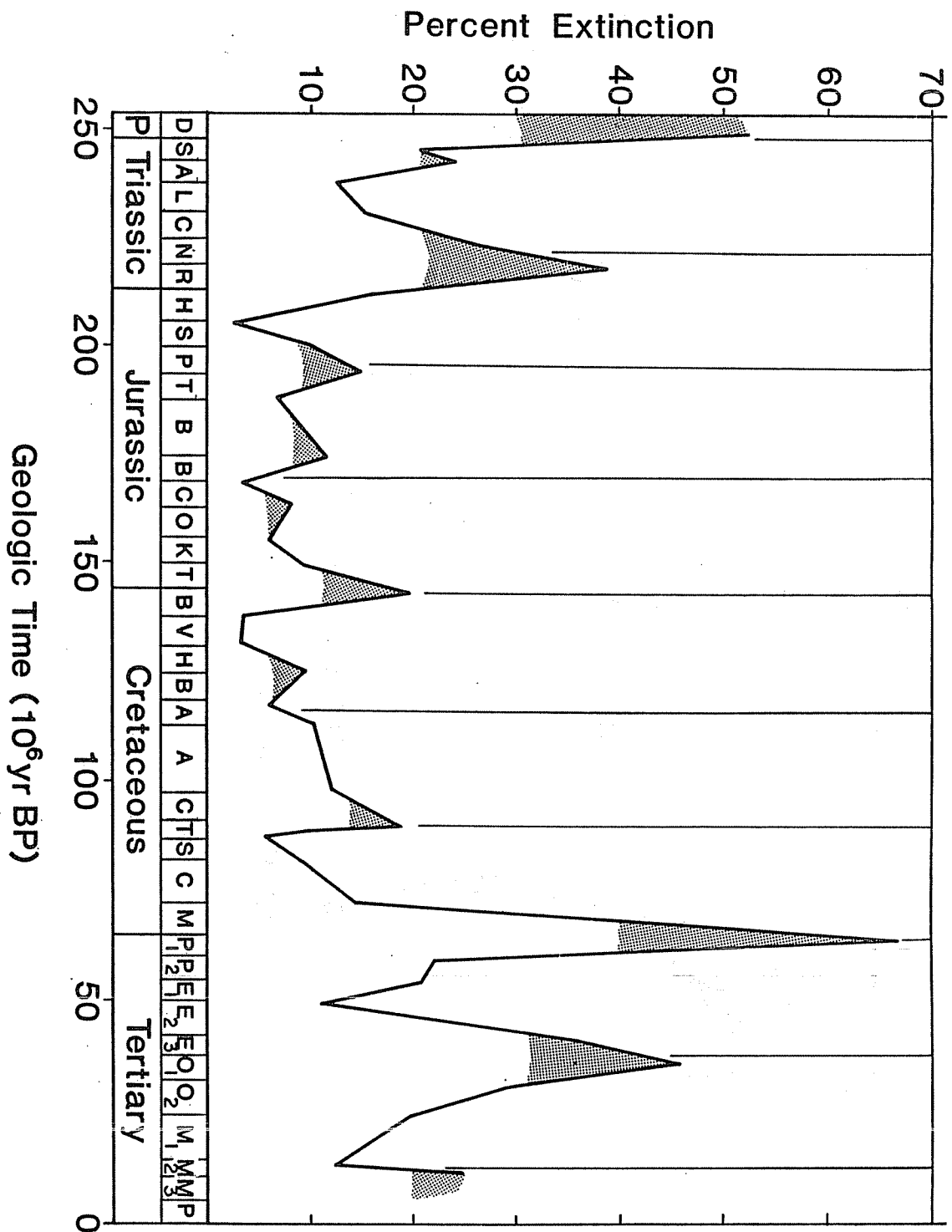


Figure 3.

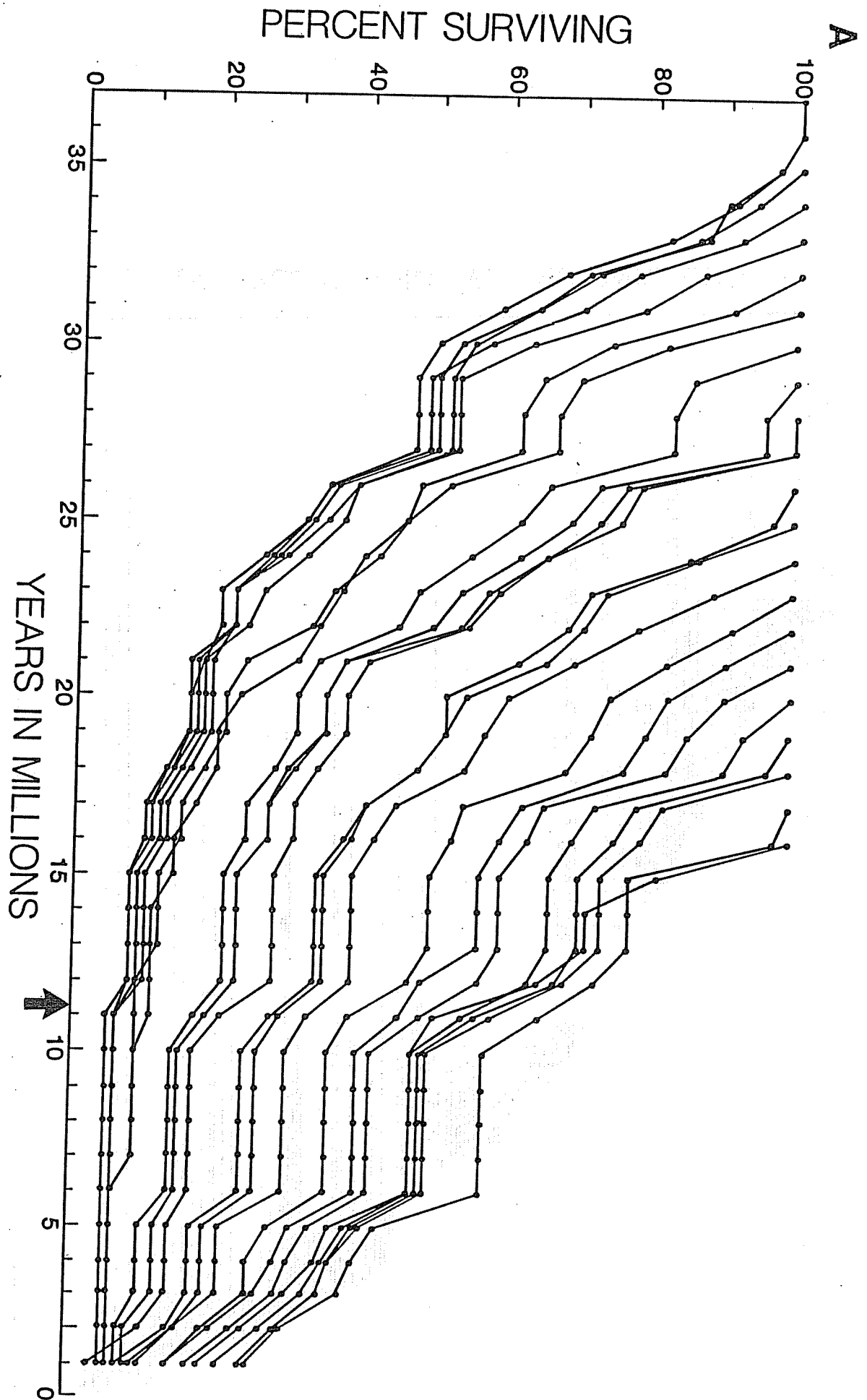


Figure 4.

ORDERING BY TIME OF DISAPPEARANCE

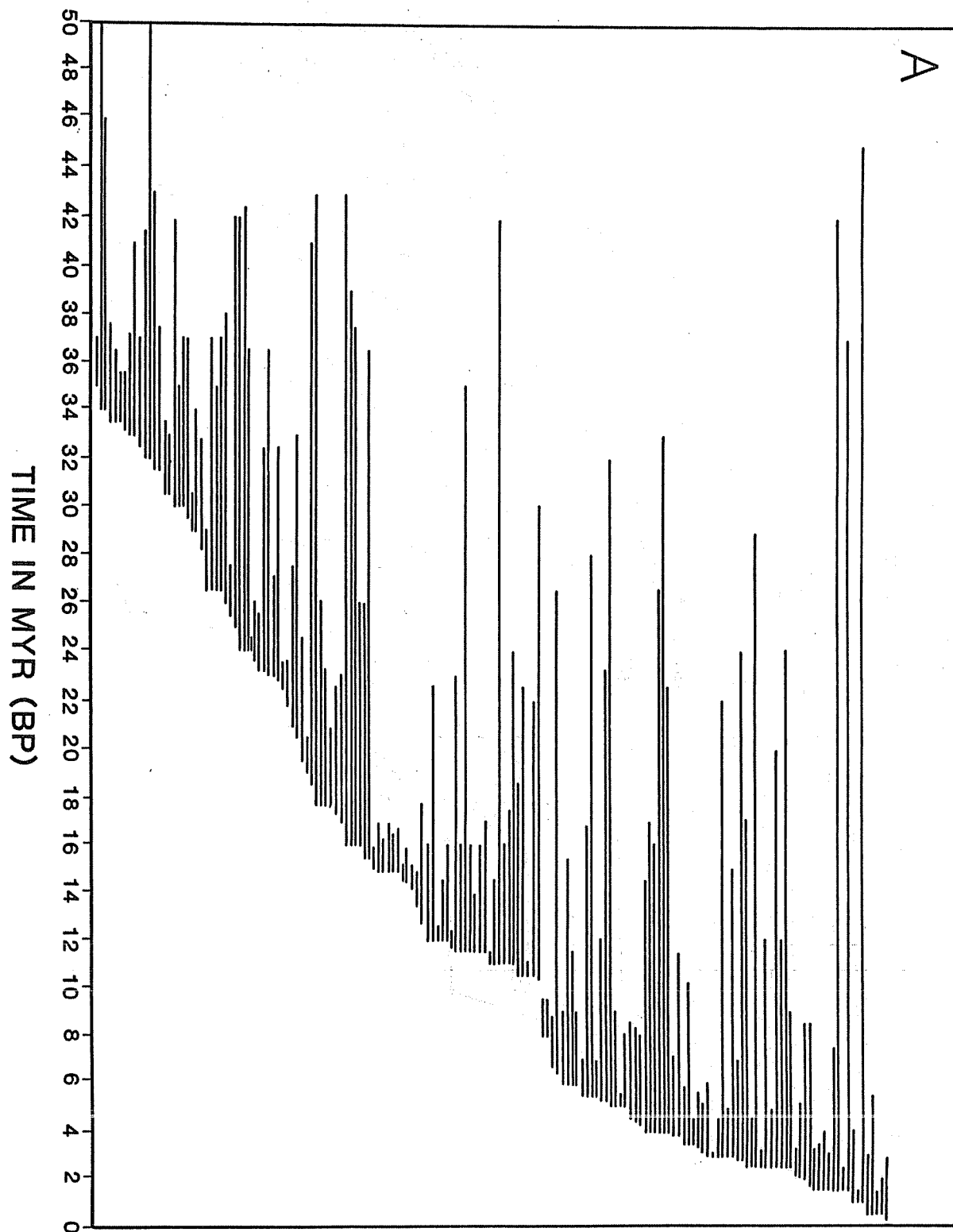


Figure 5.

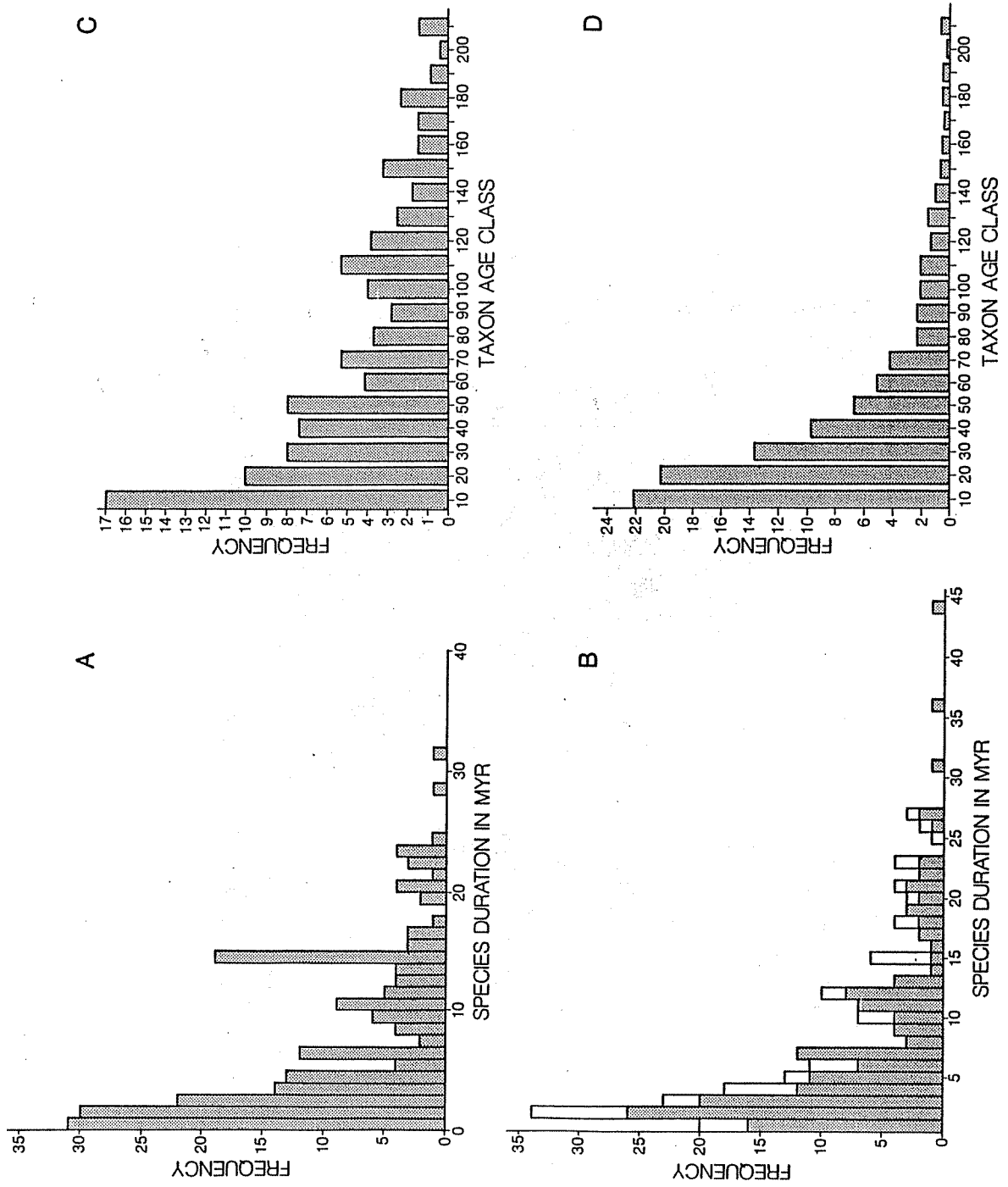


Figure 6.

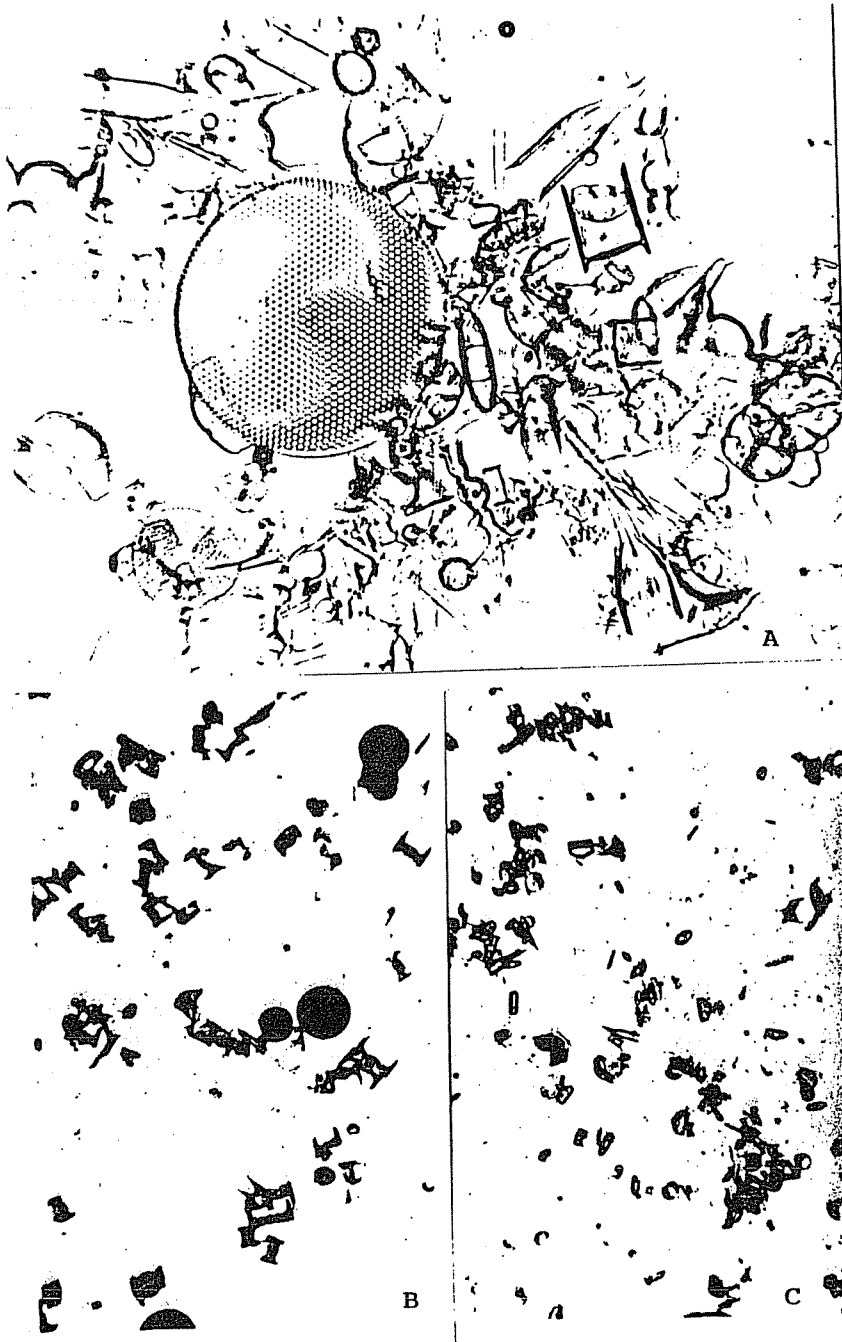


Figure 7.



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THE K/T BOUNDARY IN THE FLYSCHOID GOSAU SECTIONS OF GOSAU (ELENDRABEN) AND GAMS (KNAPPENGRABEN), AUSTRIA

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ABSTRACT: At Gosau the author has found the K/T boundary within the Zwieselalm Formation (turbidites, channel-fill deposits) and at Gams within the Nierental Formation (thin bedded turbidites, slope association). In both sections the K/T boundary layers have been deposited above a sequence of late Maastrichtian grey marly limestones (Gosau) or calcareous marls (Gams) with abundant dark grey worm tracks in the uppermost bed. The top of this bed should be defined as K/T boundary rather than a presumed geochemical boundary in the middle of a clay layer. In the Knappengraben the K/T boundary clay consists of a white-grey clay layer (3-7 mm) in the lower and a light yellow clay layer with rust-brown spots (2-7 mm) in the upper part. A calcite layer with plates up to a thickness of 8 mm cuts through the clay parallel to the bedding. A soft dark-grey clay layer (15-60 mm) with lenses of Silt (5 mm thick, 10-30 mm above the yellow clay) and a fine grained sandstone (15-20 mm) follow further upward. In the Elendraben a white clay layer (2-6 mm) is overlain by a yellow-light brown coloured clay (2-4 mm) with red-brown rusty spots and calcite plates. The sequence continues with a soft dark-grey clay (6 mm), a silt layer (4-8 mm), a dark sandy marl (20-30 mm) and a fine grained sandstone (8-15 mm).

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BIOESTRATIGRAFIA DEL CONIACIENSE Y SANTONIENSE DEL VALLE DE LOSA (BURGOS Y ALAVA). FORAMINIFEROS PLANCTONICOS, INOCERAMIDOS Y AMMONITIDOS.

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RESUMEN: El estudio reciente de la fauna de Inocerámidos en las secciones de Villaventín, Lastra de Losa, Villacián, en la provincia de Burgos, y de Fresneda en la de Alava, en el Valle de Losa, permite ahondar en la caracterización bioestratigráfica del Coniaciense y Santoniense de la Formación Losas, hecha a raíz de los estudios de la fauna de foraminíferos planctónicos y de ammonites realizados ya por dos de los autores (M.A.L. y R.M, proyecto de la CAICYT nº PR-83/2693-C2). Así se reconocen las siguientes zonas: Zona Tridorsatum (Coniaciense medio) caracterizada por la presencia en su parte superior de Forresteria (Harleites) sp. y de Inoceramus (Magadiceramus) subquadratus subsp. inc. En la Zona Margae (parte inferior del Coniaciense superior) la presencia de Protexanites bourgeoisi no es determinativa de ella puesto que también se da en la Zona Serratmarginatus (parte superior del Coniaciense superior). Esta última viene caracterizada por la presencia de Protexanites bontanti. La aparición de Texanites s.s. señala el límite con la zona suprayacente, Zona Texanus, y por lo tanto el límite Coniaciense-Santoniense. En ésta es característica la presencia de Texanites gallicus y de Inoceramus (Platyceramus) cycloides wegneri. Los foraminíferos planctónicos permiten reconocer las Zonas Concavata y Asymetrica. La primera aparición de Texanites s.s. parece coetánea con la de Sigalia carphatica seguida por la de Dicarinella asymetrica.

ABSTRACT: The recent study of the Inoceramid faunas in the Villaventín, Lastra de Losa and Villacián Sections (Burgos province) and in the Fresneda Section (Alava province) within the Losa Valley, supplies additional data on the biostratigraphic model for the Coniacian and Santonian of the Losas Formation, based on the planktonic foraminifera and ammonoid faunas (M.A.L. & R.M., CAICYT project nº PR-83/2693-C2). The following zones are recognised: Tridorsatum Zone (middle Coniacian) characterised by the presence in its upper part of Forresteria (Harleites) sp., and Inoceramus (Magadiceramus) subquadratus subsp. inc. Within the Margae Zone (lower part of the upper Coniacian) the presence of Protexanites bourgeoisi is not exclusive and it also appears in the Serratmarginatus Zone (upper part of the upper Coniacian). This latter zone is characterised by the presence of Protexanites bontanti. The appearance of Texanites s.s. marks the limit with the upper zone, the Texanus Zone, or in other words, the Coniacian-Santonian boundary. This zone is characterised by the presence of Texanites gallicus and Inoceramus (Platyceramus) cycloides wegneri. Planktonic foraminifera define the Concavata and Asymetrica Zones. The first appearance of Texanites s.s. seems to be contemporary with that of Sigalia carphatica followed by Dicarinella asymetrica.

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AN EARLY CRETACEOUS VOLCANIC SEQUENCE IN CENTRAL ISRAEL AND ITS SIGNIFICANCE TO THE ABSOLUTE DATE OF THE BASE OF THE CRETACEOUS

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ABSTRACT: Lower Cretaceous volcanics in Samaria, Central Israel, consist of a 230 m thick sequence defined as Tayasir Volcanics. It is subdivided into a Lower Basalt, a Tuff Member (a volcano-sedimentary unit), and an Upper Basalt. Concurrent, normal, faulting controlled the volcanic activity as well as the nature of the accumulation of the entire unit. K-Ar absolute ages are 144 and 148 m.a. for the lower flow and 133 and 134 m.a. for the upper flow. These represent Berriasian-Valanginian ages and suggest a slip-rate of 0.015-0.018 mm/y along the main fault system. The Tayasir Volcanics are distinguished from other younger (110-120 m.a.) Lower Cretaceous volcanic occurrences previously described both in northern and southern Israel. Lower Cretaceous age of the volcanics is supported by field relations. It is concluded therefore, that the absolute date of the base of the Cretaceous in the area, is about as the determined age of the lower basaltic flow. This conclusion is relevant to the numeric age determination of the Jurassic-Cretaceous boundary in general.

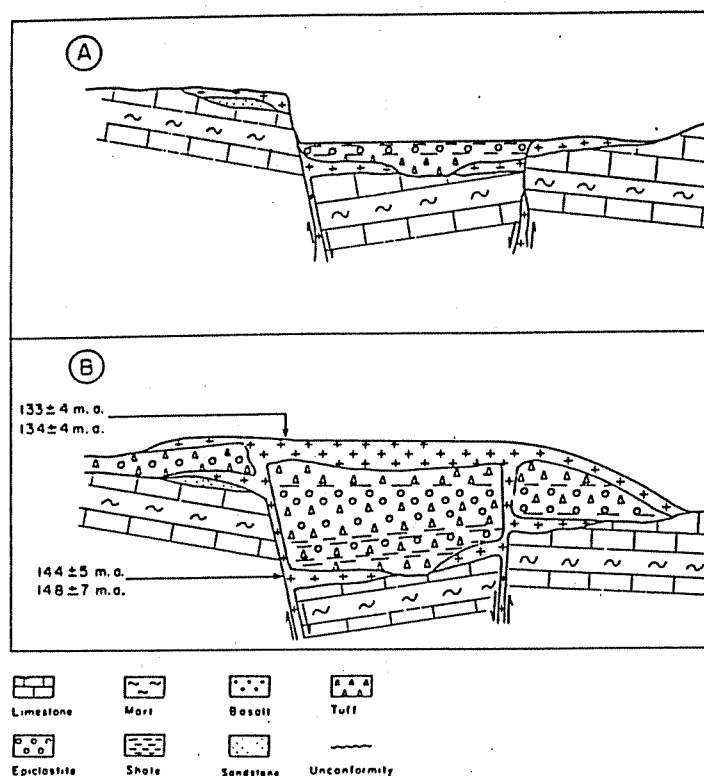


FIG. 1 —Cross-section reconstructing two stages of the deposition of the Tayasir Volcanics (modified after Mimran 1972). A—Post-deposition of lower part of the Tuff Member (Lower Valanginian). B—Post-eruption of the Upper Flow (Uppermost Valanginian). (Notice morphotectonic relief in stage A).

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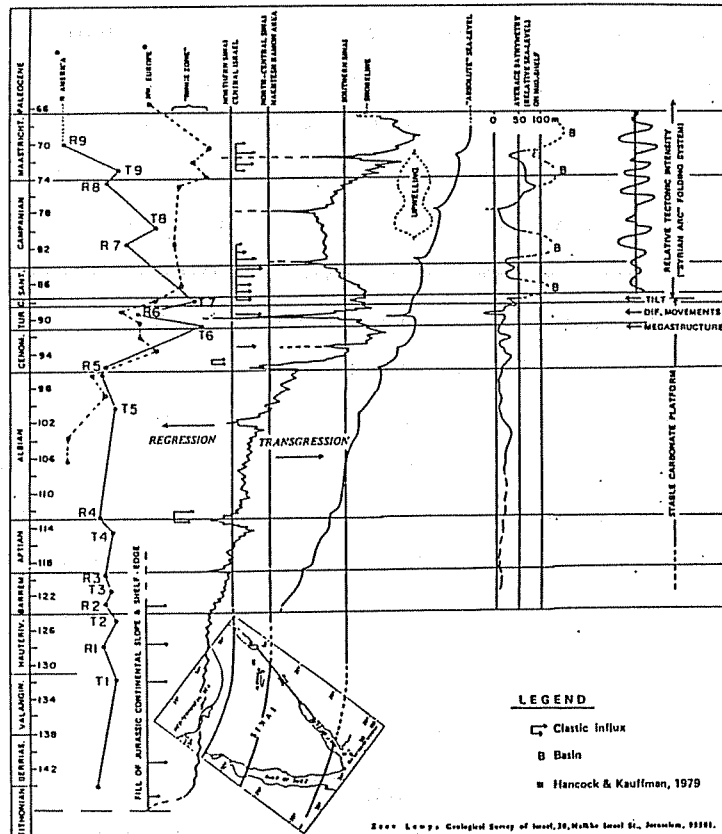
ON CRETACEOUS GEOIDAL EUSTASY AND CYCLICITY OF MAJOR SEA-LEVEL FALLS IN LIGHT OF TRANSGRESSIVE-REGRESSIVE CYCLES AND RELATIVE SEA-LEVEL CHANGES IN THE MIDDLE EAST

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ABSTRACT: The changing position of the Cretaceous Tethyan shoreline over present-day Sinai (Egyp) and Israel reflects of transgressive-regressive cycles, from which a curve of "absolute" sea-level (for constant rate of subsidence) was drawn. Relative sea-level changes were interpreted from extensive bio- and lithofacies changes in the shelf sediments. The correlation between these curves shows that some transgressions occur during regional shallowing, as indicated by extensive dolomite and brecciated chert layers. Several regressions occur during relative sea-level rise resulting from progradation (sand and clay beds extending seaward). Sea-level generally rose during the Cretaceous, interrupted by periods of stillstand and short-lasting sea-level falls. The most prominent and extensive fall took place in Middle Turonian times; minor falls occurred in the Early Campanian, middle Late Campanian and Early Maastrichtian. Regressions, probably resulting from minor sea-level falls occurred in the Early Cenomanian, Late Albian and latest Aptian. These regressive peaks are evident nearly every six million years. Some stratigraphic time-scales suggest a 6+1 Ma interval between major Mesozoic unconformities (most stage boundaries) and the decrease in duration of this interval from the Paleozoic (10, 8, 7 Ma) to the Cenozoic (nearly 5 Ma). A general sea-level rise during the Cretaceous interrupted by a very few, short-lasting falls, was noticed in North America (Hancock and Kauffman, 1979, tab. 4) and "worldwide" (Vail et al., 1977). Therefore, existence of geoidal eustasy in Cretaceous times (Mörner, 1980, 1981) cannot be tested by means of relative sea-level curves.

CRETACEOUS TRANSGRESSIVE-REGRESSIVE CYCLES, RELATIVE AND "ABSOLUTE" SEA-LEVELS, TECTONIC AND SEDIMENTARY PHASES IN SINAI (EGYPT) AND ISRAEL.

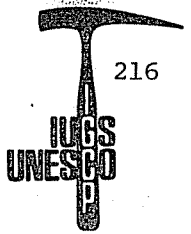


Hancock, J.M. and Kaufmann, E.G. 1979. *J. geol. Soc. London*, 136: 175-186.

Mörner, N.A. 1980. *Cretaceous Res.*, 1: 329-340.

Mörner, N.A. 1981. *Geology*, 9: 344-346.

Vail, P.R., Mitchum, R.M. Jr., Todd, R.G., Widmier, J.M., Thompson, S. III, Sangre, J.B., Bubba, J.N. and Hatelid, W.G. 1977. *AAPG, Mem.* 26.



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EXTINCTION OF UPPER DEVONIAN STROMATOPOROID - CORAL REEFS; CANTABRIAN MOUNTAINS,
N SPAIN.

G.B.S. VAN LOEVEZIJN

ABSTRACT: The Givetian age in the Cantabrian Mountains is dominated by massive biohermal stromatoporoid-coral reefs, which developed in a narrow zone of fault activity between the land area of the Asturian Geanticline in the North, and the deeper sea of the West Asturian-Leonese zone in the South. Intermittent siliciclastic supply interrupted the carbonate sedimentation several times, but each time reef building organisms reestablished. As a result of increasing uplift and erosion of the hinterland, combined with block movements in the marginal seas from the late Givetian onwards, the siliciclastic depositional regime increased, and the platform locally emerged and hindered the carbonate deposition and the development of organic build ups. Finally, during the late Frasnian, the siliciclastic input prevented the return of the last isolated stromatoporoid-coral reef biotope. This fact emphasizes that Frasnian reef extinction in the Cantabrian Mountains was not related to a sudden change or catastrophic event, but rather to a gradual change of tectonic conditions in the basin.

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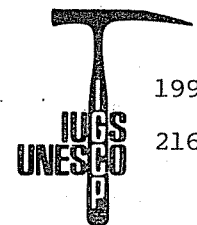
LOS INOCERAMIDOS (BIVALVIA) DEL SANTONIENSE Y CONIACIENSE DEL VALLE DE LOSA (BURGOS Y ALAVA).

Gregorio LOPEZ

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08193 Bellaterra. Barcelona.

RESUMEN: En este trabajo se estudia la bioestratigrafía de los inocerámidos del Coniaciense y Santoniense en el valle de Losa. Completándose los datos aportados por M.A. Lamolda y R. Martínez (1987) sobre el límite Coniaciense-Santoniense en esta zona, establecido en base al estudio bioestratigráfico de los ammonoideos y de los foraminíferos planctónicos. En general, el Coniaciense del valle de Losa es muy pobre por lo que respecta a la fauna de inocerámidos. Tan sólo se han encontrado inocerámidos en el Coniaciense medio, tratándose únicamente de fragmentos y ejemplares incompletos de Inoceramus (Magadiceramus) subquadratus subsp. inc. El Santoniense inferior se caracteriza por una gran abundancia de ejemplares y poca diversidad de especies. Predominando Inoceramus (Platyceramus) cycloides cycloides Wegner, que se encuentra asociado con I. (P.) cycloides ahseensis Seitz, I. (P.) cycloides wegneri Böhm e I. (P.) rhomboides rhomboides Seitz. Los ejemplares estudiados se obtuvieron durante el muestreo de las secciones estratigráficas realizadas en el Cretácico del Valle de Losa, para el proyecto PR-83/2693-C2 de la C.A.I.C.Y.T. sobre la bioestratigrafía del Cretácico superior del Surco Navarrocántabro.

ABSTRACT: This work on inoceramid biostratigraphy completes that of M.A. Lamolda & R. Martínez (1987), where new data of the Coniacian-Santonian boundary from the Losa valley were elaborated based on the ammonoid and planctonic foraminiferida faunas. As a whole, the Coniacian from the Losa valley has supplied poor inoceramid faunas. Only middle Coniacian inoceramids are represented, and all of them are incomplete specimens of Inoceramus (Magadiceramus) subquadratus subsp. inc. The Losa valley lower Santonian inoceramid faunas are characterized by a great number of specimens with a low species diversity. Inoceramus (Platyceramus) cycloides cycloides Wegner is the most common one, and it is associated with I. (P.) cycloides ahseensis Seitz, I. (P.) cycloides wegneri Böhm and I. (P.) rhomboides rhomboides Seitz. Inoceramid faunas were collected during the field work carried out in the Losa Valley, as part of the PR-83/2693-C2 C.A.I.C.Y.T. project on the Upper Cretaceous biostratigraphy of the Navarro-Cantabrian Basin.



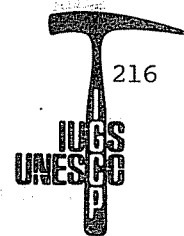
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MAASTRICHTIAN TO PALEOCENE FACIES EVOLUTION AND THE CRETACEOUS-TERTIARY BOUNDARY
IN MIDDLE AND SOUTHERN EGYPT.

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ABSTRACT: In Maastrichtian and Paleocene times open marine conditions prevailed in most parts of southern Egypt. During the Maastrichtian to Middle Paleocene mainly pelites, containing foraminiferal assemblages of middle to outer shelf origin were deposited in the centres of the southwards shallowing Dakhla-(W) and Asyut Basin (E). The synchronous marginal facies on the southern Upper Nile Platform was formed by deltaic complexes, which repeatedly prograded into the basinal facies. The siliciclastic input from the southern hinterland decreased during the climax of transgressions in Late Paleocene time when all of southern Egypt became part of a broad shelf sea, which reached further south into the Sudan. The Cretaceous/Tertiary boundary in southern Egypt usually is marked by a conglomerate, marking a hiatus of various extent (Dakhla Basin and Upper Nile Platform). The lowermost Paleocene here is attributed the planktonic foraminiferal G. pseudobulloides- or G. trinidadensis- zone respectively. In the Asyut Basin around Qena the C/T conglomerate is absent. Here the earliest Paleocene is represented by the G. eugubina- zone, the section across the C/T boundary therefore seems to be complete, although the Late Maastrichtian index foraminifer Abathomphalus mayaroensis could not yet be proved by the author. The use of Plummerita hantkeninoides is proposed instead.



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EVOLUCION Y SIGNIFICADO DE LA ESTEREOTIPICIDAD DE OICHNUS BROMLEY DURANTE EL PLIOCENO EN LA CUENCA DEL BAJO GUADALQUIVIR (S.O. ESPAÑA)

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RESUMEN: El estudio de la estereotipicidad de las perforaciones del tipo Oichnus realizado sobre representantes de Bivalvia (epi e infauna) en diferentes horizontes estratigráficos del Plioceno, ha permitido evidenciar cambios en la conducta depredadora de los organismos. Estas variaciones se detectan a nivel espacial para intervalos cortos de tiempo -el transcurrido entre los estados juvenil y maduro de las presas- y a nivel temporal, para intervalos mayores -el representado de un horizonte estratigráfico a otro-. Las variabilidades a gran escala se relacionan con la pérdida o adquisición de factores externos al sistema: presión selectiva ambiental (naturaleza del fondo, energía, competición ecológica). Las de pequeña escala están en función de factores internos: morfología, tamaño y ornamentación de las presas. Las diferencias evolutivas observadas en la estereotipicidad de los distintos tipos de Oichnus (O. paraboloides Bromley y O. simplex Bromley) prueban que su origen y producción se llevaron a cabo mediante modelos de conducta diferentes.

ABSTRACT: The analysis of the stereotypy of the Oichnus -type borings on Bivalvia (epi- and infaunal) from different Pliocene stratigraphical horizons, has allowed to evidence some changes on the predatory behaviour. These changes are detected on two levels: firstly an spatial variation for short intervals of time- between the juvenile and adult states of the preys- and secondly a temporal variation for larger episodes -between different stratigraphical horizons-. The variabilities on a large scale are related with loss or addition of external factors to the system: environmental selective pressure (type of substrate, energy, ecological competition). On a small scale the variabilities are connected with internal factors: morphology, size and ornamentation of the preys. Well-defined behaviour patterns have been revealed by evolutionary differences in the stereotypy of several Oichnus- types (O. paraboloides Bromley and O. simplex Bromley).



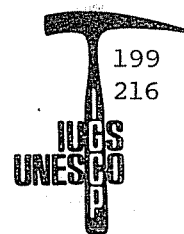
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ECOLOGICAL DYNAMICS OF THE LATE DEVONIAN MASS EXTINCTION

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ABSTRACT: The Late Devonian (Frasnian/Famennian) extinction event was an ecologically complex one, in that it was not simply due to a massive and rapid elevation of species extinction rates. On the contrary, the extinction event appears more to have been driven by species origination dynamics than extinction rates. Biological diversity does appear to drop precipitously in a single sharp pulse at the very end of the Frasnian. This event is not directly correlated with extinction rates, however, as extinction rates are elevated above "background" rates for at least 4 to 5 Myr before the actual end of the Frasnian. Many marine taxa actually show maximum extinction rates peaking long before the latest phases of the Frasnian, with declining rates during the period of diversity crisis. Marine ecosystems often show species diversity increases even during periods of maximum extinction rate. This phenomenon is due to the fact that origination rates of new species are even higher per time interval than the corresponding extinction rates. This dynamic relationship of origination/extinction rates reverses during the latest Frasnian, as origination rates sharply plummet while extinction rates remain relatively high. The sudden diversity drop in the terminal Frasnian is actually triggered by the precipitous decline in species originations.



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NEW PALYNOLOGICAL DATA AND ABSENCE OF IRIDIUM ANOMALY AROUND THE NON-MARINE CRETACEOUS-TERTIARY TRANSITION OF THE EASTERN SPANISH PYRENEES

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* Université de Provence Saint-Jérôme, F-Marseille.

** Université des Sciences et Techniques du Languedoc, F-Montpellier.

*** Centre Nucléaire de Saclay, F.-Gif-sur-Yvette.

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***** Marischal College, GB-Aberdeen.

***** Université Paul Sabatier, F-Toulouse.

ABSTRACT: Data are reported from analysis of pollen and spores, charophytes, faunas and iridium of sediments in three non-marine Cretaceous-Tertiary (C/T) sections from Barcelona and Lérida Provinces. These preliminary results indicate: 1) In the Figols-Vallcebre section, a C/T transition zone based on the distribution of charophytes as well as molluscan and ostracod faunas. 2) A high spore percentage from a Maastrichtian level of the same section as well as in samples from continental maastrichtian series in Southern France. 3) Gradual appearance of typical Tertiary pollen forms in Cretaceous assemblages, especially in the Fontllonga section, where a limit cannot be detected between Maastrichtian and Danian pollen floras. 4) No iridium anomaly has been found in the 20 samples studied so far.

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DISTRIBUCION DE LA BIOMASA Y EXTINCIONES EN COMUNIDADES DE TETRAPODOS TERRESTRES

Antonio MONCLOVA BOHORQUEZ

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RESUMEN: No siempre se dispone de los restos fósiles y datos paleoecológicos para deducir el proceso ecológico de las extinciones. Los tetrápodos terrestres presentan complejas relaciones ecológicas, adaptándose al medio con un ritmo evolutivo a menudo incapaz de absorber cambios ecológicos drásticos. La distribución de biomasa entre las poblaciones de predadores y presas muestra la actividad ecológica. Comparando la fisiología y adaptaciones de grupos fósiles y actuales deduciremos el reparto de biomasa en comunidades desaparecidas. En las comunidades de dinosaurios podemos deducir la significancia del registro fósil partiendo de las citas de los distintos géneros, de sus biomásas reales y rendimientos alimentarios, relacionándolos con sus porcentajes de individuos en la comunidad, para obtener curvas predador-presa. Las curvas varían del Jurásico al Cretácico final, permitiendo observar la estabilidad de la red trófica para, en relación a cambios ambientales, valorar los efectos negativos sobre la comunidad, relacionados con el reparto de biomasa. Durante el Cretácico las presas cambian el tamaño, en relación a cambios de vegetación, causando la inversión del patrón de distribución de biomasa en predadores, víctimas de su metabolismo y de las adaptaciones etológicas de las presas; éstas tampoco resistieron la especialización de ciertos predadores y los cambios ambientales.

ABSTRACT: It is not always possible to have the fossil remains and paleoecological dates to deduce the ecological process of extinctions. The terrestrial tetrapods show complex ecological relationships adapting themselves to their environment with an evolutive rythm frecuently unable to admit ecological drastic change. The distribution of the biomass among the populations of predators and preys indicates the ecological activity. Comparing the physiology and adaptation between fossil and modern groups it can be inferred the distribution of the biomass in disappeared communities. Among the diferent communities of dinosaurs the significance of the fossil record can be deduced using the dates of the different genera, of their real biomasses and nourishing profits, relating them to the percentage of individuals in every community in order, to get the predatory-prey curve. The curves vary from the Jurassic to the Cretaceous, allowing to observe the stability of the trophic net in order to estimate in relation to the changes in their enviroment the negative effects on the community related to the distribution of the biomass. During the Cretaceous the preys change their size, due to changes in the vegetation, causing the inversion of the standar of distribution of the biomass in the predators, as a consequence of their metabolism and the etological adaptations of their preys. These, on the other hand could not resist the specialization of certains predatories and the environmentals changes.



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THE GEOLOGY OF THE CRETACEOUS-TERTIARY BOUNDARY IN THE NORTHEASTERN APENNINES

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ABSTRACT: The Cretaceous-Tertiary (K-T) boundary in the northeastern Apennines of Italy is found in the middle part of the pelagic Scaglia Rossa Formation. This unit represents a deep water basin of subsiding continental crust enclosed between carbonate platforms to the north (Bagnolo plateau), east (Adriatic platform), and south (Lazio-Abruzzi platform), and the Liguride Ocean to the west. The paleo-basin topography was characterized by intrabasinal depocenters and structural highs which were the result of synsedimentary, extensional tectonic movements and reactivation of buried Jurassic normal faults. This activity generated synsedimentary slumps and episodic turbidity events consisting, in the distal part of the basin, of liquefaction and remobilization of unconsolidated pelagic muds. The K-T boundary occurred at a time of tectonic quiescence and pelagic sedimentation. In some localities, however, the transition from the Cretaceous to the Tertiary is incomplete due to slumping, winnowing, and erosional events that occurred in the early Paleogene. Wherever the transition is complete in the basin, the K-T boundary is consistently represented by a thin layer of clay, usually green at the bottom and red at the top, sandwiched between a whitish pelagic limestone (*Aba-thomphalus mayaroensis* Zone, uppermost Maastrichtian), and a pink, typically porcellanaceous limestone (*Turborotaloides eugubinus* Zone, lowermost Danian). The white Cretaceous biomicrite frequently contains numerous *Zoophycos* and *Planolites* trace fossils filled with pink Tertiary sediment and material derived from the boundary clay. However, the boundary clay has not been strongly affected by bioturbation, and mixtures of Maastrichtian and Danian planktonic foraminifers within the clay were found only in a few sites. The contacts between the boundary clay and the enclosing limestones are sharp and enhanced by stylolitic pressure-solution. Besides various amounts of fibrous secondary calcite formed during flexural slip folding, the boundary clay is mostly made of silt and smectite, illite, kaolinite and mix-layered montmorillonite. The sand-size fraction comprises less than 1% of the bulk rock and is mostly made of benthonic foraminiferal tests (*Textulariina* and minor calcareous benthics), and flattened spheroids of glauconite, sanidine, and titanomagnetite mixed in various amounts. Geochemical and structural analyses of these spheroids indicate that they are altered ejecta produced in a large extraterrestrial impact. This is in agreement with the anomalous concentration of siderophile elements, and rare fragments of shocked lamellae quartz and feldspars also found in the clay layer. This impact-generated material is not found in other rare clay layers analyzed above and below the boundary, but it is consistently found in similar K-T boundary clay layers worldwide, supporting the catastrophic scenario for the terminal Cretaceous mass extinction.

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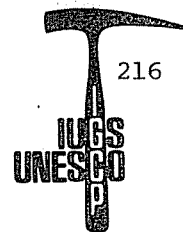
ASPECTOS MICROPALAEONTOLOGICOS DE LA CRISIS VENDICA EN LA PENINSULA IBERICA

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RESUMEN: Muy recientemente VIDAL y KNOLL (1982) dan fe de una importante crisis en el plancton marino durante el Véndico medio, que originaría la desaparición de aproximadamente el 70% de los taxones existentes y sustituidos por asociaciones de posibles cianobacterias planctónicas que florecieron en medios eutróficos. Este acontecimiento estaría relacionado con la glaciación Varangeriense. Las condiciones climáticas durante esa glaciación y en el período postglaciar Valdarnien se favorecieron el aporte de nutrientes a los océanos originando la eutrofización de los mismos. Por otra parte, las importantes variaciones climáticas y el aporte de aguas dulces a los mismos influyeron también en la creación de medios restringidos (KNOLL et al., 1981), en los que las cianobacterias planctónicas predominarían, al igual que ocurre en medios actuales con dichas características. En la península Ibérica del mismo modo que en el resto del mundo, este período se caracteriza por una gran abundancia de Bavlinella faveolata (Shepeleva, 1962; VIDAL 1976). Pizarras del Narcea, en el norte; Formación Estenilla, Formación Cíjara, Niveles Olistostrómicos y Pizarras del Pusa en el Centro (PALACIOS, en prensa) y Formación San Jerónimo en el Sur de España (LIÑAN y PALACIOS, 1983). VIDAL y KNOLL (1982) ya han indicado que B. faveolata predomina en medios marinos restringidos con influencia glacial y caracterizados por una alta productividad debido a la autotrofización de los mismos. La presencia de fosfatos sedimentarios en las formaciones del centro de la Península son un importante refuerzo a esta hipótesis.

ABSTRACT: VIDAL and KNOLL (1982) testified to an important crisis in marine plankton during the middle Vendian that must have brought about the disappearance of about 70% of the existing taxons, substituted by means of associations of possible planktonic cyanobacteria that thrived in eutrophic environments. This event must have been related to the Varangerian Glaciation. The climatic conditions during this glaciation and in the post-glacial Valdaian period favoured the contribution of nutriens in the oceans which gave rise to their consequent eutrophication. On the other hand, the important climatic variations and the flow of fresh waters into the oceans, were also factors influencing the creation of limited environments (KNOLL et al., 1981) where planktonic cyanobacteria predominated, as is the case in modern environments with the above mentioned characteristics. In the Iberian Peninsula, just as elsewhere in the world, this period is characterized by a great abundance of Bavlinella faveolata (Shepeleva, 1962; VIDAL, 1976). Shales from Narcea, in the North; The Estenilla Formation; the Cíjara Formation; the Olistostromic Levels and Shales from Pusa in the Centre (PALACIOS, in press) and the San Jerónimo Formation in Southern Spain (LIÑAN and PALACIOS, 1983). VIDAL and KNOLL (1982) have already indicated that B. faveolata predominates in limited marine environments with glacial influence and characterized by a high productivity due to their eutrophication. The presence of sedimentary phosphates in formations eated in located in the Centre of the Peninsula are an important back up to this hypothesis.



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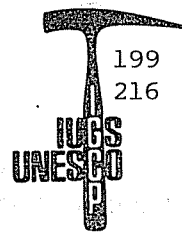
EVENTS, NATURAL SYSTEMS IN THE GEOLOGIC HISTORY AND EVOLUTION

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ABSTRACT: A great advance in the interpretation of the Geological History has been made in the last years as a result of the study on the effects of various events (extratelluric, geological, biological), and their intensity and frequency in particular. Opinions about the effects of single events on the course of macro-evolution are often controversial (over- or underestimated). For a reduction of the controversies, while studying the effects of any single event, one should remember the simultaneous effects of other events, that is, each time (and space) has its specific set of events (and specific responses of the existing systems) whose overall effects form the natural environments of a geological time (states and processes). A comparative review of events (species, intensities, frequencies, durations, coverages) throughout, the Geological History is given in this paper and their interactions elucidated, providing a better insight of the relevant factors (extra-telluric events, geological events, cyclicity, evolution rate, isolations, migrations, extinctions, etc.) of the macro-evolution and micro-evolution ("mechanism of evolution").

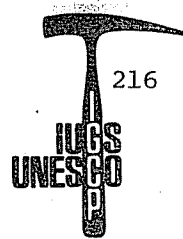


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CALCAREOUS NANNOFOSSILS AROUND THE K/T AND E/O BOUNDARIES

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ABSTRACT: A massive change in calcareous nannofossil assemblages occurs at the K/T (Maastrichtian/Danian) boundary. The rich assemblages of the uppermost Maastrichtian sediments are, however, usually also found just above or in the upper parts of the so-called boundary-clay and continue, in rapidly diminishing abundance, up into the Upper Danian. Did the coccolithophorids survive the K/T boundary events or are they reworked?. Was there a mass-mortality followed by extinctions rather than a mass-extinction at the K/T boundary?. On a family level, about 1/3 disappeared around the K/T boundary, while it was about 2/3 on a genus level and 5/6 on a species level. They were replaced by different genera and species in high and low latitudes. Survivors such as Makalius inversus, Biscutum constans, Cyclagelosphaera, Neocrepidolithus and Placozygus sigmoides soon dominated the assemblages in high latitudes, while small new forms such as Biscutum romeinii, B. parvulum and Toweius petalosus appeared and dominated in low latitudes. The calcareous dinoflagellate genus Thoracosphaera became common in all sections whereas Braarudosphaera bigelowii floods are found only at some localities. The few extinctions around the E/O boundary are spread over considerable time and are only on a species level. There is no mass-mortality and no mass-extinction near, thus also no radiation after the E/O boundary.



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MAASTRICHTIAN EXTINCTIONS OF PLANKTONIC FORAMINIFERA IN CENTRAL AND EASTERN POLAND

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ABSTRACT: Planktonic foraminifera occurring in epicontinental Maastrichtian deposits (160-270 m thick) of Central Poland (Middle Vistula River Valley) and Eastern Poland (vorehole Sawin) are characteristic of neritic zone of the Late Cretaceous Transitional Province. Of 10 genera recorded, Globotruncana, Rosita, Rugoglobigerina, Globigerinelloides, Globotruncanella, Heterohelix and Guembelitria are of common occurrence and accordingly, have been used for the reconstruction of extinction pattern. The following regularities in occurrence of planktonic foraminifera have been recorded:

1. Disappearance of last representatives of Globotruncana and Rosita at the end of Early Maastrichtian.
2. Disappearance of trochospiral forms during the Late Maastrichtian.
3. Disappearance of heterohelicids in the latest Maastrichtian.

Disappearance of globotruncanids is related to the evolutionary extinction of those species while the other changes in composition of the assemblages of planktonic foraminifera including their final disappearance are related to the shallowing of the basin due to terminal Cretaceous regression.



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THE CRETACEOUS-TERTIARY BOUNDARY CLAYSTONE IN CONTINENTAL ROCKS, WESTERN INTERIOR OF NORTH AMERICA. A PROBLEM OF ORIGIN.

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ABSTRACT: A thin bed of structureless kaolinitic claystone (1- to 2- centimeters thick) marks the palynological Cretaceous-Tertiary boundary in continental sedimentary rocks of western North America, in a narrow belt from Cimarron, New Mexico to Calgary, Alberta. Like tonsteins, which are altered volcanic ash beds, the boundary claystone has been found preserved in sedimentary sequences deposited in coal-swamp environments. It is overlain in sharp contact by the boundary impact layer, a thin 5- to 7- millimeter-thick layer of laminated, kaolinitic claystone that contains shock-metamorphosed mineral grains and high concentrations of iridium—both signatures of asteroid impact. In contrast with the impact layer, shocked-mineral grains are extremely rare and iridium much less abundant in the claystone beneath the impact layer. The few shocked grains seen in the boundary claystone probably result from downward contamination, possibly along root tubes or burrows; the iridium may have migrated down from the impact layer during diagenesis. Are both the boundary claystone and the impact layer the result of asteroid impact?. The wide distribution of this couplet suggests that they are. But the sharp contact between the two units and the restriction of shock-metamorphosed mineral grains to the impact layer on top of the boundary claystone preclude a simple graded-bed fallout model.

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LAS LINGULA DEL TRIASICO: UN ASPECTO TAFONOMICO

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RESUMEN: Este trabajo constituye la base de un primer intento de aplicar estudios ecológicos sobre braquiópodos inarticulados del género Lingula en comunidades del Triásico medio. Se estudian ejemplares de Jalance (Valencia), de edad Ladinense. Los mismos son muy frecuentes en niveles del Muschelkalk terminal (M_3) de la Cordillera Ibérica, pero nunca han sido estudiados desde el punto de vista paleoecológico. Se comienza aquí, considerando un aspecto tafonómico de interés: la deformación producida en las conchas de Lingula por la presión. Para ello, se analiza la deformación de las conchas de Lingula actual producida por presión experimental. Los ejemplares se incluyen en materiales detríticos o arcillosos y se someten a distintas presiones controladas. Las formas obtenidas se analizan mediante series de Fourier y los datos se comparan con formas de conchas sin someter a presión y con las del Triásico. La correcta interpretación de este aspecto tafonómico, puede aportar, entre otros, datos batimétricos más precisos, de los niveles triásicos que contienen Lingula.

ABSTRACT: This paper constitutes the basis for a first attempt of applying ecological studies of inarticulate brachiopoda of the Lingula genus in communities of the middle Triassic. Specimens from Jalance (Valencia) of Ladinian Age are studied here. Lingula are very frequent in the uppermost levels of the Muschelkalk (M_3) of the Iberic Range of Spain, but they have never been studied from a paleoecological point of view. The study begins considering a taphonomic aspect of special interest: the deformation produced in the Lingula shells by the pressure. To do so, the deformation produced on the recent Lingula shells by experimental pressure is analyzed. The specimens are introduced in detritic or clay materials and submitted to distinct controlled pressures. The shapes obtained are analyzed through the Fourier Series and the data obtained are compared both with data on shells that have not been submitted to this pressure and with Triassic fossil forms. The correct interpretation of this taphonomic aspect may supply us with, among other things, more precise batimetric data of the Triassic levels containing Lingula.

E61-2-01

THE ROLE OF EXTRATERRESTRIAL PHENOMENA IN EXTINCTION

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INTRODUCTION

The possibility that events in space have been responsible for major episodes of biological extinction on earth has been suggested frequently in the history of paleontology. In this century, notable examples include Schindewolf's (1962) proposal that the mass extinction near the end of the Permian was due to the effects of a nearby exploding star (supernova) and Urey's (1973) claim that several of the series-level extinctions in the Tertiary were caused by comet impacts.

Until recently, proposals for cosmic interpretations of extinction have enjoyed almost no support among paleontologists. The negative reaction has many roots, of which the most important may be: (1) the Lyellian thesis that it should be possible to explain events in earth history without recourse to "extraordinary" agents, and (2) the lack of supporting evidence for extraterrestrial influence in specific cases of mass extinction. It has been conventionally argued that hypotheses of extraterrestrial influence are fundamentally untestable and therefore not amenable to scientific inquiry. This argument is clearly flawed but has nevertheless had great weight in the scientific community.

It is indeed true that until Urey's 1973 work, there was no good observational evidence available to support the claims of cosmic influence. Urey's main contribution was to present empirical data on the timing of extinctions and

large-body impacts and to analyse these data statistically. He concluded that the similarity in timing was close enough to make a case for cause and effect. His analysis was based on few data and the statistical conclusions could have been challenged. Instead, his paper went virtually unnoticed.

The climate in this field changed dramatically in 1980 with the publication by Alvarez, Alvarez, Asaro, and Michel of data on iridium anomalies at the Cretaceous-Tertiary (K-T) boundary with the proposal that the K-T mass extinction was a consequence of a large meteorite impact (comet or asteroid). This produced a storm of controversy which continues to the present. As a result, the scientific literature devoted to mass extinction and its causes has grown exponentially to the point of being virtually out of control. Because the problem is so highly interdisciplinary, involving important elements of paleontology, geochemistry, geophysics, and astronomy, it has become difficult for any one person to make independent judgments on the merits of the many arguments and counterarguments.

My purpose in this paper is to review some of the basic evidence for and against the Alvarez claim of impact-induced extinction and to try to establish a "coordinate system" for a general evaluation of broader questions of cosmic influences in the history of life on earth. Because the literature on mass extinction has become so vast, a comprehensive review is impossible but I will attempt to identify some of the salient published papers on the subject.

THREE INDEPENDENT QUESTIONS

The current debate about the events near the end of the Cretaceous must be separated into three component questions:

- (1) Did one or more large comets or asteroids collide with earth at or near the end of the Cretaceous?
- (2) Was there a major mass extinction near the end of the Cretaceous?
- (3) If the answer to the first two questions is YES, did the collision(s) cause the mass extinction?

There has been a tendency to confuse these questions. One occasionally hears statements like: "There probably was no impact at the end of the Cretaceous because impacts do not cause extinctions." In fact, there may have been one or more K-T impacts with no biological effects.

THE QUESTION OF IMPACT AT THE K-T BOUNDARY

The recognition by geologists of large-body impacts on earth is a surprisingly recent development. Impact craters on the moon, terrestrial planets and their satellites have long been known -- although they have often been interpreted as volcanic -- but until the last few decades, geologists tended to assume that they resulted from events early in the history of the solar system and thus were not relevant to discussion of the later part of earth history. Several crater-like topographic features in Phanerozoic terrains were interpreted by some as impact features but very few of these proposals were accepted by the geological community.

This situation changed markedly in the 1960s because of several important developments, including (1) the recognition of high-pressure forms of quartz as clear evidence of meteorite impact, (2) the association of tektites and microtektites with impact, (3) photography from orbiting satellites of craters on earth, and (4) the discovery of large numbers of asteroids in earth-crossing orbits (Apollo objects).

As a result of these discoveries, geologists now have a catalog of more than one hundred well-authenticated impact features and the number is increasing rapidly (see Grieve, 1982, for list). Also, estimates of impact rates can now be made with considerable confidence although the uncertainties are still relatively high because crater loss by erosion and subduction of sea floor is high. The general conclusion is inescapable, however: the earth continues to be bombarded with large and small meteorites.

Under current estimates (Shoemaker, 1984), the Phanerozoic earth has been hit by about 3,600 objects of >1 km diameter and about 12 objects of >10 km diameter. The uncertainties in these estimates are such that the latter number may be as small as six or as large as 24. There is some indication that the impact rate has increased slightly during the Phanerozoic.

Whereas impacts on earth were once viewed by geologists with great skepticism, the phenomenon is now clearly established as part of the basic paradigm of historical geology and is seen as an integral part of Lyellian

uniformitarianism. For example, Wetherill and Shoemaker (1982) commented as follows:

"Although the physical encounter with the earth of these objects can properly be termed 'catastrophic,' in terms of the magnitude of the effects they produce, they are at the same time 'uniformitarian' in that they represent the extension of presently observed processes to earlier geologic time."

It is thus not surprising that most geologists easily accepted the evidence presented by Alvarez et al. (1980) for a large-body impact at the K-T boundary. The "signature" of anomalously high iridium concentrations was novel but totally reasonable in view of its worldwide distribution in terminal Cretaceous sediments and the well-established presence of iridium in meteorites and its near-absence in crustal rocks. If the impact had not been linked to mass extinction, it is doubtful that the geologic community would have asked for additional evidence. Without the extinction link, the Alvarez group would have merely provided one more case of large-body impact. Also, the estimate of the diameter of the impacting body (10 km), based on iridium concentrations, was completely credible because bodies of this size were expected to have collided with earth every 50 million years (on average) during the Phanerozoic.

Because of the proposed link to mass extinction, however, the scientific community demanded more evidence. Research groups in several countries added the following lines of evidence to support the impact hypothesis: (1) microtektites (Smit and Klaver, 1981), (2) osmium isotope

ratios indicating an extraterrestrial source (Luck and Turekian, 1983), and (3) shock-metamorphosed quartz typical of known impacts (Bohor et al., 1984).

At the same time, alternative interpretations of several of the impact signatures were presented. Rampino (1982) suggested that the iridium concentrations at the K-T boundary could have resulted from simple changes in ocean chemistry. Officer and Drake (1985) argued that the iridium could have come from mantle volcanism, following the report (Olmez et al., 1986) of iridium in the volatiles associated with eruptions of Kilauea volcano. It is also argued that the spherules called microtektites were incorrectly identified and that the shocked quartz could have had a volcanic origin (Officer et al., 1987). There has also been considerable debate about the meaning of the total trace element chemistry of the K-T boundary clays: some geochemists have claimed that the chemistry is clearly cosmic while others have argued for a crustal or mantle origin.

A major point of contention has been the absence of a clearly identified, large crater of terminal Cretaceous age. Some see this as a major deficiency of the impact hypothesis while others find it quite reasonable in view of the possibility that the crater would be difficult to recognize if it were in the deep ocean and because major portions of the sea floor have been lost through subduction since the end of the Cretaceous.

At present, the majority of geologists, geophysicists, and geochemists appear to accept the evidence for large-body

impact at the end of the Cretaceous but there are a few strong proponents of the volcanic alternative. In support of the latter idea is the fact that a major episode of mantle volcanism -- the Deccan traps in India -- appears to coincide with the end of the Cretaceous (Courtillet et al., 1986; see also Officer et al., 1987). There is the possibility, of course, that both points of view are correct: a large-body impact may have penetrated the crust to trigger the Deccan volcanism. This would explain the lack of an impact crater but there is no independent evidence for this interpretation.

In summary, we can conclude that the hypothesized impact at the K-T boundary is plausible and supported by considerable geochemical and geophysical evidence but that a possibly viable alternative (volcanism) exists.

There is a potentially important subsidiary question: Could there have been several large-body impacts near the end of the Cretaceous? This becomes important if one interprets the fossil record as indicating that the late Cretaceous extinctions took place in several pulses over a considerable period of time. It has been suggested that the osmium isotope data are most compatible with a multiple-impact scenario (Luck and Turekian, 1983) but this is the only direct evidence for more than one impact. On the other hand, some astronomers have argued that stars passing close to our solar system should be expected to produce showers of comets lasting for one to two million years. The question of multiple impacts must remain open until better dated evidence of individual impact events is available.

THE QUESTION OF MASS EXTINCTION AT THE END OF THE CRETACEOUS

To most paleontologists and biostratigraphers, the end of the Cretaceous was marked by one of the five most severe mass extinctions in the history of life. Indeed, it is no accident that this event marks the boundary between the Mesozoic and Cenozoic eras: times of major faunal turnover are imbedded throughout the geologic time scale. Still, there are a number of highly respected paleontologists who do not see the late Cretaceous extinctions as representing a single, discrete event. Rather, the argument is made that the extinctions are spread over a considerable interval in the late Cretaceous and that some groups of organisms passed through the interval unscathed.

Unfortunately, problems of geologic dating and of taphonomic loss of fossil record make definitive answers to the question of the suddenness and severity of late Cretaceous extinctions elusive. Although there is ample evidence that the Maestrichtian stage was a time of significantly high extinction, when compared with most other intervals in the Phanerozoic, it is at present impossible to say for sure whether the extinctions took place in a matter of a few days or years or whether they covered several million years. Whereas it is fairly clear that some major groups of microplankton and large reptiles suffered dramatic extinctions within a few centimeters (or at most meters) of the K-T boundary, a similar case is difficult to establish for the great majority of Maestrichtian extinctions. As

noted above, a theory of extinction caused by impact may be compatible either with a model of a single impact event or with one that postulates multiple events.

For the purposes of this discussion, I will adopt the view that the late Cretaceous was indeed a time of unusual mass extinction and that the event or events were limited at least to the final stage (Maestrichtian) of the Cretaceous and possibly to a much shorter interval.

THE QUESTION OF CAUSE AND EFFECT

Unfortunately, an extinction caused by large-body impact does not leave a clear signature comparable to the geochemical or geophysical signatures of impact alone. Although all geophysicists agree that a collision between earth and a 10 km body, or even a 1 km body, would have devastating consequences in human terms -- with energy release equivalent to many times the combined nuclear arsenals of the present-day world -- the effects on general biological diversity are poorly understood.

Much attention has been given in the recent literature to the so-called "dust cloud scenario" -- the blanketing of the earth by a dust-clogged atmosphere causing severe temperature changes and reduction of sunlight (Toon et al., 1982) -- but this is but one set of possible consequences of a large-body impact. Major alterations of atmospheric and/or oceanic chemistry may be much more important environmental consequences of impact. Much depends on whether the impact occurs in the ocean or on land and whether at high or low

latitudes. Some of the suggested consequences of impact would be highly selective biologically and would be expected to affect some kinds of organisms or habitats and not others. But not enough is known yet to make truly definitive predictions possible. It may turn out ultimately that the fossil record itself is the best guide to the kinds of environmental shock associated with impact -- whether at the K-T boundary or at other times in the Phanerozoic.

We are left, therefore, with only two arguments in favor of the causal link between mass extinction and large-body impact at the end of the Cretaceous -- assuming, of course, that both events occurred:

- 1) The temporal coincidence of mass extinction and large-body impact, each of which is a relatively rare event in the Phanerozoic record, and
- 2) Similar pairings of extinction and impact at other times in the Phanerozoic.

Both arguments are probabilistic and thus do not yield black-and-white answers. But they are tractable arguments, given a careful analysis of the distribution of rare events in geological time.

The mathematics of coincidence.

Much of modern statistical analysis is based on formal techniques for evaluating the probability that collections of events could have occurred by chance alone. If the probability is very low, one is justified in suggesting that the events have a common cause. If the probability is not

low, one is not justified in claiming cause and effect. Louis Alvarez (1983) presented a probability argument in the context of the similarity in timing of the extinctions and impact at the K-T boundary in Italy and I will extend this in the discussion that follows.

Suppose we are concerned with a span of geologic time (such as the Phanerozoic) with a duration of D years and with a small interval within the total span (such as the Maestrichtian) with a duration of d years. Suppose further that P physical events and B biological events are "dropped" on the total span independently and at random. Depending on the numbers of random events (P and B), the short interval may receive one or more physical and/or biological events or none at all. The probability of at least one physical event and at least one biological event occurring in the same small interval may be computed as:

$$[1 - (1 - d/D)^P] \times [1 - (1 - d/D)^B]$$

Note that this calculation does not depend on the geologic time scale being divided into equal time intervals.

As an example, suppose we are interested in estimating the probability that a rare mass extinction and a rare large-body impact could occur in the Maestrichtian stage by chance alone: let the total duration (D) of the Phanerozoic = 600 myr and the duration (d) of the Maestrichtian stage = 7.5 myr. Now, let the number of large mass extinctions (B) equal 5 and the number of 10 km impacts (P) equal 12 (from above).

Substituting these numbers into the expression given earlier yields 0.009. In other words, if the dates of extinction and impact events are known only to the stage level (Maestrichtian in this case), there is a chance of approximately one percent that the co-occurrence could have happened by chance alone -- without any causal relationship required.

If the times of mass extinction and large-body impact are better known, the probability of chance co-occurrence decreases. Suppose, for example, that both are known to have occurred in the final two million years of the Maestrichtian. In this case, $d = 2$ and the calculated probability is lowered to 0.001 or one-tenth of one percent.

These calculations suggest strongly that the coincidence between large-body impact and mass extinction near the end of the Cretaceous by chance alone is unlikely -- even if neither event is well constrained in geologic time.

There is an important related question of probability that can be asked: Given a mass extinction somewhere in the Maestrichtian, what is the probability that a large-body impact also occurred (by chance) in the same interval of time? This is simply the probability of at least one impact occurring in any given interval and can be computed as:

$$P = 1 - (1 - d/D)^D$$

Using $D=600$ and $d=7.5$, with $P=12$, the probability is 0.15.

Thus, if a major mass extinction has already been located and

the question of causation by impact is raised, there is a 15% probability that an impact would occur in the same time interval by chance alone. If time resolution is improved to two million years, as before, this probability drops to 0.039, or about 4 percent.

The foregoing calculations merely codify and make somewhat more rigorous the basic probability argument that has been used in favor of an extinction-impact link in the late Cretaceous. It is argued that two rare events in geologic history are unlikely to occur together by chance. The calculated probabilities are quite low even though the assumed accuracy of dating is conservative (7.5 or two million years in the Maestrichtian case) and this is a powerful counterargument to the claims that the dating of extinctions and impacts is too imprecise for a causal analysis.

The calculations assume, of course, that current estimates of the number of very large impacts in the Phanerozoic are reasonably accurate. If there were as many as 24 impacts of bodies >10 km in diameter, as is possible (above), then the probability of chance co-occurrence is increased somewhat.

A yet more important caveat is a problem common to all such probabilistic analyses of past events. In almost any history, very unusual events occur occasionally and it is always possible to choose pairs of events, after the fact, as candidates for causal interpretations. If, for example, a red Mercedes automobile crashes into a church in England at

precisely the same time as a politician in an Asian country is assassinated, one would not suggest that the two events are causally linked even though both events are rare. In the case of the Cretaceous extinction, the same logic could be used to discount the significance of the probabilistic arguments.

It becomes vitally important, therefore, to establish the plausibility of the extinction-impact link and this has not yet been done to everyone's satisfaction. Nevertheless, the probabilistic argument has considerable force and deserves to be taken seriously.

The obvious answer to the "Mercedes-assassination" challenge is to find out whether the extinction-impact hypothesis has predictive power. That is, can other extinction-impact pairs be found? If so, this would greatly reduce the estimated probability of co-occurrence by chance alone.

Other extinction-impact pairs.

To date, iridium and/or microtektite evidence of large-body impact has been reported for several other times of major biological extinction, as follows:

- 1) 11.7 myr BP: late Middle Miocene (Alvarez, 1987)
- 2) 38 myr BP: terminal Eocene (Alvarez, W. et al., 1982; Ganapathy, 1982)
- 3) 163 myr BP: terminal Middle Jurassic (Brochwic-Lewinski et al., 1984)

4) 248 myr BP: Permo-Triassic boundary (Sun et al., 1984)

5) 367 myr BP: Frasnian-Famennian boundary (Devonian) (Playford et al., 1984)

A few other cases could be included (such as the terminal Cenomanian at 91 myr BP and the Precambrian-Cambrian boundary) but evidence for these is not yet even reasonably firm.

With the exception of the Eocene case, all reports listed above have serious difficulties of analysis or interpretation. The Middle Miocene iridium anomaly is new, having been found in only recently in a single deep-sea core and work is proceeding at Lawrence Berkeley Laboratory to explore comparable sequences elsewhere (Asaro, pers. comm, 1987). The Middle Jurassic and Devonian cases have clear iridium anomalies but the iridium is found only in fossil bacterial mats (stromatolites) and there is the possibility that the organisms were simply concentrating ambient iridium. In the Permo-Triassic case, a strong iridium anomaly has been reported but attempts to reproduce the analyses in other laboratories have so far been unsuccessful.

The extinction-impact pairs just discussed have two additional problems. First, because of the expense of iridium analysis it has been difficult to sample the geologic record evenly. It has been inevitable, therefore, that geochemists have sampled horizons at which major extinctions are known to occur and this raises the possibility that the

finding of iridium anomalies is sample-dependent and that such anomalies are in fact common throughout the geologic record. To counter this tendency, Kyte and Wasson (1986) have reported analyses throughout the latest Cretaceous and early Tertiary records in deep-sea cores. They found only the K-T anomaly. Kyte and Wasson did not find the late Eocene anomaly probably because of the coarseness of their sampling regime. Fortunately, the problem of sampling is being eliminated because of the development and operation of the new, high-speed Iridium Coincidence Spectrometer at the Lawrence Berkeley Laboratory.

The second problem has to do with the definition and identification of major extinction events. The extinction at the end of the Middle Miocene and that at the Middle-Upper Jurassic boundary may not be significant enough to merit consideration in this context. This raises the question of the definition of a mass extinction. To some paleontologists, the term should be reserved for the five truly severe extinction events of the Phanerozoic (Ashgill in the Ordovician, Frasnian-Famennian in the Devonian, Permian-Triassic, late Triassic, and terminal Cretaceous events). To other paleontologists, an interval of time qualifies as an extinction event if its extinction rate (for the biota as a whole) stands above the normal background rate by a statistically significant amount.

Opinions on this question are quite polarized. My own view is that any event of multiple extinction that can be shown not to be a simple product of biases in fossil

preservation or study is a candidate for interpretation and that the array of possible causes, not limited to large-body impact, should be evaluated. In the context of large-body impact, there is no reason to say that the biological effects of impact must be global or truly devastating.

To summarize the evidence for impact as a cause for extinction at the K-T boundary, we have the circumstantial but rather powerful evidence from the probability calculations for the late Cretaceous and we have some supporting evidence for the general extinction-impact link from other parts of the record. But the total evidence still falls short of the ideal of absolute proof.

ALTERNATIVE EXPLANATIONS FOR EXTINCTION

Several non-cosmic explanations for the near-simultaneous extinction of large numbers of species in the Phanerozoic fossil record are available and some of these enjoy strong support in the paleontological community. The principal alternatives can be classified as follows:

- 1) Intrinsic biological factors, including competitive exclusion of taxa caused by the evolution of adaptively superior organisms,

- 2) Earth-bound environmental perturbations which develop too quickly to allow evolutionary adjustment, including changes in global climates, major transgressions or regressions of the world oceans, and unusual environmental events such as extreme volcanism.

Each of these has some evidence favoring it for the K-T event

as well as for other, selected extinction events but space does not permit a full and fair treatment of these alternatives here. Suffice to say that each should be evaluated as carefully and as rigorously as possible. This must perforce include full statistical analysis of the association in time between extinctions and evidence for the suspected causes. Taking the Phanerozoic record as a whole, there are so many extinctions and so many episodes of environmental perturbation that simple anecdotal comparisons are not sufficient. Application of the kind of probability calculations discussed earlier in this paper is clearly indicated.

PERIODICITY OF EXTINCTION

The proposals by several workers that major extinction events from the late Permian onward are uniformly spaced in time (Fischer and Arthur, 1977; Raup and Sepkoski, 1984, 1986; Rampino and Stothers, 1984; Sepkoski and Raup, 1986; Fox, in press) constitute a partially independent question bearing on the influence of extraterrestrial phenomena on biological extinction. Especially important in support of periodicity is the new analysis of generic extinctions by Sepkoski (1986).

Because similar periodicities have been found also in the records of impact craters (Alvarez and Muller, 1984) and magnetic reversals (Negi and Tiwari, 1983; Raup, 1985; Pal and Creer, 1986; Stothers, 1986), the periodicity question is germane to the question of the extinction-impact link. The

question of magnetic reversals is relevant because of empirical and theoretical arguments for impact as a cause of magnetic reversal (Glass et al., 1979; Muller and Morris, 1986).

Also, if extinctions are uniformly spaced every 26-30 million years, that fact can be an important guide to a search for further evidence for an association between large-body impact and extinction.

OTHER POSSIBLE EXTRATERRESTRIAL INFLUENCES

Although the emphasis in recent years has been on large-body impact as a possible explanation for mass extinction, there are many other aspects of our cosmic environment which must be considered to have evolutionary implications. The Phanerozoic earth has witnessed at least two complete galactic years (complete revolutions of the galaxy), a substantial increase in the luminosity of the sun, about 20 crossings of the plane of the galaxy, a significant increase in day length, and the gravitational effects of numerous passing stars, to mention just a few of the known events which may have influenced the history of life on earth.

It is not clear yet how many of these cosmic factors have had biological effects which are both significant and detectable in the fossil record. Nor is it known which, if any, could cause extinctions of species. The best candidate so far, with the exception of large-body impact, is the regime of Milankovich cycles produced by gravitational interactions in the earth-moon-sun system (Imbrie and Imbrie,

1980). From the work of Imbrie and others, Milankovich cycles on the order of 20, 41, and 100 thousand years have had a significant effect on the climate of the past 700,000 years and were probably responsible for the major advances and retreats of continental ice sheets during the Pleistocene. Although important, the glaciations may or may not have caused extinctions either through the direct effects of climatic change or through glacially-controlled sea level changes.

In view of the potential effects of the variety of known cosmic factors, it may turn out that the greatest contribution of the present debate over extinction and large-body impact will be to encourage research in other areas of extraterrestrial influence on terrestrial biology. The most important consequence of the work of the Alvarez group may thus have been to convince paleontologists that organisms have lived in a cosmic as well as an earthly environment.

CONCLUSION

The case for large-body impact as a cause of mass extinction is very strong but more study will be needed before the proposition can be said to be verified beyond all reasonable doubt.

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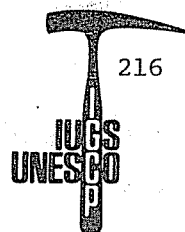
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WHAT HAPPENS AFTER EXTINCTION?

by Miquel De Renzi



SINTESIS DEL RESUMEN PROVISIONAL

En este trabajo se plantea la problemática evolutiva posterior a la extinción. Diversos autores, como Valentine, Sepkoski, etc. han tratado ya del problema. Los procesos relevantes aquí implicados van a ser de naturaleza macroevolutiva (evolución al nivel de la especie y sus consecuencias). Los procesos macroevolutivos pueden ser reducidos a los mecanismos neodarwinistas, o no. Una extinción masiva deja una multitud de nichos ecológicos libres; una situación de este tipo no sólo se da después de una extinción. Precisamente, se toma un ejemplo que no tiene que ver con extinciones, pero sí con multitud de nichos no ocupados: la gran radiación de los Metazoos al principio del Cámbrico, de la cual se sacan una serie de consecuencias aplicables a situaciones posteriores a una extinción masiva, a partir de la interpretación efectuada por Stanley de aquella radiación. El concepto de radiación adaptativa, con especiación siguiendo pautas del tipo equilibrio interrumpido, subsiguiente a muchas de estas situaciones, es discutido, en último término, a la luz de los conceptos actuales de la Biología del Desarrollo (Alberch, Gould). En otro orden de cosas, se discute también el caso de extinciones graduales, con grupos reemplazantes siguiendo modelos de cambio filético o equilibrio interrumpido. Otra cuestión comentada es la de aquellos procesos macroevolutivos que originarían tendencias no resultantes en una progresiva mejora adaptativa en el nivel de los organismos (selección de especies, de Stanley, de acuerdo con las modificaciones de Urba; hipótesis

del efecto, de Urba, etc.). Por último, se discute la cuestión azar versus procesos deterministas; es decir, la diversificación que sigue a la extinción ¿es un proceso con clave determinista o es algo resultante del puro azar? Se comentan y critican algunas ideas últimas de Hoffman sobre este punto.

PROVISIONAL ABSTRACT

This paper aims to explore the situation subsequent to an extinction. This question is concerned with macroevolutionary events (macroevolution is understood as evolution at the species level and its consequences). Macroevolution may or may not be reduced to neodarwinian mechanisms (Urba and Eldredge, 1984; De Renzi, 1986).

An important but particular process that may be produced after an extinction is diversification. Several authors (Sepkoski, Valentine, etc) have dealt with it in a general manner (diversification does not only happen after extinctions).

Valentine deals several times with the post-extinction processes (Valentine, 1977; 1980). He focuses on the diversification problems in terms of a game: the biosphere looks like a great mosaic board composed of mosaic tiles or tessera (each tile is a relatively uniform set of environmental conditions). This model is used by Valentine to explain the factors that determine the diversity in higher taxonomic categories. He assumes punctuated equilibria models (see figure 2 in Valentine, 1980). The extinction phenomena produce changes in the shape of the tessera and the model makes it possible for the author to research the post-extinction events. Other authors, such as Carr and Kitchell (1980) also deal with the problem of taxonomic diversity and how it is affected by extinction events.

The condition of evolutionary equilibrium and its perturbation is the core foundation of that paper.

The questions that I consider here are the following: many ecological niches become empty after an extinction. This fact permits other groups of unspecialized organisms, unaffected by the extinction, to occupy the niches left. As a consequence, the extinction rate (or rates) involved (gradual or catastrophic) must be taken into account.

One viewpoint with which to attack the problem is the adaptive one. However, macroevolutionary theory includes hypotheses that neglect the improvement of adaptation at the organism level, as in the Stanley's selection species or the effect hypothesis (Urba, 1983, 1984; Urba and Eldredge, 1984; De Renzi, 1986). Moreover, there is an alternative to the interpretation of classical adaptive radiation. Gould (1970) emphasizes that adaptive radiation is a group of competitive experiments to test the possibilities of a new construction (or evolutionary novelty). Then, the degree of success of each experiment is different. The survival of a little group of these experiments is the result of natural selection. This viewpoint will be taken, together with modern ideas on developmental biology, to study some features of evolutionary events after extinctions.

. . . .

The situation after a mass extinction is similar to many others in the geological record which do not involve previous extinction but rather the origin of many new ecological niches. One of these examples is an event which took place at the beginning of Cambrian times—an enrichment of the atmosphere in oxygen and an important biomass production by the autotrophic

unicellular organisms should help the appearance and diversification of the heterotrophic multicellulars. However, why do animals appear so much later? Two important internal factors are relevant for Stanley (1976a) in this scenario: 1) the absence of an evolutionary novelty (the sexuality in eucaryotic cells) as the very source of diversification of multicellular body plans, and exploitation of the empty ecological niches (adaptive radiation), and 2) the absence of predation, which maintains a low diversity in the ecosystems. The first factor means that the suitable physical conditions are not enough to occupy the empty niches. There must be a group of organisms with possibilities (their characteristics) to colonize them. It is necessary to remark on this feature, although it seems obvious. The second factor means that the diversification may be hampered by the state of the ecosystem, although the physical and evolutionary requisites are suitable.

Another important feature in the Lower Cambrian origin of Metazoa is its abrupt irruption in the biosphere, as historically referred to and recently analyzed by Stanley (1976b). This same author supposes that the rates of diversification of Metazoa are not as fast as those of other similar biotic events in the geological record. The successful and fast irruption of an unspecialized group of organisms occupying empty niches after an important extinction is also a common fact. These explosions are known as adaptive radiations. Adaptive radiations require the punctuated equilibria model -or rectangular model-, according to Stanley. However, it is also possible to imagine a situation of phyletic change different from the adaptive radiation. In this last situation there may be several kinds of ideal cases: two or more groups of organisms with the same (or different) rate of

phyletic change, and groups of organisms evolving according to phyletic change model with other groups, according to punctuated equilibria model, with different rates of change in each model. Finally, it is possible to consider the concurrence of two groups under punctuated equilibria hypothesis, with the same (or different) rate of change. Perhaps, the real cases consist generally of a single group that occupies the empty niche. The concurrence of another group may happen later.

The concurrence of groups of organisms for one set of ecological niches may be interpreted as competition. Competition is actually a very discussed concept in theoretical ecology and there are reasons to think that it is prevented in "normal" ecological scenarios; i.e. organisms become adapted to different ecological niches in an ecosystem, and the input of a new species is in such a way that it develops characteristics, which deviate it from exploitation of niches occupied by adaptively similar species already present in the ecosystem. However, it is well known today that the morphological and thus, adaptive, possibilities of the organisms are limited. The notion of constraint underlies Seilacher's constructional morphology, and Gould (1982) (in paleontology) and Alberch (1982) (in developmental biology) have remarked on this important feature. According to the latter author, a developmental system has a limited number of trajectories. Thus, natural selection cannot fashion indefinitely the adaptive characteristics of the organisms. So, morphological convergences would be very frequent and competition would take place in many cases, and one of the competing groups would become extinct.

I have to discuss something here concerning adaptive radiation. The old idea of Gould (1970) -an innovation is tested

in competitive experiments, and natural selection removes the unfit- must be reformulated. A suitable formulation is the following: developmental pathways give rise to a certain number of constructions that use an evolutionary novelty, without intermediate forms. A part of these constructions would become unfit when competition is established. This viewpoint does not conceive the morphospace as a primary continuous region of possible forms but as a primary morphological discontinuous region. This idea comes from Alberch (1982). In populational terms, there would be crowds of small populations occupying wide empty regions (e.g. mammals' postcretaceous diversification). Random genetic drift would be the principal process in action. Different selection pressures would also be possible in new conditions. Thus, developmental systems would be stressed by changes in their genetic foundations, canalization ruptures would take place, and new morphological constructions would appear in the old niches.

In a post-extinction situation, what is the proportion of free niches? Dinosaurs were replaced by mammals. Perhaps, free niches were abundant at the beginning of Tertiary times and competitive experiments would not take place. Competition would come later, when the saturation of niches was progressively attained.

A scenario with many free ecological niches is also appropriate to cases of primarily non adaptive (at the organism level) macroevolutionary processes to rule evolutionary trends, such as species selection or the effect hypothesis. Species selection works with emergent properties at the species level (Urba, 1984) and the effect hypothesis explains trends as the result of traits of the organisms or their genomes that determine

a fortiori or fortuitously the probabilities of extinction and speciation, but does not as the result of adaptation at the organism level (Urba, 1983, 1984).

These considerations do not take into account the rate (or rates) of the extinction. The extinction may be gradual or massive (see Raup, 1987). These cases must be also analysed in relation to the evolutionary rates of the replacing organisms and their evolutionary tempo (phyletic change or punctuated equilibria). Moreover, the extinction of a small group would have less consequences than the extinction of a large group (a small group is thought to be a taxonomic supraspecific entity with a very small number of species, very stenotopic, and with a low rate of speciation). Gradual extinction rates may be coordinated with the slow evolutionary rate of a replacing group (this may fit phyletic change or punctuated equilibria models) following the mosaic model of Valentine (1980). However, a fast gradual extinction rate may be also considered. Carr and Kitchell (1980) formulate an equilibrium hypothesis for it. A positive perturbation of diversity in a saturated condition results in a rapid decrease of diversity and it has a delayed recovery with a slower rate from an undersaturated condition (an example would be the the invertebrate fauna in the transition from the Permian to Triassic).

Stanley's interpretation of the Cambrian metazoan radiation teaches us still something more about another question: there may be ecological barriers that prevent the diversification of a new group, although the latter is potentially prepared for it. Moreover, to be potentially prepared for diversification is a situation that must be attained. However, this fact is not always necessarily attained. Random factors in evolution have been emphasized by Raup (1972, 1977), Schopf (1979), and other authors

in the last years. As seen above, the achievement of sexuality was very important for the diversification of the multicellular organisms at the beginning of the Cambrian. It is possible to say something similar for any novelty in a group of organisms which becomes useful in unoccupied ecological niches. However, the appearance of this evolutionary novelty may be something accidental, as Raup (1972) has shown.

As a consequence of these reasonings, it must be concluded that the replacement of the extinct groups may not be immediate, in spite of its possible achievement. The ecological barriers involved in the extinction of the precedent group can continue existing. Even though ecological barriers do not take place, the evolutionary potentialities can not yet arise in the candidate group for replacing the extinct group, and the appearance of such an innovation (or innovations) may be a random event. If the appearance of the novelties does not take place, this may also be due to random factors. A last question: the constraints imposed by the development can not make possible the morphogenesis of the necessary structures in a certain group to work successfully in the empty ecological niches.

Finally, Raup (1981) shows the idea that extinction may be an stochastic event (see also Schopf, 1979). There are not ecological causes, and so, there are no barriers for the immediate occupation of an empty ecological niche. However, the intrinsic organismic causes for later possible or impossible occupation (new suitable organisms for those environmental conditions) continue in action. If there exist new suitable organisms for the free niche, the mosaic model of Valentine (1980) is again useful. For Hoffman (1986), there is no reason to reject stochastic models of diversification and substitute them for deterministic models, as

with that of Sepkoski (1979). The latter reflects an underlying logistic process controlled by changes in origination and extinction rates with changing number of taxa.

Hoffman (1986) insists on his model, which supposes independent speciation and extinction rates changing at random. The paleontological data available do not provide support to reject this stochastic model, and speciation, extinction, origination and diversity are not dependent on global scale. Hoffman's idea is interesting but I wish to criticize it. Raup (1977) says (referring to stochastic models): "the success of the simulation does not prove the model; it proves only that the simulation represents one way in which the observed ... patterns could have developed. The logical next step is to use the model to make other kinds of predictions that can be tested with real world data. If these tests are successful, the model can be elevated to the status of a generalization or statistical law.", (the underlined is mine). Hoffman's statement fails in the underlined point: the prediction from its own model. As Hoffman (1986) tells us, its model reproduces the pattern of three of Sepkoski's evolutionary faunas (Sepkoski, 1981), but Hoffman does not say anything about the consequences of the stochastic character of the three evolutionary faunas' pattern and the possibility of testing them from the available paleontological data.

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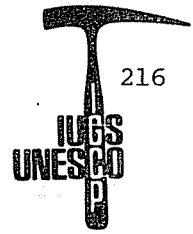
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III JORNADAS DE PALEONTOLOGIA
PALEONTOLOGIA Y EVOLUCION: FENOMENOS DE EXTINCION

ECOLOGICALLY SELECTIVE EXTINCTIONS AND THE IMPACT HYPOTHESIS.

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ABSTRACT: A trophic analysis of the bivalve and brachiopod stratigraphic record reveals a pattern at the Cretaceous-Tertiary boundary consistent with predictions based on the asteroid impact hypothesis. Impacts are expected to interrupt photosynthesis, causing higher extinction rates among suspension feeding bivalves and bivalves with zooxanthellae than among groups such as brachiopods, which have low metabolic rates, and deposit feeding bivalves. This pattern is supported by an alternative analysis based on locomotion, where active groups with higher metabolic demands are expected to have greater extinction rates than passive groups. Analysis of a Jurassic background interval does not produce the predicted pattern, suggesting that factors operating at the Cretaceous-Tertiary boundary were not the same as background processes. A similar treatment at the Permian-Triassic boundary yields mixed results suggesting that the two mass extinctions have different (non-cyclic) causes.



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PALEONTOLOGIA Y EVOLUCION: FENOMENOS DE EXTINCION

EXTRATERRESTRIAL IMPACT AT THE CRETACEOUS/TERTIARY BOUNDARY IN SOUTHERN ISRAEL.

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ABSTRACT: The Cretaceous/Tertiary boundary is well exposed in Israel, best observed in full sequences in its southern part. It grossly coincides with a sharp lithological contact between the white, chalky Maastrichtian Ghareb Formation and the green, marly shales of the Paleocene Taqiye Formation. This boundary in Israel, as in locations elsewhere, is characterized by mass extinction of planktic foraminifera and nannoplankton, nodules of pyrite and marcasite, and depletion of ^{13}C . Extraterrestrial signatures were observed in a section near Maktesh HaGadol (southern Israel). Three red chalky clay layers alternate with uniform white chalks at the uppermost part of the Ghareb Fm. (Middle-Late Maastrichtian). The lower red layer is found about 230 cm below the C/T boundary, as defined by foraminifera, the upper one almost at the stage boundary. These clays contain high concentration of Fe particles, abundant fish remains and very rare planktic foraminifera. The results of geochemical and microprobe analyses indicate anomalies of trace elements (Co, Ni, Ag, W, Au: 70-150 ppb). The determination of Ir is still under study. Green, microtektite spherules (100-200 microns), made of amorphous Fe-Mg-aluminosilicates and K-feldspar, are rather common in the upper and lower layer. The occurrence of extraterrestrial evidences within a relatively thick section assuming sedimentation rate of 1-2 cm/100 yr, suggests projectile showers lasting over a period of 100000-200000 years.

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PALEONTOLOGIA Y EVOLUCION: FENOMENOS DE EXTINCION

LA INDETERMINACION EN EL PROCESO EVOLUTIVO DURANTE LAS ETAPAS DE CRISIS

Antonio RUIZ BUSTOS

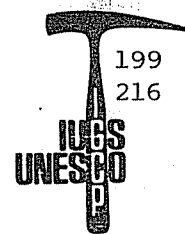
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RESUMEN: La relación entre morfología y funcionalidad consiste en que la primera es soporte material de la segunda y ésta es el efecto dinámico de la morfología, inmersa en el contexto definido por la interacción entre Medio físico-Materia viva. La Selección obliga a conseguir la mejor funcionalidad posible, lo que tiende a aproximar sus valores entre los individuos de la población. El logro de un incremento significativo en la funcionalidad por una minoría, frente al resto, es ventajoso y supone su difusión. Ello implica siempre cambios en la morfología, para ser expresión de esa mejor funcionalidad, causa de nuevas y distintas poblaciones. Todo ello origen de procesos evolutivos. La CRISIS es la perturbación rápida del ecosistema, y supone una etapa de retroceso brusco (en cierto modo un reinicio) en la Sucesión ecológica. En este período, la persistencia de unas u otras morfologías concretas, es incierta. También en la funcionalidad es posible la aparición de objetivos "polos de orientación" inéditos o diferentes a que dirigirse, adquiriendo ésta igualmente una posición incierta. En estas condiciones existe: a) La posibilidad de que nuevas morfologías y polos de funcionalidad se enlacen de manera imprevisible y surjan procesos de Megaevolución. b) Se incremente la extinción, mediante las morfologías que no logran una nueva funcionalidad o la pierden durante la crisis. c) Ambas simultáneamente, donde el porcentaje más elevado será de extinción. Unida a estas dos incertidumbres, se añade la que aporta la intensidad de la crisis, que necesita metodológicamente ser definida previamente, pues la vida supone un sistema de morfología-función capaz de superar alteraciones del ecosistema, y es necesario determinar a que entidad nos referimos. Sólo crisis grandes afectan de forma general a varios grupos, con extinciones masivas. Enunciadas estas tres incertidumbres, constituyen juntas lo que denominamos: PRINCIPIO DE INDETERMINACION EVOLUTIVA. En RUIZ BUSTOS, 1987, se describen ejemplos concretos del mismo en las faunas de Roedores. La Microevolución es el resultado de una funcionalidad encauzada por un ecosistema estable en las tendencias de su Sucesión.

ABSTRACT: The relation between Morphology and Function is such that the former is the material support of the latter. Function is the dynamic result of morphology, immersed in the context defined by the interaction between Physical Medium-Living Matter. Natural selection makes it imperative to achieve the best Function possible and tends to approximate its values between individuals in the population. The achievement of a significant increase in Function by a minority, as opposed to the rest, is advantageous and it may be assumed they will diffuse. This fact always implies changes in Morphology, it becomes an expression of this improved Function, and it is the cause of new and different populations. All this originates evolutionary processes. CRISIS is the rapid disturbance of the ecosystem, and it implies a period of abrupt recession (to a certain extent a new beginning) in the ecological succession. During this period, the persistence of some of other concrete morphologies is uncertain. It is also possible that within the Function certain objectives may appear, called "Poles of Direction", which are different or unknown and to which a course may be directed. So, Function also acquires an uncertain position. Under these conditions several possibilities exist: a) New morphologies and poles of function become intertwined in an unforeseeable way and processes of Megaevolution arise. b) Extinction increases, by means of morphologies which do not achieve a new function or which lose it during the crisis. c) Both these cases occur and the higher percentage is that of extinction. Besides these two uncertainties it may be also added the uncertainty caused by the intensity of the crisis. Previously this should be methodologically defined, as life implies a system of Morphology-Function capable of overcoming alterations in the ecosystem, and it is necessary to determine which entity we are referring to. Only important crises affect various groups in a general way, producing massive extinctions. These three uncertainties or variables constitute, as a whole, the so called: PRINCIPLE OF EVOLUTIONARY INDETERMINATION. In RUIZ BUSTOS (1987) concrete examples of this principle are described on Rodent fauna. Microevolution is the result of Function being channeled by an stable ecosystem in the trends of its Succession.

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III JORNADAS DE PALEONTOLOGIA
PALEONTOLOGIA Y EVOLUCION: FENOMENOS DE EXTINCION

THE KELLWASSER-EVENT (UPPER DEVONIAN). REGIONAL, STRATIGRAPHICAL AND GENETIC APPROACH

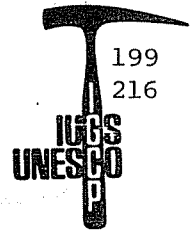
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ABSTRACT: Several localities of the Kellwasser (KW)-Horizon were investigated in the Rheinisches Schiefergebirge, the Harz-Mountains (both in W-Germany), the Montagne Noire (Southern France), and in SE-Morocco. The KW-Horizon is situated in the Uppermost *Palmatolepis gigas* - conodont zone and is connected with black limestones or black shales. The KW-Extinction-Event can be recognized at a certain level within the KW-Horizon. Analysis of the whole fauna was carried out with special respect to goniatites, ostracodes, homoctenids, conodonts and pelecypods. The conodont work was done mainly by Sandberg and Ziegler in close cooperation with the group of Göttingen. Further investigations were based on microfacies-analysis by acetate-peels. Palynological and isotopic work is under way. Although there are differences in the distinct regions it is possible to get a very high time resolution, biostratigraphically as well as lithostratigraphically. As an example the Steinbruch Schmidt in the Kellerwald area near Wildungen-Braunau (Rheinisches Schiefergebirge) is chosen. This well exposed 7.5 m-section of Upper Devonian cephalopod limestones is one of the candidates of the SDS in Frasnian/Famennian-boundary discussion. As this section:

- the extinction occurs about at 11 cm below the top of the 40 cm thick Upper KW-Limestone within one single layer,
- the extinction can be detected by the following parameters:
 - (1) lithological change (change to coarser grain).
 - (2) extinction of pelagic homoctenids (abruptly).
 - (3) occurrence of shallow-water pelecypods
 - (4) increase of shallow-water conodonts.

Looking for possible interpretations of these facts - adding the observations from other sections - leads to the assumption that there must be more than one reason for this extinction-event. Among a multicausal spectrum of effects an oceanic overturn and a remarkable shallowing effect represent the main causes triggering the cessation of a great number of faunal elements at the Kellwasser-Event.



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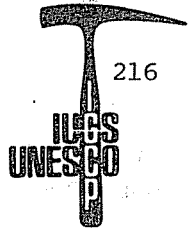
PALEONTOLOGIA Y EVOLUCION: FENOMENOS DE EXTINCION

THREE UNUSUALLY COMPLETE SPANISH K/T BOUNDARY SECTIONS: CARAVACA, AGOST, ZUMAYA

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ABSTRACT: Three (hemi)pelagic sections across the Cretaceous-Tertiary boundary in Spain have much in common: all three show a 1-2 mm "ejecta" rich lamina at the K/T boundary, which coincides with the mass-extinction level of large Cretaceous Planktonic foraminifera. The extinction in all three sections is within 1/2 mm of section. It is not preceded by a decline in species abundance, a decrease in carbonate content or a major trace element pattern change. This 1/2 mm translates -via (local) Cretaceous sedimentation rates- in an extinction within 10 years. Most likely it took place as a single event, although some simple morphotypes continue for a while in the overlying boundary clay. The "ejecta" lamina contains the -probably direct- aerial fall-out products of a single or multiple impact event: all three contain about the same iridium concentration; 35±5 ppb. All three contain diagenetically altered microtektites of similar size, about 0.4-0.5 mm. All three contain Mg-Al-Cr rich quenched spinels. Such spinels are extremely rare in terrestrial rocks. They probably originated within a molten mixture of basaltic (ocean floor) target rocks with a 10% of meteorite, which quickly cooled off to form quenched crystals. The repopulation by the new Paleocene forms appears more abrupt in the new KT section near Agost than previously assumed. At 6.5 cm (± 2500 kyr) above the impact ejecta layer the repopulation takes place within 0.5 cm (± 200 yr). Almost all species known from the Eugubina Zone appear at almost the same time, which implies that the initial speciation from an -as yet unknown- ancestor must have taken place elsewhere. Magaritz et al., reported a FAD of G. eugubina well below the extinction horizon in the Negev of Israel (HorHaHar and Ein Mor sections). This outlier of the Tethys could have been one of the hypothesized refugia where the (allopatric) speciation of Paleocene forms may have taken place. Unfortunately these shallow marine KT sections were bioturbated to such a degree (numerous crab remains and burrows were found) that LADs and FADs of Cretaceous and Paleocene plankton, and the eventually once present boundary clay were homogenized over several decimeters. The LAD of Cretaceous plankton was even smeared over 1 m up section. Just the lack of bioturbation at K/T time in all three Spanish sections allows the inference of an abrupt extinction followed by rapid evolution of new plankton species. However, the latter only after the extinction of the dominant Cretaceous planktonics.



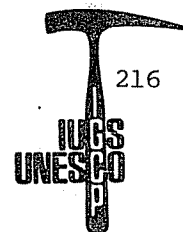
III JORNADAS DE PALEONTOLOGIA
PALEONTOLOGIA Y EVOLUCION: FENOMENOS DE EXTINCION

SPECIES DURATION AND EXTINCTION PATTERNS IN CENOZOIC NON-MARINE OSTRACODA,
WESTERN UNITED STATES

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ABSTRACT: About 250 species of non-marine Ostracoda appeared and, for the most part, became extinct during the approximately 65 million years of the Cenozoic Era in the western United States. Lacustrine sequences containing the ostracode faunas in the Colorado Plateau and Great Basin total as much as 10000 m. Important new appearances occurred in early Paleocene, Late Paleocene?-early Eocene, late Eocene-early Oligocene?, late Oligocene?-early Miocene, and late? Pliocene Epochs. Major extinctions took place in the late Eocene, late Miocene and post-Pliocene Epochs. Duration of individual species appears to have been of the order of one to five million years, but evidence for both shorter and much longer species duration also exists. More highly ornamented species had typically shorter life spans than did the simpler forms. Climatically and tectonically controlled onset of lacustrine conditions and the rapidity with which eutrophication developed was mainly responsible for the appearance of new populations. Modification of the populations and their demise seems to have been largely the result of volcanic activity, progress toward alkaline or saline conditions, prevailing temperatures, and other environmental factors. Homeomorphic series of species comparable to, but not matching in age, those of Chinese Cenozoic lake sequences can be recognized.



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EL EVENTO KAČAK-OTOMARI Y SU CARACTERIZACION EN EL DOMINIO PALENTINO (ZONA CANTABRICA, NO DE ESPAÑA)

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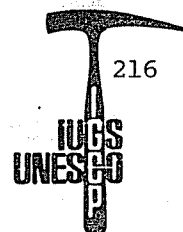
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RESUMEN: El estudio de eventos constituye una actividad de gran aplicación en correlación y cronoestratigrafía. Faltan, empero, definiciones inequívocas de los distintos tipos de eventos y hasta del propio concepto de "evento". La denominación de los fenómenos no contribuye tampoco a aclarar su naturaleza. Se propone identificarlos mediante términos litoestratigráficos correspondientes a unidades y localizaciones donde se manifiesten con especial claridad. Se analiza el notable grado de ambigüedad e imprecisión que existe en torno al bioevento devónico Kačak-Otomari. En el Dominio Palentino, la mejor caracterización de dicho suceso sería entre la extinción de Pinacites, en una secuencia de pizarras negras, y la proliferación de nuevos ammonoideos (especialmente Cabrieroceras spp. y Sobolewia), en las calizas del Miembro Man, fenómeno desarrollado a lo largo de un ciclo T-R. La aparición del suborden Tornoceratina, que suele asociarse con el mismo fenómeno, se registra en Palencia en una pulsación transgresiva claramente diferenciada de la anterior. Esto indicaría que debe tratarse de un bioevento distinto, con gran potencial como límite estratigráfico o como herramienta de correlación.

ABSTRACT: The study of Geological events constitutes an activity of the maximum importance in solving correlation and chronostratigraphical problems. Nevertheless, accurate definitions for the various types of events and also for the "event" concept itself are lacking. Even the way in which the various events are denominated does not help either to clarify their nature. Identification using lithostratigraphical terms corresponding to the settings and units where they develop is proposed here. The remarkable vagueness and inaccuracy around the Kačak-Otomari event is discussed. Within the Palentine Domain, the event is best characterised between the Pinacites extinction, in a black-shale succession, and an important ammonoid radiation (mainly of Cabrieroceras spp., and Sobolewia), in the Man Member limestones. This event corresponds there to an almost complete T-R cycle. Appearance of the suborder Tornoceratina, coupled usually with the Kačak-Otomari event, occurs in Palencia in a later transgressive pulse; this would indicate a different bio-event with a great potential value as stratigraphic boundary or correlation tool.

Deciphering biological catastrophes in the past:
a key for planning the future.

WALLISER, Otto H. *



It will be given a report about the goal and activities of the IGCP Project 216 "Global biological events in earth history". After three years of international cooperation, the state-of-the-art is the following: global bio-events are manifold in respect to causes and extent. Three main patterns can be recognized:

- (1) Innovation-events, which show a rapid spreading and diversification of new constructive achievements;
- (2) Radiation-events, documenting short phases of adaptive diversification by an increased evolutionary rate;
- (3) Extinction-events, indicating a high rate of extinctions either stepwise within a short phase or simultaneously and sudden. The extinctions may happen in only one ecological level or comprise several to many ecological realms.

Probable causes for the global bio-events are

- (1) Cosmic causes, such as (1a) changes caused by the revolution of the solar's system within the galaxy or (1b) impacts of cosmic bodies. In both cases a certain cyclicity must be assumed.
- (2) Earth-born causes, such as
 - (2a) biological causes, as for example biological innovations; those may have played an important role especially in the early history of the evolution (e.g. innovation of photosynthesis, of bisexuality, of mineralization, etc.)
 - (2b) Geological causes, of which the following are of great importance: changes of sea-level, of the ocean water chemistry, of the oceanography, of the atmosphere chemistry and of climate, as well as extraordinary volcanic activities.

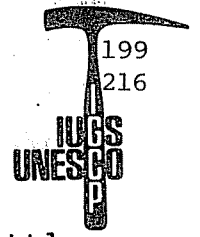
The phases of major or mass extinctions play an important role for the evolution. Causing ecological niches, they trigger an increase of the evolutionary rate, documented by also relatively short phases with radiations.

The investigation of global bio-events leads

- (1) to a high-resolution event-stratigraphy;
- (2) to the recognition of regularities -- or even to natural laws -- in respect to long-term processes which, at the one hand, lead to global changes or which, on the other hand, are triggered by global events. This concerns the interdependency of processes within and between the biosphere and the geosphere. In so far, the event-investigation is of great importance for a sensible planning of mankind's future.

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The Maastrichtian molluscan fauna recovered from Zumaya,
Spain: a status report.



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Introduction

The asteroidal impact theory proposed by Alvarez et al (1980) to explain the terminal Cretaceous extinctions has been the target of skeptics for almost a decade. In spite of the best research efforts of many workers, however, the idea of some sort of extraterrestrial impact as the cause of the widespread extinctions marking the end of the Cretaceous Period remains to be disproved, although the hypothesis has evolved somewhat, with many scientists now favoring multiple impacts ("comet showers"), with resultant "step-wise" extinctions. Three facts have kept "non-impacters" on the defensive: 1. The geochemical signature and associated glassy spherules found at most K-T boundaries cannot yet be explained by terrestrial causes, such as volcanism, in spite of great efforts in this area of research. 2. There was indeed a great mass extinction during the Maastrichtian Stage of the Cretaceous, with marine plankton showing the greatest decline very close to the boundary in the most complete stratigraphic sections. 3. Complete stratigraphic sections with the K-T boundary are usually characterized by a pronounced lithologic change immediately above the K-T boundary.

Paleontological research continues to play a major part in the K-T extinction controversy, and indeed the only major retreat of the Alvarez hypothesis has been caused by paleontological

findings. The Alvarez hypothesis as originally formulated demanded that the majority of latest Cretaceous extinctions were directly caused by the impact of a single bolide, estimated at about 10km diameter. Disputes concerning the final appearances of groups disappearing before the impact (the controversy surrounding the "last" dinosaur, for instance), were argued on the basis of preservation potential and stratigraphic completeness. It seems logical that the larger and rarer the organism, the less likely that final occurrences will be found at the boundary itself. Paleontologists have now examined many boundary sections in minute detail (and in my mind, the greatest accomplishment of the impact hypothesis has been the tremendous increase in knowledge of latest Cretaceous biostratigraphy as a by-product of more detailed sampling and study). These studies have shown that extinctions during the Maastrichtian were not clustered immediately before the terminal Maastrichtian event that produced the well-known, iridium-rich clay layers. Instead, discrete intervals of extinction prior to the final "event" have been recognized in both macro- and microfossils (Alvarez et al, 1984, for summary). The major problem here is stratigraphic and sedimentologic. Extinction "steps" can be produced by the removal or non-deposition of strata in a local section. The notorious difficulty of recognizing diastems in sedimentary sections puts the burden of proof for "stepwise" extinctions into the domain of the sedimentologist.

Two avenues of research continue to be explored by paleontologists working on the K-T extinction problem. First,

the exact biostratigraphic levels of taxa need to be further documented. Although this process is well-advanced for microfossils, it is less well known for macrofossils. This type of work can only be done by patient, detailed collecting. Secondly, paleontologists will look at the history of both surviving and terminating lineages with the goal of determining whether any, or many groups "saw the extinction coming". As extinction is the fate of all species, the null hypothesis to the impact theory is that the terminal Cretaceous extinctions had a terrestrial, ecologically driven cause. If major players in the K-T drama showed recognizable trends or ecological shifts prior the boundary, it can perhaps be argued that extraterrestrial causes for extinction need not be invoked.

In this short contribution I propose to examine information about ammonites and their relation to the terminal Cretaceous extinction. As my information comes from limited collecting from a single stratigraphic section, located in Zumaya, Spain, I will not attempt to make generalizations about the relation of ammonites and the K-T boundary. Rather, I will summarize current information.

The role of the ammonites in the controversy

Ammonites are perhaps the most important of the larger macrofossils to have disappeared at the end of the Cretaceous. In spite of vigorous investigation of supposedly "complete" sections, however, it is still unclear exactly when the ammonites did disappear. I have argued elsewhere (Ward, 1983, 1986) that the ammonites, shelled cephalopods common in Paleozoic and Mesozoic seas, showed marked shifts in morphology (and therefore

presumably in ecology), prior to their Cretaceous demise. These shifts included an increase in heteromorphic forms, and a reduction in shallow water, moderately to highly ornamented species characterizing the middle parts of the Cretaceous. Available evidence (facies distributions and functional morphology studies) suggests a shift towards deepwater habitats for most ammonites. Among those species staying in shallow water, an increase in streamlining and swimming efficiency can be observed. In terms of the tempo of extinctions near the end of the Cretaceous, the most pronounced ammonite extinctions of the Late Cretaceous occurred during the Campanian, not the Maastrichtian.

Information about the last ammonite occurrences currently comes from three areas: the Danish chalk sections (Birkelund, 1979), Antarctica (Macellari, 1986) and Zumaya, Spain (Ward et al, 1986). Additional information will soon be forthcoming from work in progress by Hansen and Kauffman at the Brazos River, Texas, sections.

The careful collecting of Birkelund in the chalk sections at Stevns Klint showed that a fairly diverse ammonite fauna (representatives of seven genera) could be collected at levels up to within several centimeters of the fish-clay horizon that marks the K-T boundary at Stevns Klint. Birkelund's use of ammonite protoconchs for biostratigraphic data was a pioneering effort, which greatly increased the resolution of ammonite datum surfaces. The supposed synchronicity of the final ammonite levels with the actual K-T boundary (Birkelund, 1979) is still

problematical, however. The Stevns klint section was deposited in fairly shallow water, and has discontinuities and omission surfaces at many levels, including the Cretaceous Tertiary boundary itself. Birkelund and Hakansson (1982) noted that ammonites range up to a hardground "capping the Maastrichtian bryozoan mounds", and that the "fish clay" unit marking the K-T boundary is clearly erosional. The amount of Cretaceous strata removed is unknown. Depositional rates in this section were fairly slow, thus marring resolution. A more favorable area of study in this depositional area would be the section at Nye Klov, located more centrally (and deeper) in the basin. Unfortunately, the ranges of ammonites in this section are not documented in the literature. Based on the Stevns Klint evidence, ammonite existed in the Danish chalk basin certainly for the last million years of the Maastrichtian, and probably during the last 100, 000 years. Beyond that, however, no estimate can yet be made.

The ammonite fauna found at Stevns klint is dominated by baculitids and scaphitids. Other common cephalopod fossils include belemnites. Nautiloids are either rare or absent. An unfortunate aspect of the chalk lithofacies of Stevns klint is the scarcity of planktonic foraminifera. These fossils are now considered the best means for intercontinental correlation of the Maastrichtian Stage. Unfortunately, the ammonite occurrences at Stevns klint are not correlated with the internationally recognized planktonic foram zones.

A second area where the ranges of ammonites immediately beneath the K-T boundary are well - documented is Seymour Island in Antarctica. The careful, detailed collecting of Carlos

Macellari (1986) has yielded a good record of Maastrichtian ammonites. These ammonites are exquisitely preserved with their original aragonitic shells unaltered by post-death diagenesis. The ammonites at Seymour Island are numerically dominated by members of the family Kossmaticeratidae. Very few ammonites from Seymour Island Ross co-occur at Stevns klint.

Although it is clear that most of the Maastrichtian Stage is represented on Seymour Island, it is impossible to know if the section is complete at the K-T boundary because of a lack of information about microfossil zones in this section. Macellari (1986, and pers. comm.) believes that the section is complete or virtually so. He noted (1986) that ammonites (of his uppermost Pachydiscids ultimus Zone) have been collected to within several centimeters of the proposed K-T boundary. As at most other K-T sections the boundary at Seymour Island co-incides with a lithological change. Without more precise information about planktonic foram zones, however, the relationship of ammonite ranges and the K-T boundary cannot be determined at this time.

Ammonite occurrences at Zumaya, Spain

Ammonites from the seacliff exposures at Zumaya, Spain, have been studied since the 1960's by Prof. Jost Wiedmann and his students. In 1982 I was invited to recollect this exposure in the company of Dr. Wiedmann. Since that time I have made two additional collecting trips to Zumaya. The results of these trips included reports on the limestone-marl lithofacies (Mount and Ward, 1986), the oxygen and carbon isotopic ratios of the strata (Mount et al, 1986), and the ranges of macrofossils

collected during the three trips (Ward et al, 1986). All three of these contributions were offered as preliminary reports only. The Zumaya exposures turn out to be an excellent reference section both for documenting late Cretaceous macrofossil stratigraphy as well as yielding valuable information about the patterns of extinction immediately prior to the K-T boundary.

The seacliff exposure near Zumaya contain a conformable sequence of Upper Cretaceous and Lower Tertiary marine strata. These strata were deposited in the Flysch Trough of the Basque-Cantabric Basin (Lamolda et al, 1981). This basin was one of several forming along the boundary of the European-Iberian Plates during the Late Cretaceous. During the Campanian and Early Maastrichtian ages, sediments deposited in this basin were mainly of turbidity current origin. During the Late Maastrichtian there was a change in depositional patterns, caused by a both a reduction in siliciclastic material influx, as well as basin-wide shallowing and regression (Lamolda et al, 1981). The result is that Lower Maastrichtian flysch is overlain by Upper Maastrichtian limestone-marl rhythmites (Mount and Ward, 1985). Sedimentation rates dropped, with Lower Maastrichtian accumulation rates estimated at 200 bufnoffs (m/m.y., compacted) compared to 60 to 80 bufnoffs (m/m.y., compacted) for the Upper Maastrichtian. Immediately following the K-T transition there was an even more dramatic reduction in siliciclastic influx into the basin, resulting in the deposition of pink coccolith limestones during the Danian

The measured section for the stratigraphic studies of Mount and Ward (1986) and Ward et al (1986) extends upward from the

waterfall locality to the K-T boundary. The Waterfall locality roughly corresponds with the changeover from flysch to limestone-marl. The section is 240m thick. Mount and Ward recognized two principle lithofacies groups: 1) light colored limestone-marl rhythmites, and 2) a dark red to purple marl. These lithofacies are approximately equally distributed in three cycles, culminating at the K-T boundary (Fig. 1). In general, the purple marls are erosionally recessive compared to the limestone-marl lithofacies. As the strike of the Zumaya beds is perpendicular to shoreline, the geography of the region is strongly controlled by lithology.

Macrofossil biostratigraphic patterns

The Zumaya exposures are of importance in revising Maastrichtian biostratigraphy for the following reasons. First, there is 100% exposure of outcrop. Secondly, macrofossils, while not abundant, can be collected from virtually any part of the measured section of fig.1 given enough effort. Third, there is a good understanding of the ranges of microfossils from the section, allowing integration of planktonic foram zones (Herm, 1965), nannofossil zones (Percival and Fischer, 1977) and molluscan macrofossils. On the basis of their collections, Ward et al (1986) proposed a three zone scheme for the upper 240m of Cretaceous section at Zumaya (fig.2). One of these zones is upper Lower Maastrichtian, while the other two are Upper Maastrichtian. Details of this proposal are found in Ward et al, 1986.

Two findings from the Zumaya section merit discussion. First, we showed that inoceramids disappear at the top of the

Lower Maastrichtian. Although an inoceramid-like bivalve (Tenuipteria) is found in the uppermost part of the Zumaya Maastrichtian section, true inoceramids (Inoceramus, Endocostea, Platyceramus) can be found only in the Lower Maastrichtian. All are gone by the start of the A. mayaroensis foram zone. This is not a case of collection failure. Inoceramids are common in the upper part of the Lower Maastrichtian at Zumaya: they virtually form pavements along bedding planes. Specimens up to a meter in length are common. Their disappearance coincides with a lithological change, and their disappearance is quite sudden. Three species are common in the Lower Maastrichtian part of the section at Zumaya; all then disappear over a stratigraphic distance of 40m. The Zumaya pattern may not be unique; I have yet to find any documentation of upper Maastrichtian inoceramids (other than Tenuipteria). If step-wise extinctions are eventually accepted for the K-T extinctions, this may be the first, and perhaps most important "step".

The disappearance of the inoceramids coincides with faunal turnover among the ammonites as well. The well known Lower Maastrichtian ammonite fauna with Hauericeras and Pseudophyllites disappears at this point, while the first of the Upper Maastrichtian pachydiscids, including Anapachydiscus fresvillensis, appears.

The uppermost ammonite faunule, found in the upper 25 m of the Zumaya Cretaceous section, is also of interest. There are two episodes of extinction in the upper part of the Zumaya section, one at about 40 m below the K-T boundary, with disappearance of five species of ammonites, and a second at about

20m below the boundary, with the disappearance of three more species which had been long-ranging in the section (fig 2). It is above this last extinction episode that the uppermost faunal first appears. It is composed of Pachydiscus colligatus (sensu Seunes; Kennedy, in press, has determined that P. colligatus ss is a Campanian form, and that P. colligatus sensu Seunes, found only in the uppermost part of the Maastrichtian in several parts of the world is a different taxon. Kennedy will be revising this nomenclature). The other ammonite found in this faunule is Vertebrites sp., also known from uppermost Maastrichtian deposits elsewhere.

One of the most interesting findings of the Zumaya work to date has been the 12m gap in ammonite occurrences at the top of the Cretaceous section. A great deal of effort has gone into collecting this upper part of the section. Only a single fragment of cephalopod has been found, within a meter of the K-T boundary. This specimen is tiny (about 1cm diameter), incomplete, and is so poorly preserved that it is impossible to determine whether it is an ammonite or nautiloid. Other macrofossils can be recovered (echinoids, Tenuipteria) but other cephalopods have eluded recovery so far. Perhaps this will change in the light of new collecting about to start at Zumaya.

The absence, or at least rarity of ammonites in the uppermost ten meters or so of the Zumaya section has created some controversy. If this finding holds, it indicates that ammonites disappeared in this area well before the K-T boundary. Based on sedimentation rates, this disappearance was a minimum of 100 to

200,000 years before the K-T boundary event. There are certainly mitigating circumstances. The final 15 to 20 m of Cretaceous section occurs in a strongly recessed bay. The strata are purple marls; their orientation is such that bedding planes cannot be observed. Jan Smit (pers. comm.) has argued that the absence of ammonites in this part of the section is due to collection failure only, because of the different mode of stratal exposure in this part of the section. This is certainly a possibility. It is harder to collect from this lithofacies, and ammonites are found much more easily on bedding planes than on exposures (such as the final 15 to 20 m of the Cretaceous section at Zumaya) striking perpendicular to coastline. It should be noted, however, that an identical lithofacies and regressive coastline lower in the section has yielded numerous ammonite specimens. Further collecting will hopefully clear up this controversy.

One of the most curious aspects of the Zumaya ammonite fauna is not so much what is present, but what is not. Studies on the nearby chalk faunas of France (Kennedy, 1986,) and in the Petite Pyrenees (Kennedy et al, 1986) show ammonite faunas dominated by numerous baculitids and Hoploscaphites constrictus. Although baculitids are fairly common at certain levels low in the Zumaya section, scaphitids are rare or absent. The Zumaya fauna is numerically dominated by tetragonitids and pachydiscids.

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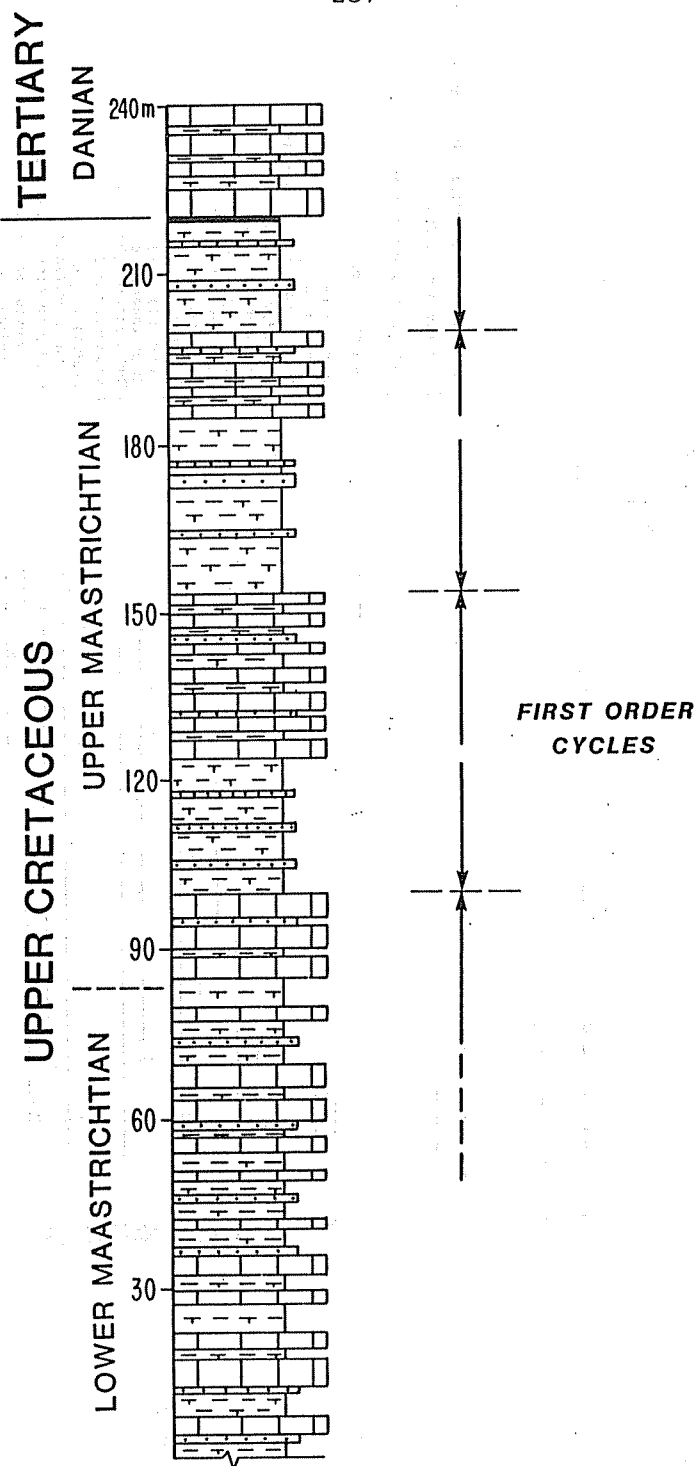


FIG. 1 — Stratigraphic section of the uppermost Lower Maastrichtian through lowermost Danian at Zumaya, Spain. First-order cycles, illustrated here, are composed of a basal half-cycle consisting predominantly of marl which is overlain by an upper half-cycle consisting of interbedded limestone/marl (see text for explanation). Thin, calcareous sandstones are interbedded throughout both half-cycles. Thickness in meters.

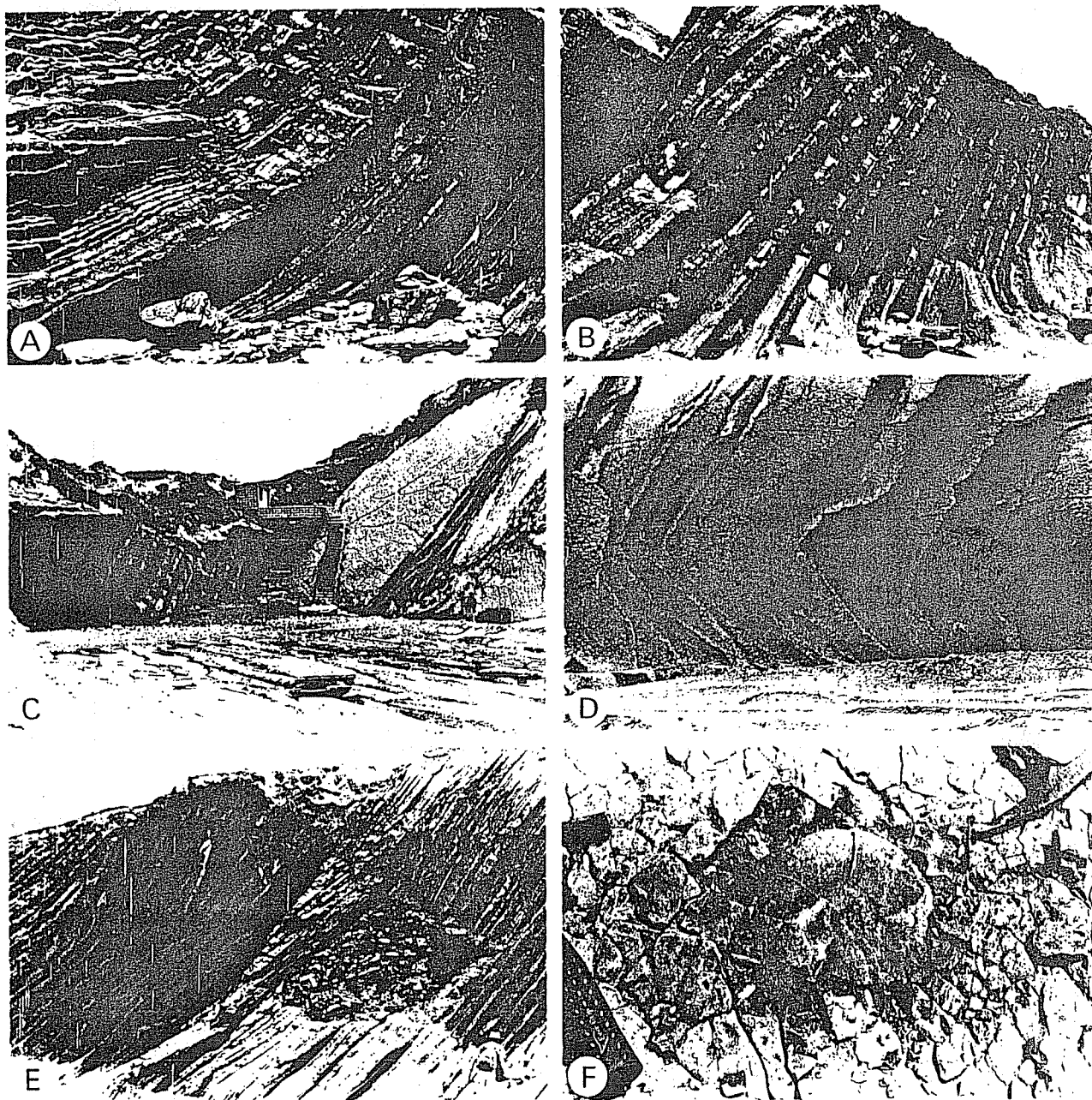


Fig. 3.- Lithologies at Zumaya, Spain. A. Cretaceous-Tertiary boundary. B. 20-40 meters below K-T boundary. C. Stairwell access, Zumaya beach. D. Bedding planes exposed 60 m below K-T boundary. E. Lower Maastrichtian portion of Zumaya section. F. Typical ammonite preservation.

III JORNADAS DE PALEONTOLOGIA
PALEONTOLOGIA Y EVOLUCION: FENOMENOS DE EXTINCION

THE CRETACEOUS-TERTIARY BOUNDARY EVENT OF TIBET

WAN Xiaoqiao

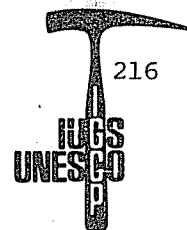
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ABSTRACT: The marine Cretaceous-Tertiary boundary occurs over a widespread area in southern Tibet, as well as in the Gangdisê Mountains in Northern Tibet. The uppermost Cretaceous layer is the Zongshan Formation, and the Tertiary strata can be divided lithologically into the Jidula Formation, the Zongpu Formation, and the Zhepure Formation. The key in locating the Cretaceous-Tertiary boundary lies in the age of the Jidula Formation. Recently some new Bivalvia, Ostracoda and Foraminifera have been found in the Jidula Formation, testifying that it was deposited in the Paleocene. The fossils found in the Jidula Formation are different from those in the underlying Zongshan Formation, and identical to those in the overlying Zongpu Formation. Both contacts are conformable. The change in fossil groups coincides with the evolution of life between the Cretaceous and Tertiary. Thus, the Cretaceous-Tertiary boundary is in between the Zongshan Formation and the Jidula Formation. Some stratigraphers believed that "the Jidula sandstone" is synchronous with the Pab sandstone in Pakistan.

In the author's opinion, deposits formed in transgression of regression tend to be diachronous. It has been demonstrated that the sandstone formed in the Lower Indus Basin during the Middle Maestrichtian, and in the Upper Indus Basin during the Late Maestrichtian. It extends across the boundary of the Cretaceous-Tertiary in the Zongba region, and belong to the Paleocene in Gamba and Tingri. The age of the sandstone becomes younger and younger along the direction of regression (Fig. 1). The "mass extinction" event at the end of the Cretaceous period is very clear, especially in the case of Foraminifera. The history of the Tethys-Himalayan Sea during the Late Maestrichtian is marked by a regression. The analyses of foraminifera biofacies including the statistics of the number of species, and Oxygen and Carbon isotope measurements of foraminiferal tests give a picture of environmental fluctuations. At the end of the Maestrichtian, a regression started in both the East and West, and withdrew towards the Gamba-Tingri Basin. The regression gave rise to the deposition of sandstone of varying thickness in the entire Himalayan region. The temperature of the sea was changeable. The Cretaceous Foraminifera, especially planktonic and larger forms extinct at this period. The regressive stage was followed by the Danian transgression. The environment became suitable for new foraminifera groups, which burst even more abundantly (Table 1). The conclusion of the author is that the Foraminifera were "victims" of the late Maestrichtian regression and the temperature change, involving the near-synchronous global annihilation of numerous taxa, which was a biological catastrophe in the marine realm.

fossils	age	Maestrichtian	Danian
<i>Fraeglobotruncana anomala</i> Wan			
<i>Heterohelix globulosa</i> (Ehrenberg)			
<i>H. cordatus</i> Wan			
<i>Globotruncana coronata</i> Bolli			
<i>G. stuartiformis</i> Dalbliez			
<i>Orbitoides tissoti</i> Schlumberger			
<i>O. media</i> (d'Archiac)			
<i>O. apiculata</i> Schlumberger			
<i>Omphalocyclus macroporus</i> (Lamarck)			
<i>Rotalia dukhani</i> Smout			
<i>R. conoidalis</i> Wan			
<i>R. crassata</i> Wan			
<i>R. fornicata</i> Wan			
<i>R. hensoni</i> Smout			
<i>R. lenticularis</i> Wan			
<i>R. orientalis</i> Cushman et Bermudez			
<i>R. pinarensis</i> Cushman et Bermudez			
<i>R. plana</i> Wan			
<i>R. trochidiformis</i> Lamarck			
<i>R. venusta</i> Hu			
<i>Lockhartia altispira</i> Smout			
<i>L. conditi</i> (Muttal)			
<i>L. cushmani</i> Applin et Jordan			
<i>L. haimel</i> (Davies)			
<i>L. hunti</i> Ovey			
<i>L. megapulata</i> Hu			
<i>L. tipperi</i> (Davies)			
<i>Smoutina corpuscula</i> Hu			
<i>S. cruyssi</i> Droogei			
<i>S. grandis</i> Wan			
<i>Keramosphaera tergestina</i> (Stache)			

Table 1, The Range Chart of Foraminifera at the Cretaceous-Tertiary Boundary of Southern Tibet



III JORNADAS DE PALEONTOLOGIA
PALEONTOLOGIA Y EVOLUCION: FENOMENOS DE EXTINCION

EVENTOS INTRINSECOS VERSUS EXTRINSECOS EN LA EVOLUCION DE LOS OSTRACODOS MESOZOICOS

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RESUMEN: El registro de la distribución, origen y extinción de todas las especies de ostracodos mesozoicos permite ilustrar las fluctuaciones más importantes en la evolución, así como de la diversidad de las especies. En varios casos, hay importantes cambios en la actividad evolutiva y/o diversidad específica, que parecen estar relacionados con límites estratigráficos durante el Mesozoico y/o con eventos geológicos globales. Ejemplos de ésto, pueden verse en los límites entre el Triásico y Liásico, el Tithónico y Neocomiense, el Neocomiense y Aptienense y el Albiense y Cenomaniense. En otros casos, los incrementos en la velocidad de la evolución y en la diversidad específica, parecen estar relacionados con la adquisición evolutiva de caracteres más sofisticados, en particular aquellos relacionados con la articulación de las valvas y con la mejora de la capacidad sensorial. El advenimiento de la charnela entomodonta en el Jurásico medio, el fuerte aumento del número de especies con charnela anfidonta en el Cretácico y del incremento en el número de poros radiales anteriores, que se observa en varios linajes, son buenos ejemplos de lo referido.

ABSTRACT: By recording the stratigraphical distribution, origination and extinction of all ostracod species throughout the Mesozoic, it is possible to illustrate major fluctuations in evolutionary activity and in specific diversity. In many instances marked changes in the level of evolutionary activity and/or species diversity appears to correlate with major Mesozoic stratigraphical boundaries and/or global geological events. Examples of these, often dramatic changes, can be seen at the Triassic-Liassic, Tithonian-Neocomian, Neocomian-Aptian and Albian-Cenomanian boundaries. At other times, enhanced rates of evolution and species diversity seem to be associated with the evolutionary acquisition of more sophisticated bio-characters, particularly those associated with carapace articulation and improved sensorial ability. The advent of the entomodont hinge in the Middle Jurassic and the dramatic increase in species with amphidont hingement in the Cretaceous, together with the increase in many lineages in the number of anterior radial pore canals, provide good examples.

THE BASQUE COASTAL SECTIONS OF THE CRETACEOUS-TERTIARY BOUNDARY.
A KEY TO UNDERSTANDING MASS EXTINCTION IN THE FOSSIL RECORD

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The coastal section of Zumaya, province of Guipúzcoa (Spain), is one of the best sections to study and to elucidate the K/T boundary problem. It fullfills the following premisses

- (1) sedimentary completeness across the boundary
- (2) no facies change at the boundary
- (3) predominance of pelagic and nearly complete absence of turbiditic sedimentation in the boundary layers
- (4) sedimentation above CCD and probably also above ACD
- (5) relatively high sedimentation rate, important for biostratigraphic resolution
- (6) presence of macro- and microfossils throughout the section, and
- (7) absence of tectonics in the boundary layers.

For the present purpose the macro-invertebrate, mainly ammonite fauna of the Maastrichtian, was investigated, thereby allowing the determination of a Maastrichtian ammonite sequence based on stratigraphic evidence. The problem of "mass extinction" at the K/T boundary was studied and found to contradict the much propagated picture of a single cosmic catastrophe at the boundary itself.

Ammonites - as well as inoceramids - show a gradual decline through the late Maastrichtian. Only 7 ammonite species can be recorded from the last ammonite-bearing level, but this level is still 12.5 m below the boundary itself. This means that the final decline of ammonites occurred - with one exception - about 130.000 years before the so-called Iridium Event. Similar observations were made on the decline of inoceramids. Only the turnover in calcareous nannoplankton and planktonic foraminifera remains fixed to the boundary level as was stated previously. But it needs to be stressed that no boundary clay is present at Zumaya nor iridium has been detected.

To elucidate the importance of the Zumaya section, a short review of the other available K/T boundary sections may be useful, especially since they are very restricted in number. A large number of these sections is highly pelagic in nature and up to now devoid of any macro-invertebrates (e.g., the DSDP-ODP cores in the Atlantic, the Caravaca section in southern Spain, the Lattengebirge, Northern Calcareous Alps, or the Gubbio section in which the iridium anomaly was detected first, but interestingly not confirmed later on). The nearby section of Sopelana, province of Biscay, is unfortunately tectonized; these tectonics were the reason for the previous record of "Tertiary" inoceramids. In the likewise nearby Biarritz section macro-invertebrates have not been investigated so far. If, however, macro-invertebrates are present (e.g., the Maastrichtian sections, the Danish boundary sections at Stevns Klint and in northern Jylland, and even the very thick Vistula River section in Poland) condensation and redeposition are widespread near the boundary.

There are four possibly important sections from which macro-invertebrate records are available at least from the early Maastrichtian. This is obviously due to incompleteness of the section in case of the Krappfeld Gosau Beds, Carinthia, as well as the Quiriquina Beds in Central Chile. The proposed "hypostratotype" for the K/T boundary at El Kef, Tunisia, is complete but devoid of macro-invertebrates in the upper, more interesting portion. The same can be stated for the Agadir section, Morocco. Whether the recently described Maastrichtian ammonite sequence of Seymour Island, Antarctica, is complete towards the top or not, is very difficult to decide due to the high percentage of endemic species.

From this brief review the importance of the Zumaya section is stressed again. It can now be added to the information available from the Zumaya section that also the decline of belemnites - restricted to the Temperate Maastrichtian - is found to be gradual; belemnites, however, seem to have persisted into the uppermost Maastrichtian levels.

In addition to ammonites, belemnites and inoceramids, the extinction pattern of marine and terrestrial reptiles is also by no means catastrophic but likewise gradual; most of them experienced their final decline before the end of the Cretaceous.

"Mass extinction" or better turnover at the K/T boundary can therefore drastically be restricted to the groups of oceanic surface plankton (calcareous nannoplankton, foraminifera) and maybe to some angiosperms (the Aquilapollenites Province), in case stratigraphic correlation is correct.

There are, however, a few groups of invertebrates flourishing at the time of the "boundary event". These are bryozoans and specialized crinoids as recorded from the K/T boundary beds of Jylland, Denmark. Since both groups are very sensitive to changes in salinity and oxic conditions, these two factors can now be ruled out from having contributed to the K/T boundary event.

Peaks of increasing and decreasing temperature were recorded from the boundary level. If their interpretation is correct, these could be related, indeed, with the presumed impact, but they are again unrelated with the gradual decline in most macro-invertebrates and vertebrates.

But one of the main problems still remains: the interpretation of the iridium concentrations. These concentrations seem to be restricted to those sections in which boundary clays are developed. In most cases this clay was deposited under starved conditions. In this case, however, natural sources of iridium precipitation are available and there is no need of its cosmic origin.

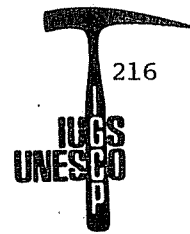
Since ammonite decline is not only gradual but also fluctuating in nature - if the Cretaceous or the whole course of ammonite evolution is considered - one has to look for other causes than catastrophic events. Periodic events paralleling the course of ammonite diversity through time are, however, sea level changes which, indeed, have played a major role in the late Mesozoic. The above-mentioned faunal decline both on the marine shelves and on the nearby continental borders can be related with the very pronounced late Cretaceous sea level fluctuations without difficulty.

Obviously, the problem of turnover in the marine surface plankton requires a special treatment since it seems to be more or less instantaneous. Whether it was the consequence of a cosmic impact and/or fluctuations in temperature at the boundary level itself, cannot be decided with certainty so far. From the available observations we can conclude that the faunal and floral break at the K/T boundary was most probably not a monocausal phenomenon, but the result of a more complex scenario of both fluctuating and instantaneous factors.

These observations are moreover in agreement with the conclusions we have drawn some time ago in revising ammonite evolution across the Mesozoic System boundaries:

Summarizing the result on all these boundaries it can be demonstrated that there is neither an abrupt and world-wide extinction, nor a spontaneous replacement by new elements at these caesuras as had been generally supposed to have occurred at the Triassic-Jurassic boundary, for example. Instead, one can recognize three distinct phases in the sequence of events: (1) a continuous disappearance of the "antique" faunal elements; (2) a similarly continuous, gradual, and largely synchronous appearance of, or substitution by, qualitatively distinguishable "modern" elements in small populations, yet in various parallel lineages (mosaic evolution); (3) a quite revolutionary, and quantitatively very sudden, diversification of these new elements, occurring at or with some delay above the boundary.

Thus one can demonstrate both continuous evolution of the modern faunas ("preadaptational phase"), as well as "discontinuous" spontaneous revolution, which does not produce qualitatively new characters and must be explained by diversification or adaptive radiation. This means that no further explanation by internal factors or by higher mutation rates resulting from the impact of cosmic rays becomes necessary. It is believed that, preceded by high extinction rates, world-wide ecological factors promoting higher niche diversity suffice to explain these adaptive radiations. The high degree of provincialism, endemism and specialization of the "antique" faunas and the constant survival of smooth oxycones - regarded as inhabitants of a deep-sea environment - demonstrate that marine regressions and transgressions were the most effective ecological factors.

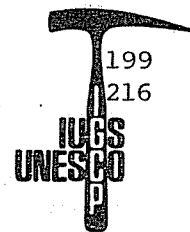


III JORNADAS DE PALEONTOLOGIA
PALEONTOLOGIA Y EVOLUCION: FENOMENOS DE EXTINCION

VERTICAL ADVECTION FROM PYCNOCLINAL AND DEEPER WATERS. A MECHANISM FOR RAPID EVOLUTIONAL CHANGE.

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ABSTRACT: The main biomass of the ocean is in the surface wind-mixed layer (0-100 m depth), dependent on light or primary production based on photosynthesis. Waters from the main pycnocline (100-1000 m) or deeper contain decay products which can inhibit photosynthetic growth or are toxic or debilitating to respirors. Global to regional scale vertical advection of such waters into the surface mixed layer could create an environmental crisis for marine groups through reduction of their food supply, direct toxicity, or chronic debilitation caused by contact with such waters. After long duration of cool climates with oxic deep waters, such crises are caused by upwelling of metals concentrated at depth and result in reduced primary productivity as well as metal toxic and chronic reactions. During warm climates with anoxic and potentially sulfidic waters in the pycnocline, the crisis may be the result of anoxic waters with a maximum effect on respirors with minimal to enhanced effect on phytoplankton. The effect will be selective due to the differing limits of toleration of organisms and as a function of the depth of toxic water, surface mixing, duration of upwelling and ratio of upwelled area to natural range.



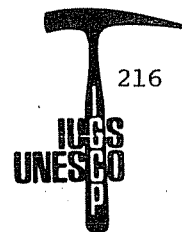
III JORNADAS DE PALEONTOLOGIA
PALEONTOLOGIA Y EVOLUCION: FENOMENOS DE EXTINCION

AN ASTRONOMICAL BACKGROUND TO EXPLAIN THE PERIODIC MASS EXTINCTIONS

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ABSTRACT: Since D.M. Raup and J.J. Sepkoski Jr. raised the question of periodicity of mass extinctions, some astronomers are interested in this phenomenon. Periodic comet showers have been discussed, but what is the original cause of these periodic comet showers? Some people have suggested different models. One of these model is that mass extinctions are caused by a distant solar companion. But where is the solar companion? Here an answer will be given for the last model. From astronomical data, in fact we already know a small star group named Multiple Star. This will be discussed in our paper.



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EARTH'S CATASTROPHE AS A MAJOR DYNAMIC CAUSE FOR EVOLUTION OF ORGANISMS: VERIFICATION AND MECHANISM

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ABSTRACT: Mass disappearances are frequently followed by mass appearances and both are coupled to almost all of inter-Period boundaries throughout the Phanerozoic Eon. Most of these boundaries signal some globally catastrophic events of lithospheric, hydrospheric, atmospheric or even astrospheric origin. Such unique association of biotic events and abiotic events implies a causal relationship between them to a great extent. Mass disappearances, particularly mass extinctions have been largely ascribed to the abiotic catastrophes. The most significantly biospheric effect of catastrophes is, nevertheless, mass appearances, especially mass originations or diversifications. This can be justified not only by many macroscopic statistics, but also by some microscopic scrutinies of stratigraphic sections, particularly those of K-T and P-Tr boundaries that seem to be the optimal candidates for catastrophic events. The argument can be also attested theoretically, because a catastrophic event could create multitudinously different opportunities for evolution of organisms in the catastrophic region. These opportunities come from the undersaturated ecosystem on the one hand, but, more importantly, they come from numerously and variously renewed habitats established directly by the catastrophic events. Both opportunities attain the maximum in the central region, but the abiotic stress is so high that extinctions are commonly far greater than originations in respect of rates. Therefore, this region is predominated by mass disappearances. In the peripheral region, however, higher abiotic stress is in favor of evolution of organisms and all opportunities tend to be optimum. So, mass speciations are prevailing and characterized by the Gigantoevolution. After the event, many organisms would enter the central region where the ecosystem was extraordinarily undersaturated.



