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The Cretaceous-Tertiary Boundary and the Last of the Dinosaurs [and Discussion]

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The Cretaceous–Tertiary boundary and the last of the dinosaurs

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Disaster theories of the K–T extinctions, more specifically dinosaur extinctions, are presently engendering much controversy. They require (*inter alia*) that those extinctions were sudden and simultaneous worldwide and that they coincided with an allegedly causal disaster at the K–T boundary. This paper reviews the evidence for and against those temporal requirements. The other major requirement is of a biological nature, namely an indication of the manner in which the specified disaster might have extinguished the organisms concerned; yet this causal mechanism, whatever it might have been, apparently had no effect whatever upon other, very similar organisms.

In any particular geographical region, the precise stratigraphic level at which dinosaurs became extinct can be determined only if there is a virtually unbroken succession of potentially dinosaur-bearing continental beds that pass up from the level of the highest dinosaur known to a level well above the K–T boundary. Unfortunately there are surprisingly few regions where such conditions prevail. The problem is further complicated by the difficulties of worldwide stratigraphic correlation and by the fact that specialists in different fields define the position of the K–T boundary on different criteria. Although some alleged discoveries of Palaeocene dinosaurs have long been discredited (the beds were not Palaeocene, or the bones were not dinosaurian), there does seem to be some evidence that dinosaurs died out at different times in different places, sometimes surviving whatever it was that produced the iridium anomaly and sometimes co-existing with Palaeocene palynomorphs and Tertiary-type mammals, or both. In such cases it does not seem unreasonable to postulate a Danian age for the animals in question.

Introduction

It is evident that groups of organisms do not die out in an entirely random manner, unaffected by any external causes. If that were so, it would be expected that the rate of extinction, the proportion of all groups dying out per unit of time, would remain fairly constant. On the contrary, at certain times in the Earth's history the number of groups dying out per unit of time appears to be much greater than at others. Such bursts of extinction, if they seem to have taken place within a sufficiently short interval and to have affected a sufficiently wide diversity of organisms, are called 'mass extinctions'. One such mass extinction seems to have occurred at the end of the Cretaceous, more or less on the K–T boundary.

This variability of the extinction rate leads to several questions.

1. Do such 'mass extinctions' actually occur, or are they illusions resulting from imperfections of the fossil record and from our methods of classification?

2. If there are such things as 'mass extinctions', do they take place at regular intervals?

3. What is the manner of extinction of each particular group? Was it sudden, with all its various member-species disappearing simultaneously everywhere? Or was it gradual, with its

member-species dying out at different times? (The actual extinction of any group, of course, be it a single species or a taxon of higher category, must itself be an instant phenomenon; it takes place at the moment of death of the last surviving individual.)

4. What is the reason for each extinction?

It is obvious that to attempt to answer any of these questions, one needs to know when each extinction occurred, not necessarily in absolute terms, but in terms of a standard strato-chronological scale, uniform worldwide, that is just as useful for making comparisons and correlations. In the case of the third question we need to know the time of extinction of each member-species with some considerable precision.

In recent years, special interest has been attached to what might be termed 'disaster theories' of mass extinctions, in particular the end-Cretaceous extinction and, most especially, the extinction of the dinosaurs as part of that extinction. (I prefer the term 'disaster theory' to the more usual 'catastrophe theory' because the latter term has a special, altogether different meaning in mathematics and could therefore be ambiguous when used in a palaeontological sense.)

Archibald & Clemens (1982) defined a palaeontological catastrophe (i.e. disaster) as 'a single event that set in motion a chain of other events, thereby causing major biological changes and extinctions within at most a few thousand years.' The best known of the many such theories is that originally propounded by Alvarez *et al.* (1980) (see also Alvarez *et al.* 1984) in which they suggested that, at the end of the Cretaceous, the Earth was struck by a huge meteorite. They believed that one consequence of this event was the formation of the so-called 'iridium anomaly' in the stratigraphic column; another – so they alleged – was the 'end-Cretaceous mass extinction', dinosaurs included.

I have shown (A. J. Charig, unpublished paper read at the Lyell Meeting of the Geological Society of London and the Palaeontological Association on 'Catastrophes and the history of life', held on 25th February 1987) that, to establish as a credible hypothesis any such theory of the extinction of the dinosaurs, indeed any 'disaster theory', it is necessary to do four separate things.

1. Show that the extinction of the dinosaurs was sudden and simultaneous, worldwide.
2. Show that the time of that extinction coincided exactly with the time of the disaster concerned.
3. Suggest a causal mechanism by which the disaster might reasonably have caused the extinction of the group(s) in question.
4. Explain why that same disaster, that same cause, did not lead to the extinction of other, similar groups of organisms.

This article briefly reviews our knowledge of the timing of the extinction of the dinosaurs in certain parts of the world in terms of the standard strato-chronological scale. Such knowledge is essential to any demonstration of items (1) and (2) above. This includes the question of the relation of the extinction of the dinosaurs to the position of the Cretaceous–Tertiary boundary, in particular the sporadic claims that have been made that dinosaurs survived into the Tertiary.

The Cretaceous–Tertiary boundary

In attempting that task, one great difficulty lies in there being many different ways of defining the boundary, none of them entirely satisfactory. Strictly speaking, the various

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divisions of the stratigraphic column – systems, stages – are defined on the type-sections that stratigraphers have agreed to accept as the global standard for each. Those type-sections, however, are inevitably from different parts of the world, which means that the top of each division is unlikely to coincide exactly with the bottom of the division above; such a succession of disparate type-sections is bound to include many gaps or overlaps between them. We therefore use only *bottoms* in defining the stratigraphical column. Thus, for example, the Permian system runs from the bottom of the Permian type-section (in Russia) to the bottom of the Triassic type-section (in Germany).

A survey of the literature and questioning of my colleagues shows that, in practice, at least five distinct ways of defining the Cretaceous–Tertiary boundary are in common use:

1. *On the fauna and/or flora*

This, the commonest method of stratigraphic correlation, is a somewhat dangerous procedure in so far as it makes one totally unwarranted assumption: that a given species of fossil organism, wherever it appears in the world, is of the same geological age. After all, some species are very long-lived; a species may survive in one part of the world much longer than in another; and its presence or absence may depend very much upon the nature of the local environment. Correlation based upon a single species must therefore be viewed with suspicion. On the other hand, correlation based upon a whole fauna or flora of disparate elements is likely to be more reliable.

2. *On the lithology*

This is even more variable than the palaeontology. It may be employed within a limited area for the recognition of a stratigraphic boundary, but even within such limits it may well be diachronous.

3. *On the geochemistry*

4. *On the 'iridium anomaly' of Alvarez et al.*

Geologists continue to argue as to whether or not this feature is a single, simultaneous, worldwide phenomenon (as well as to whether its origin is terrestrial, i.e. volcanic, or extra-terrestrial).

5. *On magnetic reversals (magnetostratigraphy)*

It is not unreasonable to assume that these at least are simultaneous worldwide. However, it is not always easy to distinguish one reversal from another; to do so may require the use of the adjacent fossils.

Questions put to my colleagues also revealed a remarkable diversity in the methods that they use for dealing with this problem. Those concerned kindly agreed that I might quote them.

C. R. Hill (on Mesozoic plants) states that the terrestrial megaflora passes through the K–T boundary without dramatic change; there is far more change within the Lower Cretaceous and again at the Palaeocene–Eocene boundary. It follows from this that palaeobotanists who study large fossils, wishing to ascertain the position of the K–T boundary, are obliged to use a wide range of fossils from other groups, mostly animal fossils. (On the other hand the calcareous nannoplankton does show a distinct change at that boundary; and, less certainly, some palynologists claim a 'fern spike', a sudden and short-lived abundance of fern spores, at or a little below the K–T boundary.) (Personal communication.)

C. G. Adams (on the Foraminifera) sees a very marked change in planktonic foraminifera and in larger shallow-water benthic foraminifera below the K–T boundary. Whole families disappeared suddenly and simultaneously at the end of the Cretaceous (e.g. the family Globotruncanidae, with about 50 species living at the end of the Maastrichtian). Then, in the Palaeocene, the impoverished fauna was gradually enriched as new forms slowly developed to replace the old ones. Shallow-water foraminifera were affected to a much lesser extent. Adams defines the K–T boundary on the overall marine fauna. (Personal communication.)

E. F. Owen (on Mesozoic brachiopods) reports a situation in his group of animals that is not unlike that of the terrestrial plants. The brachiopod fauna shows no sudden break at the K–T boundary, many genera passing across it with remarkably little change and some persisting even to the present day (e.g. *Crania*, *Terebratulina*). As brachiopods cannot be used in this connexion, and because the lithology is equally useless, fossils from other groups must be employed as indicators of the position of the K–T boundary. Incidentally, observations of the succession in the Netherlands and in Denmark suggest that there was some ecological change at that boundary. (Personal communication.)

M. K. Howarth (on cephalopods) draws the K–T boundary above the last ammonite or belemnite. It is, he says, a less than satisfactory way of drawing a system boundary because it marks the extinction of a group or groups (as evidenced by the fossil record); nevertheless he is forced to use this method for purely practical reasons. The best approach to the defining of a system boundary is, where feasible, to draw it at the first appearance of an incoming fauna. (Personal communication.)

C. Patterson (on Mesozoic fishes) cannot recognize any significant changes in the fossil fishes across the Cretaceous–Tertiary boundary. He is therefore obliged to recognize that boundary upon other elements in the fauna. (Personal communication.)

R. T. J. Moody (on testudinates, *inter alia*) believes that the boundary is marked by a recognizable, though not drastic, change in the turtle fauna; he says that the beginning of the Tertiary era is marked by the appearance of some new cheloniids and of much smaller pelomedusids. With specific reference to the strata of Niger in the southern Sahara, Moody comments that the K–T boundary is not obvious. Its position is best recognized on the lithology of the limestones in the relevant part of the succession, on the presence of the ammonite *Libycoceras* beneath it, and on sharks' teeth; it is hoped that the application of geochemical techniques will prove useful. (Personal communication.) (On the subject of sharks' teeth, Capetta (1987) notes striking changes in the selachian fauna at the K–T boundary, with about 45% of the genera disappearing.)

Also worthy of note are the observations of Whalley (1988). He concluded that evolutionary changes in the Insecta over the K–T boundary provide no evidence of abrupt or catastrophic changes.

Thus there is a considerable diversity of approach to the problem. Incidentally, more than half of the authorities mentioned stated unequivocally that the diverse groups of organisms in which they specialize – megafossil plants, brachiopods, insects, bony fishes – pass across the Cretaceous–Tertiary boundary virtually unchanged. (That fact, though not strictly relevant to the subject of this article, constitutes a remarkable commentary upon the alleged 'universality'

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of the end-Cretaceous extinction.) Such people are therefore obliged to base their determination of the position of the boundary upon the stratigraphic correlation of a selection of fossils from outside their own area of study.

The extinction of the dinosaurs

The title of this article implies that dinosaurs are extinct. Not everyone, however, accepts that that statement is true. Unbelievers fall into two distinct categories:

1. Users of a purely cladistic classification. It is now generally accepted that birds evolved from theropod dinosaurs (Ostrom 1973); therefore, to a cladist, birds *are* theropod dinosaurs. But birds are alive today; therefore, to a cladist, *dinosaurs* are alive today, and cannot be regarded as extinct (figure 1). Cladists have no term for dinosaurs in the usual sense of that word, for they deny that such a group is 'natural', whatever that may mean (e.g. Wiley 1981: 70 *et seq.*).

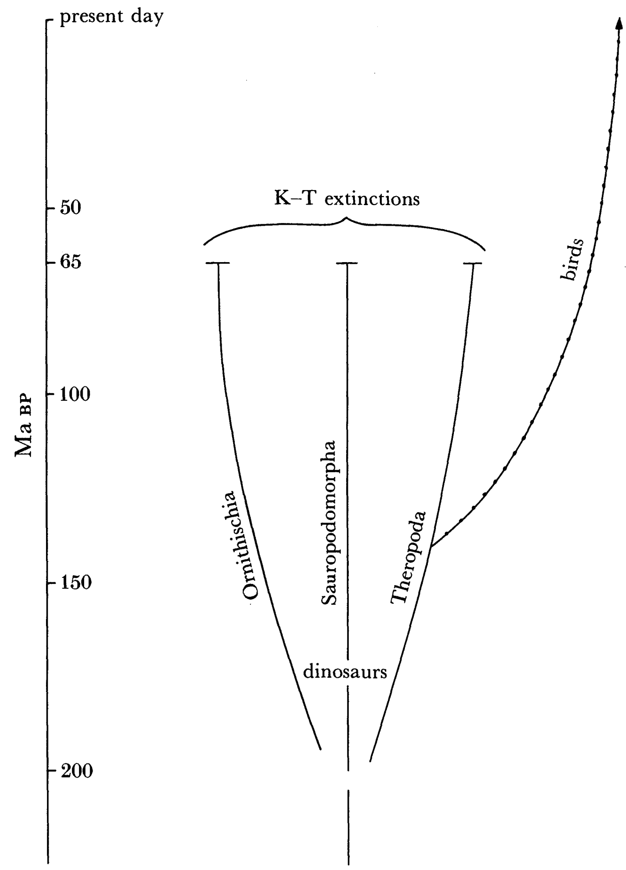

Figure 1. The phylogenetic relationship between 'proper' dinosaurs and birds. In a cladistic classification it is obligatory to include the birds *within* the theropod dinosaurs.

This point of view serves only to demonstrate the impracticability of cladistic classification, which classifies organisms according to their phylogeny and not according to their actual characters. Dinosaurs are a clearly defined group of animals, a group that appears to be wholly extinct; the fact that long before they died out there evolved from one of their lineages an entirely different group of animals, the birds, that survived them and persisted right through to the present day is completely irrelevant to any discussion of dinosaur extinction. In any case,

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the lack of a name by which to refer to the dinosaurs proper (i.e. the dinosaurs *sensu stricto*, as usually understood by most people) must surely be a serious hindrance in any discussion that concerns them.

2. Those who believe that dinosaurs *sensu stricto* are still alive today. They draw a parallel with the coelacanths, which, like the dinosaurs, appear to be absent from the fossil record throughout the entire 65 Ma of the Cainozoic, but which were discovered alive and well in the Indian Ocean in 1938 (Smith 1956). This category of people includes a few – a very few – people from the academic world, one of whom (Dr Roy Mackal of Chicago University) has even initiated and led expeditions into the forests of Africa in search of the fabulous 'Mokele-Mbembe' (Agnagna 1983, Bright 1984). Needless to say, his expeditions have proved unsuccessful.

The parallel with the coelacanths, however, is not strictly valid. It is true that the coelacanths show, yet again, the inadequacy of the fossil record; their apparent absence from all Cainozoic rocks serves only to create an illusion. On the other hand, the present-day coelacanths have escaped total extinction until now because they long ago retreated to a highly specialized ecological niche; and for that very reason – because they were animals of modest size, living in the depths of the sea and away from human beings – they escaped our notice until 1938. The dinosaurs present an altogether different case; a group of large terrestrial animals still living on the surface of a well-explored globe populated by some five thousand million people could hardly exist without occasionally leaving some tangible remains or traces of that existence, or without affording some opportunity for a photograph.

For our present purposes, therefore, we shall take it that dinosaurs are truly extinct.

Dating the last of the dinosaurs

We all tend to take it as a well-established fact that dinosaurs *everywhere* died out at the end of the Cretaceous, which, today, means at the end of the Maastrichtian stage. But that is not so; the 'fact' is merely an assumption, a false assumption, for rarely can such dating be logically justified. Fossils, reasonably enough, are generally dated on the strata that contain them; but it is often forgotten that, a century ago or less, the strata themselves may well have been defined by those same fossils. Indeed, the Cretaceous–Tertiary boundary has sometimes been defined as the stratigraphic horizon at which dinosaurs become extinct. Thus, for example, Archibald & Lofgren (1989) cite old coal surveys of the U.S. Geological Survey, in which 'the K–T boundary...was believed to lie about 2–3 cm lower, based upon the highest remains of unreworked dinosaurs'. In those circumstances it is hardly surprising that the dinosaurs seem to vanish simultaneously on that very boundary in various parts of the world! A better example of the circular argument would be hard to find.

We should also remember that the Danian stage, which follows the Maastrichtian and is now regarded by everyone as the basal stage of the Palaeocene (*above* the K–T boundary), was at one time included by many in the Cretaceous rather than in the Tertiary. However, this potentially unwelcome complication may be safely ignored in the present assessment.

Further difficulties are caused by the fact that Upper Cretaceous beds with fragmentary remains of dinosaurs have sometimes been dated to precise stages within the Cretaceous, e.g. to the Campanian or the Maastrichtian, simply on the evidence of the dinosaurs that they contain.

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It is, of course, logically impossible to recognize the last dinosaur in any sequence with absolute certainty. The assertion that a given individual is the last dinosaur in that sequence is based upon negative evidence, namely the apparent absence of dinosaur remains in all later beds, and it is therefore capable of falsification by the subsequent discovery of dinosaurs in those later beds.

That apart, the conditions required for a reasonable attempt at such recognition and at relating the position of the last dinosaur to that of the K–T boundary are remarkably stringent. The sequence in a given area needs to consist of a virtually continuous succession of sedimentary rocks of continental origin, potentially dinosaur-bearing, passing up from the level of the last recorded dinosaur for some considerable stratigraphic distance and, if possible, well into the Palaeocene. Only then can we verify, with a reasonable degree of assurance, the absence of later dinosaur remains in younger beds. Disconformities *below* the level of the last recorded dinosaur are, of course, totally irrelevant. An unbroken succession of continental beds, uninterrupted by marine intercalations with well-documented faunas of known age, is very difficult to date and is also less likely than a marine deposit to contain an 'iridium anomaly'. We have here a type of 'Catch 22' situation.

Let us now look at some of the more important parts of the world that have yielded Late Cretaceous dinosaurs.

1. *Western North America, east of the Rockies; especially Montana*

In Montana, detailed studies of continuous stratigraphic sequences across the K–T boundary (Archibald 1982; Archibald & Clemens 1982) have revealed some interesting facts. It had already been claimed many years ago (Sloan & Van Valen 1965) that certain orders of mammals, once thought not to have evolved until the Palaeocene (i.e. the earliest Tertiary; *after* the disappearance of the dinosaurs) had in fact originated in latest Cretaceous times, when they coexisted with dinosaurs and typical Mesozoic mammals. Samples from three different levels in the Hell Creek Formation have now shown that these 'new' mammals increased gradually in both numbers and diversity, whereas the dinosaurs (to be more precise, *Triceratops*) and the older, Mesozoic mammals simultaneously showed a tenfold drop in relative abundance. It has also been noted that the disappearance of the dinosaurs in various regions appears not to be synchronous but to vary in time from one region to another – generally occurring later in more southerly regions with a tropical climate (Van Valen & Sloan 1977). This suggests a gradual climatic change.

On the other hand, doubts were subsequently cast upon these opinions by Smit & van der Kaars (1984). All the 'mixed' faunas of the Hell Creek Formation occur in stream-channel deposits; Smit & van der Kaars believe that the streams were of Palaeocene age, that they cut through the K–T boundary and then re-worked the washed-out remains of dinosaurs and mammals from the Mesozoic rocks, incorporating them with those of the newly dead Palaeocene mammals. However, with the passage of time the beliefs of many of the people concerned (Sloan *et al.* 1986; Smit *et al.* 1987) seem to be approaching a consensus. Stated very briefly, this is that most of the localities concerned are certainly Palaeocene in age, some are certainly Maastrichtian, and others they are not quite sure about. Archibald & Lofgren (1989) remain equivocal.

Meanwhile yet another combination of these workers (Rigby *et al.* 1987) have agreed that six of the dinosaur-bearing localities in the uppermost part of the Hell Creek Formation are definitely to be dated as Palaeocene. They base their view upon the stratigraphic position of the localities and upon their having yielded fossil pollen of unmistakable Palaeocene aspect.

2. *The American Southwest: New Mexico and Texas*

Equally strong support for the idea of Palaeocene dinosaurs, so it seems to me, is afforded by the American Southwest.

The Javelina Formation in the Big Bend region of Texas, according to Stone & Langston (1975), yielded an incomplete, partly articulated skeleton of a large sauropod determined as *?Alamosaurus sanjuanensis*. The matrix in and around the bones, especially the femur, contained many fairly well-preserved palynomorphs (up to 45 species in all); it is not impossible, however, that some are reworked. None of the taxa is restricted to the late Cretaceous. Some appear first in the late Maastrichtian and range up to the present day; pollen of the Chenopodiaceae–Amaranthaceae group, which includes only one Maastrichtian species and is otherwise exclusively Palaeocene to Recent, is well represented. The flora as a whole shows a strong Palaeocene affinity.

Fassett (1982) suggested that the upper part of the Ojo Alamo Sandstone in the San Juan Basin of New Mexico, known to contain abundant dinosaur bones, lay *above* the K–T boundary. The iridium-enriched layer, which should coincide with that boundary, is missing in the San Juan Basin itself; it has been found, however, in the Raton Basin a little to the east, from which its theoretical position in the San Juan Basin has been worked out on the correlation of fossil pollen and spores (figure 2). It is presumed that the central part of the Ojo Alamo had been eroded away before the upper part containing the dinosaur bones was deposited. This means that the dinosaurs must have survived whatever event produced the iridium anomaly.

The most recent mention by the Alvarezes and their fellow-workers of dinosaur extinction in the San Juan Basin (1984) refers only to the magnetic stratigraphy and the question of

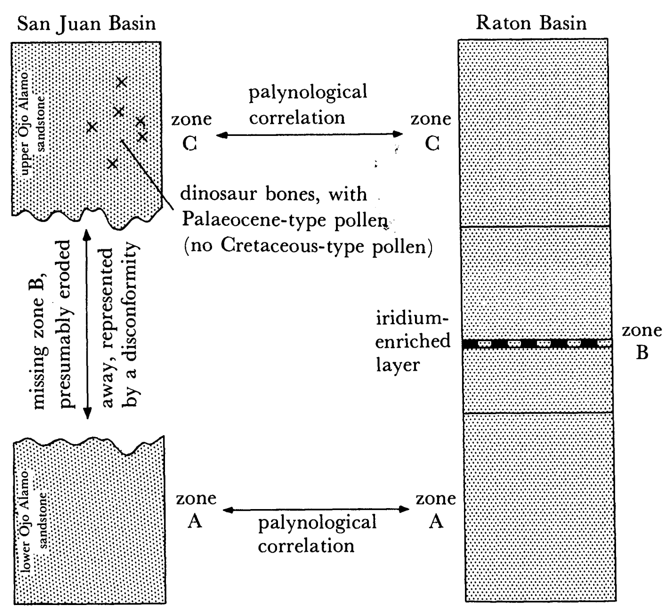

FIGURE 2. Stratigraphic relation of the dinosaur remains in the upper part of the Ojo Alamo Sandstone in the San Juan Basin (New Mexico) to the iridium-enriched layer in the Raton Basin to the east.

whether the extinction occurred in zone 29N or 29R; this can have no conceivable bearing upon the relative positions of the K–T boundary (as determined by the pollen) and the dinosaur extinction. If the pollen correlation used by Fassett is correct (and it was done by Robert H. Tschudy, of the U.S. Geological Survey in Denver – a palynologist of excellent repute), then the impact hypothesis of dinosaur extinction, indeed all disaster theories, fall to the ground.

More recently still Fassett *et al.* (1987) have produced more evidence that tends to confirm Fassett's original findings. Palaeocene-type pollen has been found in the upper part of the Ojo Alamo Sandstone, in one place with a dinosaur bone loose on the surface (which *could* have been reworked) and at another place that appears to be not with, but at the same stratigraphic level as dinosaur material *in situ*. There is no Cretaceous-type pollen at or above the level of the dinosaur bone, and there seems to be no unconformity between the bones and the pollen. This suggests that the Ojo Alamo dinosaurs, if not reworked, are of Palaeocene age, possibly throughout the entire San Juan Basin.

It is surprising that neither of the papers written by Fassett cited above makes any mention of the paper by Stone & Langston.

3. *Mongolia*

Maleev (1954) referred to what he called the 'ankylosaur horizon' at the Bain-Shire locality. According to his stratigraphic table, that horizon contains the genus *Talarurus* and lies above the 'Nemegetu' (= Nemegt); the table equates the upper part of 'ankylosaur horizon' to the Lance and Hell Formations of Montana, placing those two in the Laramie stage and citing the age of all three as Danian. However, even as recently as 1954, Maleev still considered the Danian to be the uppermost stage of the Cretaceous rather than the lowermost of the Palaeocene; he maintained that assignment to the Upper Cretaceous in subsequent papers (for example, in 1955).

Elsewhere the highest deposits of the Mongolian Cretaceous are called the Upper Nemegt Beds. Gradziński *et al.* (1968) declared that their fauna indicated a Campanian or Maastrichtian age. More recently, (1983) Karczewska & Ziembińska–Tworzydo (1983) have stated, on charophytan evidence, that 'the Nemegt Formation is not younger than the Lower Campanian'. Archibald & Clemens (1982) stated that, except for one locality of latest Cretaceous or Palaeocene age, the Gobi Desert succession stops short of the K–T boundary by about 10 Ma. Tatarinov has confirmed (personal communication) that nowhere in Mongolia do the Upper Cretaceous Beds reach the top of the Maastrichtian, that even the highest beds contain dinosaur remains, and that, in consequence, it is impossible to determine the precise level of dinosaur extinction.

4. *Southern France*

Ashraf & Erben (1986), working in the basin of Aix-en-Provence, have located the K–T boundary (defined palynologically) about 60 m *below* the highest of the *in situ* dinosaur eggs.

5. *Transylvania*

The Szentpeterfalva Beds of Transylvania, though not widely exposed, contain a diverse fauna of dinosaurs that were originally described by Nopcsa in a series of papers (1900, 1902, 1904, 1915, 1923, 1928, 1929). There has been much controversy in the past as to the age of the beds. Nopcsa simply believed them to be late Cretaceous; more specifically, they have usually been described as Campanian to Maastrichtian (e.g. Jeletzky 1960), but others have suggested that they might be Danian. There has been no definitive correlation until now. However, the beds and the fauna are presently under study by Grigorescu and Norman & Weishampel, all of whom are quite certain (personal communication) that they are of latest Maastrichtian age. The overlying strata are dated as Oligocene.

6. *Nigeria*

Nopcsa (1925) described a quantity of reptilian material from beds in Sokoto Province, Nigeria, that are regarded by everyone as of Lower Tertiary age (probably Eocene, Landenian). It included several vertebrae that he regarded as dinosaurian – some more specifically as trachodontid.

Swinton (1930, pp. 34–35) showed that these vertebrae were almost certainly crocodilian.

7. *Other regions*

Other parts of the world where allegedly dinosaur-bearing deposits have at one time or another been referred to the Danian stage include Belgium, Spain, Portugal, Austria, India, China, Alaska, Peru and Argentina. But the relevant information published on those regions is either very limited in extent and difficult to assess or is altogether non-existent. They will not be considered here.

Conclusions

Surprisingly enough, the only region where the fossil record extends almost unbroken from the Upper Cretaceous into the Lower Tertiary and appears to document the disappearance of the dinosaurs is western North America (east of the Rockies); we have no direct evidence as to when the dinosaurs disappeared elsewhere, not to within millions of years. It was because of this that the late Thomas J. M. Schopf wrote in 1981 'the problem of the extinction of the dinosaurs boils down to the rather trivial question of what happened to a score of species inhabiting the river and flood-plain habitats adjacent to the North American Western Interior seaway.'

Thus there is no direct evidence to support the idea that the extinction of the dinosaurs was a simultaneous phenomenon, worldwide. It is also true that there is not much evidence to support the opposite contention, that dinosaurs in different places died out at different times; but, without any substantial evidence pointing in either direction, one should logically adhere to the more general solution to the problem, the solution that might reasonably be expected in any comparable case. As to the question of whether or not the dinosaurs survived beyond the Cretaceous–Tertiary boundary, that inevitably hinges upon subjective opinions on the identification of fossil remains found in the field, on whether those fossils were *in situ* or reworked, on stratigraphic correlation from one area to another, and on what constitutes the K–T boundary. Nevertheless there does seem to be a modest amount of reliable evidence suggesting that in certain regions (notably Montana, New Mexico, Texas, Provence and, *fide* Professor Jaeger's comments (below), India) some dinosaurs did survive into Danian times and beyond the alleged catastrophe, or both.

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Discussion

M. J. Benton (*Department of Geology, Queen's University of Belfast, U.K.*). 1. The recent proposal that the dinosaurs died out as a result of a temperature-induced change in the sex ratio is an attractive, but unlikely idea. The eggs of modern turtles and crocodilians may hatch as either males or females depending on environmental temperatures early in development. This may have been true for the dinosaurs too – we shall never know – but the late Cretaceous crocodilians and turtles were apparently unaffected by any postulated change in temperature at the time.

2. The statement that paraphyletic groups mask extinction events has to be questioned. Sepkoski (1987) stated that 'the dinosaurs, the symbol of the Cretaceous–Tertiary extinctions, constitute a paraphyletic taxon', and this apparent paradox has been taken up by the present author. However, I would argue that this is mere word-play: the dinosaurs did die out, whether one judges it at the level of species, genera, or families. Indeed, six or seven monophyletic dinosaurian families disappeared at the end of the Cretaceous. This does not alter the suggestion that paraphyletic higher taxa may be of only limited use in macroevolutionary studies.

3. Dr Charig has gone to some length to catalogue the 30 or more findings of supposedly Palaeocene dinosaurs. He has also shown that, on further study, nearly all of these turn out not to be dinosaurs, reworked dinosaurs, or not Palaeocene in age. Because of these disproven cases and the natural desire of palaeontologists to find the 'last' dinosaur, is it not probable that there were no Palaeocene dinosaurs? The search for such beasts, on past performances, is unlikely to be successful.

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A. J. Charig. 1. If the sex of a dinosaur **was** affected by the ambient temperature early in its development, the critical temperature need not have been the same as for modern reptiles.

2. Dr Benton writes that 'The statement that paraphyletic groups mask extinction events has

to be questioned.' What I said in my lecture (and have now written in my article) was the exact opposite thereof. To paraphrase my wording, it would be the use of **holophyletic** groups (i.e. complete clades, as required in a cladistic classification) that would mask extinction events; thus the dinosaurs, if they are considered to include birds, do **not** become extinct at the K–T boundary. Dr Benton (who has adopted a cladistic approach) argues 'that this is mere word-play: the dinosaurs did die out [because all the constituent] monophyletic dinosaurian families disappeared at the end of the Cretaceous.' That statement, however, is meaningful only if Dr Benton is using the word 'dinosaurs' in a paraphyletic sense, excluding the bird families, in a manner contrary to cladistic thinking. I wholeheartedly disagree with the suggestion in Dr Benton's final sentence.

3. I strongly dispute that I have 'shown that ... nearly all of these findings of supposedly Palaeocene dinosaurs turn out not to be dinosaurs, [to be] reworked dinosaurs, or not Palaeocene in age.' The final sentence of my 'Conclusions' (above) clearly demonstrates otherwise. If I had rejected *nearly* all the findings of supposedly Palaeocene dinosaurs, there would still be no logic in Dr Benton's suggestion that that fact in itself makes it unlikely that there were any Palaeocene dinosaurs at all. As for 'the natural desire of palaeontologists to find the 'last' dinosaur', is it not just as natural for those who are strongly committed to a belief in mass extinctions to be embarrassed by the apparent existence of dinosaurs in the Tertiary?

J.-J. Jaeger (*Laboratoire de Paléontologie des Vertébrés, Université Pierre et Marie Curie, Paris, France*). The Deccan Traps of India have been shown to be another place in the world where the age of dinosaur extinction has been precisely dated. The most recent remains are located in inter-trappean deposits dated at 65.7 ± 2 Ma by $^{39}Ar/^{40}Ar$ dating and showing reverse magnetic polarity. This reversal, during which almost 80% of the Deccan Traps lavas were deposited, is currently supposed to represent anomaly 29 R.

In the Aix Basin of southern France, several methods failed to yield only precise dating of the numerous dinosaur egg shell localities. In these cases, no iridium anomaly could be located.

A. J. Charig. I am very grateful to Professor Jaeger for this important information, previously unknown to me. If the last dinosaur remains in the inter-trappean deposits of India do indeed occur within magnetic reversal zone 29R, then the Indian dinosaurs became extinct at about the same time as those in the San Juan Basin of New Mexico, which means that they too may have survived into Palaeocene times. Considering the abundance of dinosaur eggshell material in the Cretaceous of southern France, the apparent absence in the Aix Basin of an iridium anomaly is particularly unfortunate.

G. B. J. Dussart (*Christ Church College, Canterbury, Kent, U.K.*). Is there not a systems component to extinctions? One consistent aspect of the evolution of dominant groups appears to have been the success of more homeostatic systems over less homeostatic systems. Thus one might expect the succession of homoiotherms over poikilotherms to be a literally universal occurrence. Topological catastrophe theory tells us, however, that catastrophes are often made up of the coincidental occurrence of one or more events that are not, in isolation, capable of bringing about the catastrophe. Thus dinosaurs might have been under pressure from being behavioural rather than physiological homoiotherms. It would then only take a minor catastrophe such as a bolide impact to give the mammals an opportunity to take over. An alternative promoter of the succession might have been the assumption of egg-eating by mammals at the time. This behaviour could have spread rapidly amongst mammals; as physiological homoiotherms, they might have pursued this mode of life at night, when reptiles were less active and capable of protecting their eggs. Appropriate evidence might be that most of the modern reptiles and birds make elaborate precautions for protecting their eggs. Even though we know that there were dinosaurs which protected their eggs, they might not have done so very successfully, as they are not with us today. A scenario of egg-eating by relatively unspecialized mammals (whose small size might preclude much fossilization) could explain the sudden demise of some of the dinosaurs and the acknowledged lag between the end of the dinosaurs and the ascendancy of the mammals.

To summarise: the main factor of physiological homoiothermy might have operated in concert with subsidiary secondary factors. The second factor might have been a bolide impact in the area currently occupied by North America, egg eating by mammals in other parts of the world, and possibly direct competition between viviparous (but poikilothermic) icthyosaurs and physiologically homoiothermic cetaceans in the seas. Perhaps when considering extinctions, it might be useful to think in terms of causes and triggers. The underlying cause might have been general, but the triggers for extinctions might have been local. The cause produces the contemporaneity of the extinction but the trigger produces the geographic heterogeneity. Similar processes can be seen operating today. Trees are dying in the Harz Mountains of north Germany. The underlying cause is that the trees were planted and grown close to their tolerance thresholds but the trigger is acid rain, which is pushing them into local extinction.

A. J. Charig. Dr Dussart's concept of direct competition between ichthyosaurs and cetaceans is, I believe, completely untenable. The last ichthyosaurs known are from the base of the Upper Cretaceous, whereas the first cetaceans are from the top of the Lower Eocene – more than 50 Ma. later!

L. B. Halstead (*Department of Pure and Applied Biology*, *University of Reading*, *U.K*). I should like to support Dr Charig in his analysis of the end of the dinosaurs. The work of Sloan *et al.* (1986) and Sullivan (1987) has demonstrated that the dinosaurs were declining in both numbers and diversity for the last 5 Ma of the Cretaceous period. The final 300000 years witnessed a striking acceleration of this decline so that at the end there were only some 12 species distributed among eight genera. It becomes difficult to speak of the final extinction of the dinosaurs as a sudden mass extinction.

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A. J. Charig. I thank Dr Halstead for his support.

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