

THE ENIGMA OF THE EXTINCTION OF THE DINOSAURS

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INTRODUCTION

One of the more interesting contributions of paleontology to general knowledge is evidence that giant reptiles were once the dominant life forms on our planet. During the past two centuries some 5000 skeletal fragments of these creatures have been excavated from Mesozoic sediments. Many are objects of public wonder in museum displays around the world.

It is difficult to contemplate the skeletons of dinosaurs or large marine reptiles without also being reminded of their mysterious disappearance. In spite of a voluminous literature on the subject, there is no consensus regarding the stresses which drove the giant reptiles to extinction. It has become apparent, however, that they vanished in a general biotic crisis, and in recent years more attention has been focused on theoretical models which would produce stresses on a global scale.

The problem of the extinction of the dinosaurs is thus clearly an interdisciplinary one. Unfortunately, the competence of a single author is necessarily limited. The review that follows represents the perspective of one student of the great reptiles who is greatly vexed by their apparently sudden disappearance at the end of the Mesozoic Era. The peculiarities of this extinction are summarized and various possible agents of biotic stress are briefly discussed.

The Cretaceous-Paleocene (Mesozoic-Cenozoic) boundary, corresponding to the extinction event during which the dinosaurs disappeared, occurred about 65 million years ago. The Maastrichtian Stage is the final major biostratigraphic division of the Cretaceous and the Danian Stage the first of the Paleocene. For examples of current geochronologic scales, see Van Hinte (1976) and Berggren (1971), noting that the absolute ages given are only approximations of actual values (Jeletzky 1978).

THE TERMINAL CRETACEOUS EXTINCTIONS

Upper Cretaceous sediments, representing the final 30 million years of the Mesozoic Era, have yielded abundant remains of large reptiles, both terrestrial and marine, around the globe. The following generalizations are drawn from this record:

1. There is no evidence of a decline in diversity or of a meridional restriction in the geographic distribution of large reptiles toward the end of Cretaceous time. Their skeletal remains have been recovered from terminal Cretaceous (Maastrichtian) sediments in southern Argentina and in the Queen Elizabeth Islands of arctic Canada (Russell 1975, 1979).

2. The occurrence of large terrestrial reptiles was probably more precisely correlated with high rainfall and abundant plant growth than with swampy environments near the sea (Béland & Russell 1978). Dinosaurs occur in diversity and abundance in sediments deposited over 1500 km from the nearest strand line in central Asia (Russell 1970).

3. Remains of small, unspecialized, and often relatively intelligent dinosaurs (e.g. possessing enlarged endocranial cavities; Hopson 1977) are abundant (although usually disarticulated) in late Upper Cretaceous sediments and show no evidence of a terminal Cretaceous decline. (Remains include members of the Caenagnathidae, Dromaeosauridae, Hypsilophodontidae, Ornithomimidae, Pachycephalosauridae, Protoceratopsidae, Saurornithoididae, and Thescelosauridae; see Béland & Russell 1978, Galton 1974, Gradzinski et al 1977, and references cited therein.)

Vertebrate microfossil evidence, which is interpreted as indicating a gradual replacement of the terminal Cretaceous dinosaurian community by a basal Paleocene mammalian community over a period of approximately 100,000 years, is presented by Van Valen & Sloan (1977) and Archibald & Clemens (1977). The model is not strengthened by the occurrence of articulated dinosaur remains and vertebrate microfossil associations typical of terminal Cretaceous sediments in strata deposited contemporaneously with "transitional" microfossil assemblages (cf Béland & Russell 1978, Russell 1979). It could be argued with equal validity that several microvertebrate communities co-existed in terminal Cretaceous time, and suffered unequally in the subsequent extinctions.

The highest level of articulated dinosaurian remains in terrestrial sequences can be traced laterally into marine sections in several localities. There it coincides with a profound marine extinction event marking the Maastrichtian-Danian boundary. Large marine reptiles are also found throughout the world in Upper Maastrichtian strata, but unworked remains have never been recovered from sediments of Danian age (Russell

1975, 1979, and references cited therein). The marine extinctions were evidently more severe than those which took place in terrestrial environments (Table 1), probably because they were exacerbated by profound secondary trophic disturbances.

In both continental and marine sections the extinction datum is often accompanied by lithological changes (Russell 1977, Figures 3–8). An abrupt coarsening of clastic particles in continental strata could be interpreted as evidence of more tenuous plant cover, for the basal Paleocene sea was transgressive in the northern interior of the United States (Frye 1969) and evidence of relatively lower-energy fluviatile sedimentation would otherwise be expected. Interestingly, Davies et al (1977) link low abyssal sedimentation rates during Paleocene time with continental aridity and low rates of river discharge into the oceans. They also document sustained low abyssal sedimentation rates later in Cenozoic time, unaccompanied by a comparably severe depression in biotic diversity.

Changes in deep oceanic circulation are postulated to have caused fluctuations in basinal carbonate compensation surfaces (and carbonate deposition-solution patterns) both prior to and following the terminal Cretaceous extinction event. However, a genetic link between the two phenomena is not obvious (Thierstein & Okada 1979). Other lithologic changes may be related to a widespread late Maastrichtian–early Danian withdrawal of epicontinental seas (Naidin 1976; see also section on regressions).

It is clear that the biosphere exerts an influence on rates of terrestrial erosion and biogenic deposition in the oceans. Sedimentological processes probably would respond to the partial collapse in planetary ecosystems, and physical evidence of this response should be carefully sought at the Cretaceous-Paleocene boundary.

The extinction event can often be identified with a bedding plane in sedimentary successions, and it is generally recognized to have taken place within a relatively short period of geologic time. Current estimates of the local duration of the extinctions vary between essentially instantaneous to 10^4 – 10^5 yrs (Thierstein & Okada 1979, Van Valen & Sloan 1977, Kent 1977). On the basis of the occurrence of the Cretaceous-Paleocene boundary in a zone of negative geomagnetic polarity in northern Italy, and a zone of positive polarity in New Mexico, Kent (1977) suggested that the extinction occurred 500,000 years later in the latter region. However, the boundary also occurs in a zone of positive polarity in Alabama and at several other localities within the western interior of North America (G. P. L. Danis, J. A. Foster, D. A. Russell, manuscript in preparation). It is probable that the time scale of biotic and geomagnetic events during the Cretaceous-Paleocene transition is at the limit of stratigraphic resolution.

Table 1 Number of genera of fossil organisms currently recognized as having lived prior to and following the terminal Cretaceous extinctions (for sources of information see Russell 1977, p. 15)

	A: Before extinctions ^a	B: After extinctions	B/A × 100
<u>Fresh-water organisms</u>			
cartilaginous fishes	4	2	
bony fishes	11	7	
amphibians	9	10	
reptiles	12	16	
	36	35	97
<u>Terrestrial organisms</u> (including fresh-water organisms)			
higher plants	100	90	
snails	16	18	
bivalves	10	7	
cartilaginous fishes	4	2	
bony fishes	11	7	
amphibians	9	10	
reptiles	54	24	
mammals	22	25	
	226	183	81
<u>Floating marine microorganisms</u>			
acritarchs	28	10	
coccoliths	43	4	
dinoflagellates	57	43	
diatoms	10	10	
radiolarians	63	63	
foraminifers	18	3	
ostracods	79	40	
	298	173	58
<u>Bottom-dwelling marine organisms</u>			
calcareous algae	41	35	
sponges	261	81	
foraminifers	95	93	
corals	87	31	
bryozoans	337	204	
brachiopods	28	22	
snails	300	150	
bivalves	399	193	
barnacles	32	24	
malacostracans	69	52	
sea lilies	100	30	
echinoids	190	69	
asteroids	37	28	
	1976	1012	51

Table 1 (continued)

	A : Before extinctions ^a	B : After extinctions	B/A × 100
Swimming marine organisms			
ammonites	34	0	
nautiloids	10	7	
belemnites	4	0	
cartilaginous fishes	70	50	
bony fishes	185	39	
reptiles	29	3	
	332	99	30
Totals overall	2868	1502	52

^a A generally signifies the last 20 million years of the Cretaceous; B the first 10 million years of the Cenozoic. In the case of marine microfossils and terrestrial organisms the interval is usually much closer to the extinction event, but in several groups of marine macrofossils it is larger. The record of terrestrial organisms is here limited to North America; for marine organisms coverage is global, although existing information is more complete from North America and Europe.

There are very tenuous indications of two nearly synchronous pulses of extinction with different biologic effects. An earlier pulse may have more strongly affected terrestrial plants and some planktonic organisms; a later pulse, other planktonic organisms and terrestrial vertebrates (Boersma & Shackleton 1979, Doerenkamp et al 1976, Russell & Singh 1978). Foraminiferal assemblages of a peculiar but transitional aspect apparently occur within a narrow (30 cm or less) stratigraphic interval at the boundary in some marine sections (Boersma & Shackleton 1979). That the stresses which caused the extinction were of relatively short duration is also suggested by the rapid diversification of surviving organisms in early Cenozoic time (see Béland 1977).

Newell (1962, Figure 6; 1966, Figures 2–5) graphically demonstrated that the terminal Cretaceous extinctions constituted one of the most dramatic extinction events known to have occurred during the last 500 million years. A survey of paleontologic literature suggests a general drop in generic diversity across the Cretaceous-Paleocene boundary of approximately one-half (Table 1, Russell 1977). Because the number of species within genera also declined, Russell (1977) postulated that a total reduction of 75% took place in species diversity during the extinctions. These figures imply a crisis far more severe than that which took place on a scale of 10⁴ yrs from the end of the Pleistocene through to the present (Berggren & Van Couvering 1974; Webb 1969, Figure 2; Russell 1976), or that which would follow an essentially instantaneous discharge of one-half of the world's stockpile of nuclear weapons (Nier et al 1975).

SOURCES OF BIOTIC STRESS

There are at least two widely shared points of view among paleontologists concerning the extinction of the dinosaurs: 1. The reason for their demise is unknown, and none of the explanations which have been advanced is supported by a convincing body of evidence (Jepsen 1964). 2. The dinosaurs died as a result of a complex of interrelated and mutually reinforcing stresses which have not been satisfactorily separated and identified in the geologic record (Newell 1975). In the present state of knowledge both points of view can be defended. In this review sources of biologic stress on a planet-wide basis are evaluated with respect to what is known of the Mesozoic-Cenozoic boundary crisis. It is very doubtful that only one of them was operative during the extinction interval and therefore uniquely responsible for the totality of events which took place.

Trophic Effects

Phytoplankton lie at the base of the food chain in the open oceans. Extinction among this group of organisms (cf Tappan & Loeblich 1972, Gartner 1977, Russell 1977) was probably a factor in the simultaneous disappearance of some organisms in higher trophic levels, including marine reptiles. This proposition is consistent with the survival of most of the fresh-water vertebrates, which derived much of their nourishment from terrestrial plant communities (see Table 1). Enormous reserves of oxygen in the atmosphere (Reid 1977, pp. 142–43), coupled with the relatively greater productivity of terrestrial plants (Woodwell et al 1978), render it unlikely that a decline in oxygen production due to marine phytoplankton extinctions would threaten the survival of terrestrial vertebrates. In turn, it would also seem improbable that during the Cretaceous-Paleocene transition continental relief was so low and tectonic activity so reduced (see sections on regressions, volcanicity) that land-derived nutrients dwindled everywhere to the point of causing an abrupt, world-wide extinction of a great number of planktonic organisms in the sea.

Although many taxa of terrestrial plants became extinct (Tschudy 1971), the total change was much less dramatic than in marine phytoplankton (see Jarzen 1977, Hickey 1977, Gartner 1977). In central Alberta Canada, terminal Cretaceous dinosaurs may have briefly survived the palynofloral change elsewhere associated with the Cretaceous-Paleocene boundary within the western interior of North America. The floral change in itself, we can infer, was not severe enough to eliminate large terrestrial vertebrates (Russell & Singh 1978). One could argue whether minor changes in terrestrial floras were as important to dino-

saurian consumers as the cessation of dinosaurian browsing, with the extinction of the large herbivores, was to prevailing patterns of ecological succession in plant communities. The demise of several lineages of marsupials, however, could have resulted from a removal of carrion from the food web after the extinction of the giant reptiles (cf. Archibald & Clemens 1977).

The diversification of flowering plants through Upper Cretaceous time (Norris et al 1975) was accompanied by a simultaneous diversification of herbivorous dinosaurs (Ceratopsidae, Hadrosauridae). With no evidence for a late Cretaceous decline in dinosaurian diversity, and in view of the possibility that they survived the palynofloral change associated with the Cretaceous-Paleocene boundary, there is little basis for supposing that dinosaurs became extinct for want of nontoxic plant fodder (Swain 1976).

Marine Regressions

It is widely held that the epicontinental seas of the globe declined greatly in extent from late Cretaceous through Cenozoic time (Hallam 1977), and that this regressive trend constituted a major environmental change which has profoundly affected the biosphere (Newell 1971). Superimposed on the general pattern of withdrawal of seas from the continents, a relatively brief but profound regressive event corresponding to a sea level drop of about 100 m (inferred from Jeletzky 1978, p. 8, Figures 3–7), and coinciding with the terminal Cretaceous–basal Paleocene interval, is often postulated to have produced a global environmental deterioration culminating in the extinctions which brought the age of reptiles to a close (Cooper 1977, Kauffman 1977).

The precision with which global changes in sea level are reflected in regional strand line movements has been questioned by some. Yanshin's (1973) graphs, based on the distribution of epeiric seas over much of the Earth's continental lithosphere, show no pronounced, long-term regressive trend through Upper Cretaceous and Cenozoic time. There would seem to be little parallelism in degree of continental emergence. The graphs relate the position of ancient strand lines to the limits of sialic crust, rather than to existing strand lines (cf Hallam 1977). Bond (1978) has also presented evidence suggesting that widespread post-Miocene epeirogenic uplift (~100 m) has occurred in Africa, while Europe, Australia, and the Americas remained relatively stable.

Short-term eustatic changes in sea level, such as the terminal Cretaceous withdrawal of the seas, are frequently, if not usually, masked by regional tectonic activity (Bond 1976, Jeletzky 1978). Even geologically brief, glacially induced changes in sea level (85 m, CLIMAP Group 1976) may

be locally modified by changing undulations in the equipotential surface of the Earth's gravity field (-70 to $+50$ m, Mörner 1977). Jeletzky (1978, p. 36), affirming the widespread evidence for a terminal Cretaceous (terminal Maastrichtian) regression, noted that it has been preserved not so much due to its unusual amplitude, but because it occurred during a tectonically quiescent period. Furthermore, according to Reymont & Mörner (1977), the terminal Maastrichtian–basal Danian interval was characterized by advancing seas in the lands bordering the South Atlantic.

The terminal Maastrichtian regression was preceded by a comparably well-defined regressive event during early Campanian time (Jeletzky 1978, p. 16) which was not accompanied by extinctions of exceptional severity. Adams et al (1977) postulate that a global eustatic regression of 40–70 m took place during the late Miocene Messinian crisis, coinciding with hiatuses in carbonate sequences and a general cooling. However, no major discontinuity occurred in Miocene-Pliocene faunal development (Berggren & Van Couvering 1974, Webb 1977). There is little compelling evidence that changes in sea level comparable to those observed during the Maastrichtian–Danian regression would produce large-scale extinctions. Indeed, the availability of large areas of continental shelf to colonization by highly productive terrestrial plant formations should not in itself have constituted an event detrimental to the survival of dinosaurs.

Temperature

Oxygen isotope temperature studies of marine microfossils near the Cretaceous equator in the Pacific (Douglas & Savin 1974, Savin et al 1975) and of belemnites in Cretaceous mid-latitudes in Europe (Spaeth et al 1971) and New Zealand (Stevens & Clayton 1971) indicate a thermal minimum during mid–early Cretaceous time, followed by an early–Upper Cretaceous (Cenomanian–Turonian) maximum and a return to levels comparable to those prevailing during the early Cretaceous minimum near the close of the Cretaceous (Lower Maastrichtian). Their data suggest that tropical surface ocean temperatures during the Lower Maastrichtian were similar to those existing in low latitudes today (28°C), with minimum high-latitude temperatures of approximately 10°C .

Isotopic evidence is in harmony with a late Maastrichtian warming of epicontinental seas in many regions (Stevens & Clayton 1971, and references cited therein). This trend is supported by paleontologic and chemical evidence in northern Europe (Voigt 1964, Jorgensen 1975) and micro-faunal data in the western interior of North America (North & Caldwell

1970), although isotopic paleotemperature determinations remain constant in the latter region (Tourtelot & Rye 1969). Saito & van Donk (1974) report a 5°C cooling of oceanic waters during Upper Maastrichtian time in the South Atlantic, and isotopic data suggestive of temperature fluctuations at the Cretaceous-Paleocene boundary in the southern oceans was cited by Margolis et al (1975). Boersma & Shackleton (1979), on the basis of isotopic ratios preserved in foraminiferal tests, found evidence of a thermal rise across the Cretaceous-Paleocene boundary in Atlantic waters, where basal Paleocene temperatures were significantly warmer than during the latest Cretaceous.

It has been postulated (Hughes 1976, McLean 1978) that massive extinctions were precipitated when an Upper Cretaceous warming trend ("radmax") passed a biologically critical threshold at the end of the period. Large reptiles are known to be particularly vulnerable to heat stress (Cloudsley-Thompson & Butt 1977). However, isotopic temperature data suggest that the "radmax" occurred during early Upper Cretaceous time, although a very brief, terminal Cretaceous heating event would not appear to be ruled out.

Changes in terrestrial floras across the Cretaceous-Paleocene boundary have not been viewed as indicative of warmer climates. Instead, a slight but general cooling is usually postulated, accompanied by increased seasonal fluctuation in temperature and rainfall (e.g. Tschudy 1971, Hickey 1977). As evidence of this Krassilov (1975) noted that smooth-margined leaves, typical today of perennially warm, moist environments, are more abundant in terminal Cretaceous strata of mid-latitude sections than in supradjacent sediments of basal Paleocene age, where they tend to be replaced by serrated-margined leaves. Jarzen (1977) cited a shift from animal- to wind-pollination across the boundary as an effect of increased seasonality. The possibility that the decline in the proportion of plant taxa with entire-margined leaves could be the result of local increases in seasonal aridity (cf Gentry 1969) should be examined.

Information sufficient to document consistent global paleotemperature patterns through Maastrichtian-Danian time is, accordingly, unavailable at present. Accepting the uniform validity of existing interpretations, it could be concluded that thermal minima occurred at different times in different regions, and did not necessarily coincide with the terminal Cretaceous extinction datum. Thermal declines of this general magnitude had occurred earlier in Mesozoic time, but were not associated with comparably severe extinctions.

With this in mind, it may be useful to examine the possible consequences of a brief (~100,000 yrs) but marked thermal decline (10–5°C) in oceanic

bottom waters near the Eocene-Oligocene boundary about 38 million years ago (Kennett & Shackleton 1976). In contrast to the rapid and massive extinctions of planktonic organisms at the Cretaceous-Paleocene boundary, it was the benthonic forms that suffered an abrupt decline in diversity. Differences between Eocene and Oligocene marine macrofaunal assemblages are gradational in character and strongly influenced by lithofacies changes (Berggren 1971). In northern mid-latitudes, meridional displacements in the distributions of arborescent plant taxa have been interpreted as resulting from rapidly declining mean annual temperatures (Wolfe 1971, 1972). The floral changes in turn are generally seen as responsible for concomitantly high turnover rates, which were unaccompanied by significant diversity changes, in terrestrial mammalian communities (Webb 1977, and references cited therein). The pattern and severity of the terminal Cretaceous extinctions were evidently not duplicated.

Volcanism

The thermal effect of volcanic dust veils has often been invoked as a reason for a proposed temperature decline at the end of the Cretaceous, although at present such veils have not been known to depress mean annual temperatures by as much as 1°C (Miles & Gildersleeves 1978). Late Cretaceous levels of volcanicity were presumably inferior to those existing during the Pleistocene (Vogt 1972) and mean temperatures departed more greatly from the biologically critical 0°C threshold. It has been suggested that the injection of biologically deleterious substances into the biosphere through volcanism may have brought about the terminal Cretaceous extinctions (e.g. Vogt 1972, Feldman 1977, pp. 137–38). Sediments could be examined for the appropriate chemical residues, but the gradual, episodic nature of terrestrial volcanicity is not in harmony with the sudden and sharp biostratigraphic datum marking the Maastrichtian-Danian boundary.

The occurrence of pathologic and relatively thin shells in dinosaur eggs from the higher levels of the Cretaceous in southern France has been provisionally linked either to the passage of unusually severe atmospheric cold fronts (Thaler 1965) or to the appearance of toxic substances in the environment (Erben 1972). R. Dughi and F. Sirugue (personal communication, 1975), however, note that pathological eggs occur throughout late Cretaceous exposures in the region, and that eggs with thin shells belong to different dinosaurian taxa than do those with thick shells. Thus, according to them, the apparent thinning of shells toward the upper limit of the Cretaceous implies faunal change, not necessarily increasing environmental degradation.

Collisions of Comets and Large Meteorites

Urey (1973) cited a series of biological stresses which might follow the collision of a comet with the Earth's oceans. Among these are a sudden and possibly lethal heating of the atmosphere and oceanic surface waters. However, Urey also noted that a tektite shower, which occurred in the Australasian region about seven hundred thousand years ago and suggested an impact energy consonant with his calculations, produced only a minor stratigraphic discontinuity. Evidence of a cometary collision could be sought in tektite fields and concentrations of certain rare-earth elements (cf Vostrukhov 1977) at the Cretaceous-Paleocene boundary.

The collision of a large meteorite has also been considered as a possible agent of mass extinction. The Popigai crater is the largest Phanerozoic meteor crater known. It measures 95–100 km in diameter and impacted sometime between 29 and 47 million years ago (Masaitis 1975). Although the blanket of ejecta and the air blast may have been lethal over a region two to three times the diameter of the crater (M.R. Dence, personal communication, 1978), no permanent floral or faunal change has yet been linked to the event. The distribution of ancient craters on cratonic areas suggests that a large asteroid (about 4 km in diameter) should fall into the oceans on an average of one per ten million to 100 million years, creating an impact wave which could easily be 5 km high (M. R. Dence, personal communication, 1978). The effects of such an event, as suggested by McLaren (1970, p. 812),

would certainly spread to all shelf and epicontinental areas connected with the open ocean. The turbulence of the tidal wave and accompanying wind, followed by the gigantic runoff from the land would induce a turbid environment far longer than could be survived by bottom dwelling filter-feeders, and their larvae. The hypothesis of meteoric impact in the ocean explains equally the nonextinction of many other forms of both marine and terrestrial life. There must have been many regions where plankton and nekton could have survived, (as well as) epiplanktonic and rocky-bottom attached organisms . . . (and) land plants and animals . . .

The pattern does not appear to conform to the survivorship pattern following the Cretaceous-Paleocene crisis. However, the biological consequences of collisions with large extraterrestrial objects deserve careful study, as several such events have probably occurred since the beginning of the Phanerozoic.

Ultraviolet Radiation

It is well established that the Earth's ozone layer shields the biosphere from potentially lethal solar ultraviolet radiation (Margulis et al 1976). The ozone layer is vulnerable to partial or complete destruction as a

result of the coincidence of a colossal solar flare (10,000 times more intense than any so far observed) with a reversal of the terrestrial magnetosphere, or of the arrival of a blast of high energy radiation from a nearby supernova. The biosphere could thereby be subjected to essentially unattenuated solar ultraviolet radiation, short term atmospheric instability, a reduction in the transmission of visible light through nitrogen dioxide absorption, and a global cooling as much as 0.5°C. These effects would endure for only about 10 years after the arrival of an initial pulse of radiation (Reid 1977, Roy 1977, Tucker 1977, K-TEC Group 1977, pp. 144–48, Hunt 1978). It is unlikely that the cooling effect would have stimulated the formation of continental glaciers during late Cretaceous–early Paleocene time, for high latitude temperatures exceeded 0°C much more than at present (Savin et al 1975).

The reaction of planetary ecosystems to increased levels of UV exposure is very poorly understood. It is possible that plastids of green plants are more vulnerable to UV radiation than the host cell or animal cells (Margulis 1968). Transient reduction in atmospheric ozone in the wake of nuclear detonations on an unprecedented scale would apparently produce a greater incidence of UV damage among terrestrial and aquatic plants than among terrestrial vertebrates (Nier et al 1975, pp. 90–93, 141–51). Electromagnetic (but not particulate) radiation from an extra-terrestrial source capable of damaging the ozone layer would not reach ground level (Tucker 1977, Clark et al 1977). This mechanism could account for some of the disturbances in terrestrial and aquatic plant communities which approximately coincided with the extinction of the dinosaurs.

Ionizing Radiation

Tucker (1977, p. 121) estimated that a nearby supernova could generate a rise in background radiation at the base of the atmosphere to levels of the order of 300 roentgens per year. These levels would be sustained for about ten years, coinciding with the passage of the relativistic blast wave.

Accepting the general accuracy of this estimate, the ensuing disturbances in marine ecosystems would probably be less than on land (Nier et al 1975, pp. 126–41). The most vulnerable terrestrial plant formation, the forest, would for the most part respond by little more than a slight inhibition of growth (Woodwell 1963, 1967). However, some conifers (Taxaceae, Pinaceae, Cupressaceae; cf Dugle & El-Lakany 1971) would be more severely affected, for their greater chromosome volume reduces resistance to ionizing radiation. Seeds, including those of conifers, are significantly less vulnerable than parent plants.

Large vertebrates (*Homo sapiens*) are about as radiosensitive as are the

above conifers (Woodwell 1963). Here, however, the relationship between chromosomal volume and radiosensitivity tends to be obscured by the greater physiological complexity of the organisms (cf Vorontsov 1958, United Nations 1958, Bond et al 1965). An inverse correlation between reproductive rates and increasing size nevertheless militates against resistance to chronic ionizing radiation (G. M. Woodwell, personal communication, 1978). This would imply that dinosaurs would have been more vulnerable than, for example, lizards. No terrestrial vertebrate exceeding about 25 kg in body weight is known to have survived the terminal Cretaceous extinctions.

On the balance, then, it is probable that exposure rates quoted by Tucker would be seriously detrimental to some terrestrial organisms (Woodwell, personal communication, 1978), whether resulting from a supernova or some other cause. Further, it is not unreasonable to expect that large terrestrial vertebrates would be more adversely affected than terrestrial plants. The dinosaurian extinctions would seem to be in conformity with an increase in background radiation to levels suggested above.

It has been proposed that the presence of high concentrations of radioactive minerals in fossil bones of late Cretaceous age was the result of a contemporaneous increase in background radiation (Salop 1977). There is in fact no correlation between bone radioactivity and stratigraphic proximity to the Cretaceous-Paleocene boundary (Jaworowski & Pensko 1967, Bell et al 1976).

Supernovae

For about two weeks these colossal stellar explosions radiate as much energy as about ten billion suns, or as much as all the stars in a galaxy combined. Terrestrial environments could be affected at distances of up to one hundred light years. Several lines of astrophysical evidence suggest that these explosions occur at a rate of about one every fifty years per galaxy, showing some association with spiral arms. This translates into an average of one supernova within 50 light years of the Earth every 70 million years (Tucker 1977, Clark et al 1977).

At a distance of 50 light years the stresses exerted on the biosphere by a nearby supernova would not be instantaneous. An initial burst of electromagnetic radiation would be injected into the atmosphere over an interval of a few hours. It would be followed in three to thirty years by an intense flux of cosmic rays at the leading edge of a relativistic blast wave. High levels of background radiation (~ 300 r) would persist for about 10 years. Some 3,000 to 30,000 years later, the Earth would be immersed in the expanding shell of the supernova remnant, implying radiation doses of about ten roentgen per year for thousands of years (Tucker 1977).

The effects of the initial electromagnetic wave and the following pulse of cosmic radiation might be correlated respectively with disturbances in plant communities and the extermination of the dinosaurs. Presumably the damage sustained by the ozone layer in the wake of the cosmic ray blast (Tucker 1977) would be somewhat less effective, biologically, due to the previous elimination of UV sensitive forms when the layer was disrupted by the initial wave of electromagnetic radiation. There is as yet no compelling astrophysical evidence for a 65 million year old supernova remnant near the solar system, but it is rather unlikely that one would have remained over such a great length of time (Feldman 1977).

Periodic Galactic Events

The solar system revolves around the center of the galaxy once in approximately 200 million years. During the galactic orbit the Earth passes through the equatorial plane of the galaxy several times, where it is exposed to increased levels of cosmic radiation for hundreds of thousands of years (Hatfield & Camp 1970). Terrestrial temperatures are postulated to increase during the perigalactic passage and decline near the apogalactic point, producing long-term climatic cycles (Meyerhoff 1973, Steiner & Grillmair 1973). Encounters with major spiral arms of the galaxy, occurring at 100 million year intervals, may expose the Earth to short-term environmental stresses. The brief immersion of the solar system within dense clouds of interstellar matter could affect terrestrial climates (Talbot et al 1976). Clark et al (1977) note that in the course of the ten million year transit through a spiral arm the Earth is exposed to a high incidence of nearby supernovae, which result from the explosion of massive stars created in the compression lane of the arm.

Thus the galactic environment may produce both episodic and acute stresses within the biosphere. The effects of the galactic milieu in Earth history will continue to be an interesting area of research

CONCLUSIONS

The stratigraphic record suggests that well over half of the species of organisms inhabiting the planet became extinct in a general biotic crisis at the end of the Mesozoic Era. Although secondary trophic effects are difficult to isolate, it would appear that large terrestrial vertebrates, such as dinosaurs, pterosaurs, and giant crocodilians, and planktonic marine organisms were exterminated as a direct result of the primary causes of the extinction. The length of the crisis is currently estimated to be within the range of one-half million to a few tens of years. It may have occurred in two, nearly simultaneous pulses, one affecting terrestrial and marine

plants more severely and another affecting terrestrial vertebrates more severely. Extinctions on the scale of those which took place during the Cretaceous-Paleocene transition are rare events in Earth history.

A coincidence of terrestrial stresses, such as marine regressions, global temperature changes, and increased volcanicity, has been invoked to account for the terminal Cretaceous extinctions (Ager 1976). This is unlikely, for the time scale of such changes is substantially greater than that of the extinctions themselves. During the last two million years the biosphere has been subjected to relatively rapid alternations of glacial and interglacial climatic regimes. The period was characterized by changes of strand line and temperature, as well as levels of volcanism, which were at least as great as those which occurred during the late Cretaceous and early Paleocene. Rates of turnover among large terrestrial mammals were high in North America, but diversity remained approximately constant until postglacial time (Webb 1969). There were no massive extinctions of planktonic marine organisms (cf Berggren & Van Couvering 1974).

The biosphere is probably well adapted to coping with the type of biological stresses that occur relatively frequently through geologic time. Episodic changes of the kind described in the preceding paragraph may be considered to belong to this category, as are fluctuations in solar radiation and stresses generated by the infall of comets and asteroids. The solar system, on the whole, has provided an environment favorable for the long-term survival and development of life on our planet.

The solar system is in turn protected by its isolation within the vastness of the galaxy. In human experience there is little visible evidence of a cosmos beyond the sun other than the strangely disquieting beauty of a starlit night. Through the centuries supernovae have occasionally appeared in the sky, even during the day (Stephenson & Clark 1976). They represent the only objects known in our region of the galaxy capable of damaging the terrestrial biosphere even at great distances.

The major stresses resulting from a nearby supernova are postulated to occur in two pulses, each of about a decade's duration, separated by a somewhat longer, relatively stress free interval. A chronic increase in background radiation may endure for several thousands of years. Because the occurrence of a nearby supernova is such a rare event and its effects would be so sudden and so massive, there is little likelihood of the biosphere developing an adaptive response in the way that it is able to adjust to episodic environmental changes.

Unfortunately, when organisms are confronted with any environmental pressure which they can neither tolerate nor evade they can only respond by dying. Even communities of organisms respond to a variety of pres-

tures (cooling, aridity, chemical pollution, radiation) by returning to a formation resembling an earlier stage in the development of a successional climax (Whittaker & Woodwell 1971). Accordingly, the fact of the disappearance of an organism or a community of organisms may not reveal the stresses which brought about its demise. The spectrum of metabolic systems represented by organisms that became extinct at the end of the Cretaceous greatly exceeds the extremes postulated in the current debate on dinosaurian metabolism (Marx 1978). Whether large dinosaurs were warm- or cold-blooded is of uncertain relevance to the problem of their extinction.

There is, consequently, ample justification for geophysical studies of the Cretaceous-Paleocene boundary to more precisely identify agents of biological stresses. For example, increases in cosmic ray intensities from nearby supernovae may produce concentrations of cosmogenic isotopes in the sedimentary record (Higdon & Lingenfelter 1973). Evidence of meteorite impact can be sought through trace element analyses (see Christensen et al 1973), and cometary collisions may be revealed through the identification of tektite fields. Several series of sedimentary samples spanning the Cretaceous-Paleocene boundary in North America, Europe, and New Zealand are housed in the Paleobiology Division, National Museum of Natural Sciences (Ottawa) and are available for such studies. The time period over which the extinctions took place should also be more precisely delimited through detailed magnetostratigraphic studies (see Foster 1977).

Of all the hypotheses which have been advanced to account for the extinction of the dinosaurs, only one involving the explosion of a nearby supernova currently seems plausible to this writer. However, firm astrophysical evidence of a supernova in the vicinity of the solar system about 65 million years ago is as yet unavailable. The probable effects of the collision of supernova ejecta with the atmosphere, and the physical reflection of these effects within sedimentary processes, must be carefully evaluated. Only then can the stratigraphic record be examined meaningfully for physical data which will uphold or negate the hypothesis that a nearby supernova coincided with the biologic catastrophe which occurred at the end of Cretaceous time. In the present state of uncertainty it would not be too surprising if a fundamental deficiency were found in the supernova model. If such should prove to be the case, the disappearance of the dinosaurs would remain an outstanding mystery of the geologic record.

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