THE TERMINAL CRETACEOUS EXTINCTION EVENT

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OPSOMMING

Die oorsake van massauitsterwings in die geologiese verlede bly nog 'n fassinerende onderwerp vir bespreking. Die moontlikheid van katastrofiese ekstraterrestriële oorsake word tans nog druk bespreek en wissel van supernova tot die wyd gepubliseerde asteroïedimpakteorie van Alvarez en medewerkers wat op die aanwesigheid van groot hoeveelhede iridium op die grens tussen Kryt en Tersiêr gebaseer is. So 'n impak kon moontlik 'n wêreldwye vuur en gevolglike as tot gevolg gehad het wat die son se strale gekeer en 'n sogenaamde kernwinter veroorsaak het; die moontlikheid van suurreën is ook nie uitgesluit nie.

Baie outeurs verwerp egter die ekstraterrestriële teorie en meen dat massauitsterwings aan verskillende terrestriële oorsake toegeskryf kan word. Moontlikhede is die verlaging van watertemperatuur in oseane, die terugtrekking van die see sodat tussengetydiere aan droë toestande blootgestel word, die oorstroming van die land deur seewater en geofisiese aktiwiteite van die aarde. Die idee dat baie diergroepe, soos die dinosouriërs, nie skielik uitgesterf het nie, maar geleidelik, het ook heelwat aanhangers. Biotiese faktore soos siektes of die akkumulering van letale gene kon waarskynlik slegs 'n rol in agtergronduitsterwing gespeel het, maar kon nie massauitsterwings veroorsaak het nie. Groot veranderinge in ekostelsels kon egter wel tot massauitsterwings gelei het.

Soos belangstelling in massauitsterwing gedurende die laaste aantal jare toegeneem het, is daar baie gegewens vir die meeste uitsterwingsgebeure versamel. Een belangrike onbeantwoorde vraag is of die sogenaamde katastrofiese gebeure - soos di teen die einde van dieKrytperiode - sowel kwalitatief as kwantitatief van die talle ander kleinskaalse uitsterwingsgebeure verskil. 'n Aspek wat almal nog dronkslaan is die selektiwiteit ten opsigte van groepe wat tydens sekere periodes uitsterf. Die oorsake van massauitsterwings is waarskynlik 'n sameloop van

omstandighede soos die area van habitat en die klimaat en chemie van die atmosfeer en oseaan.

Organic diversity is a response of living matter to the diversity of environments, and to opportunities for different modes of life. The many kinds, sizes, shapes, activities and habitats of living beings are bewildering but life has been highly diverse throughout long spans of time. Creationism holds that the world's plants and animals have been decreasing in diversity by extinction, but the fossil record indicates quite the opposite. As faunas and floras replaced their ancestors through time, new organisms appeared more frequently than outmoded groups disappeared.

The geological record of fossils follows a single, invariant order throughout the world. The oldest rocks contain only single-celled creatures; invertebrates dominate later strata, followed by the first fishes, primitive amphibians and reptiles, dinosaurs, mammals and man. Fundamentalists resolve the problem of this invariable order in the earth's strata by invoking Noah's flood: all creatures were churned together in the flood and their fossilized succession reflects the order of their settling as the waters receded. Could exceptionless order possibly arise from a contemporaneous mixture by such dubious processes of sorting? If, however, the strata represent vast stretches of sequential time, then invariant order is an expectation, not a problem. No fossilized man keeps company with a dinosaur, because man was still 60 million years in the future when the last dinosaur perished. But, what could have caused the several mass extinctions during geological time? The answer to this question is not self-evident.

Because it is calculated that 99 per cent of all the species which have ever existed are now extinct, it could perhaps be more instructive to discover why species vanish than why they appear. There is a mass of palaeontological evidence to show that it is usually the most highly adapted creatures which vanish. Life continues by the evolution of less specialized ancestors; it is creatures which evolve least which last longest. The periodical occurrence of extinctions in which a wide range of orders and even whole phyla are wiped out simultaneously remains a long-standing and highly puzzling problem. These major catastrophes seem to have occurred at the end of geological periods and are in fact used to date the latter. One of the most drastic of all these mass extinctions was the one which occurred at the end of the Cretaceous Period and affected organisms right across the broad spectrum of life. About a quarter of known animal families succumbed: sixteen orders or superfamilies perished, including marine reptiles, flying reptiles and dinosaurs; several types of fish gave up the struggle for existence as also many belemnites and ammonites. It is an extinction event which shows up so clearly in the geological record that it has been taken to mark the end of the Cretaceous (the age of dinosaurs) and the beginning of the Tertiary (the age of mammals). This Mesozoic-Cenozoic contact not only serves as a model for an era boundary but also as an outstanding example of a biological crisis and as a focus for many hypotheses on the causes of wide spread extinction.

Toward the close of the Cretaceous period - some 70 to 65 million years ago - the earth was a very different place. The Atlantic Ocean was forming as the New and Old World continents were drifting apart, the Indian subcontinent was an island on a collision course with Asia, and Australia was just beginning its drift north from Antarctica. There were no ice caps at the poles, and plants with some of the characteristics of subtropical vegetation reached as far north as the present Arctic Circle; this was an indication that the higher latitudes were then far warmer. On land, angiosperms were dominant in both the Northern and Southern hemispheres. Dinosaurs occupied the highest levels of the food web, and a host of other vertebrates - fish, amphibians, reptiles such as crocodiles, turtles and lizards, birds, and mammals - are known to have existed. The Cretaceous oceans and epicontinental seas harboured reef-forming bivalves (rudists), ammonites, and a variety of marine reptiles that, like dinosaurs, were soon to become extinct.[1]

There is a popular fascination with the possible reasons for the total extinction of a once flourishing group of organisms. Speculation runs riot. However, the animals whose extinction usually arouses most curiosity are dinosaurs, especially their final late Cretaceous extinction. Some notion of the various extinction hypotheses that have been proposed is given by Jepsen (1964):[2]

"Authors with varying competence have suggested that dinosaurs disappeared because the climate deteriorated (became suddenly or slowly too hot or cold or dry or wet), or that the diet did (with too much food or not enough of such substances as fern oil; from poisons in water or plants or ingested minerals; by bankruptcy of calcium or other necessary elements). Other writers have put the blame on disease, parasites, wars, anatomical or metabolic disorders (slipped vertebral discs, malfunction or imbalance of hormone and endocrine systems, dwindling brain and consequent stupidity, heat sterilization, effects of being warm-blooded in the Mesozoic world), racial old age, evolutionary drift into senescent overspecialization, changes in the pressure or composition of the atmosphere, poison gases, volcanic dust, excessive oxygen from plants, meteorites, comets, gene pool drainage by little mammalian egg-eaters, overkill capacity by predators, fluctuation of gravitational constants, development of psychotic suicidal factors, entropy, cosmic radiation, shift of Earth's rotational poles, floods, continental drift, extraction of the moon from the Pacific Basin, drainage of swamp and lake environments, sunspots, God's will, mountain building, raids by little green hunters in flying saucers, lack of even standing room in Noah's Ark, and paleoweltschmerz."

What really caused this and other mass extinction events still remains a contentious issue of enduring fascination, as witnessed by the large number of papers which appeared during the last decade. The traditional darwinian view has it that organisms evolve and become extinct primarily as a result of competitive interactions, with changes in the pshysical environment being of subordinate importance. It has, however, become increasingly apparent in the last few years that organic turnover through time is characterized by long periods of relative stability punctuated by geologically brief episodes of mass extinction, during which a significant proportion of the biota of the earth is killed off. Evolution is seen to have had a substantial opportunistic component, with (lucky?) survivors radiating into the ecological niches vacated by extinction.[3]

EXTRATERRESTRIAL CAUSES OF THE MASS EXTINCTION

The puzzle of the event on the Cretaceous-Tertiary (K-T) boundary, so far as a uniformitarian explanation goes, is that there is no physical difference in the rocks on either side of the event. Whatever happened, probably happened quickly and seemingly left no trace. Once, however, the possibility of a catastrophe is admitted, other solutions become plausible. For a while, the theory of Russel & Tucker[4] came close to being accepted. They suggested that a supernova - the catastrophic explosion of a massive star at the end of its life cycle - emitted colossal amounts of lethal radiation into the interstellar medium. Even 100 million light years away, it would have disrupted the protective upper atmosphere (ozone layer), exposed the earth to cosmic rays, and brought about a marked and prolonged drop in temperature as a result of the formation of high-altitude ice clouds.[5] Larger plants and animals would have been unable to cope with the cold; smaller ones, and less highly evolved marine creatures, could survive and adapt. The duration of the events that caused the Cretaceous-Tertiary extinctions according to the supernova theory is uncertain; it might have been as little as hundreds of years or as great as two million years.[4]

One of the more recent and most widely publicized hypotheses advocating a catastrophic, extraterrestrial cause is the asteroid impact theory of Alvarez et al.[6] They discovered abnormally large traces of the heavy element iridium in a marine formation near Gubbio in the Apenine mountains of Italy. The iridium was concentrated in a layer of clay, one to two centimetres thick, that separates marine limestone of late Cretaceous age from an overlying marine limestone of early Palaeocene age. The limestone below the clay contains fossil marine organisms typical of the latest part of the Cretaceous. No organisms are preserved in the clay. In the limestone above the clay the Cretaceous organisms are absent; they have been replaced by the organisms typical of the Palaeocene. Iridium is one of several elements geologists call siderophiles and it is rarely present in the rocks of the earth's crust but is comparatively abundant in meteorites. The steady rain of micrometeorites on the surface of the earth results in modest concentrations of iridium and other siderophilic elements in the sediments that accumulate in the ocean basins.[7]

Alvarez et al. argued that the most likely reason for the increase in iridium was the impact of an extraterrestrial body such as an asteroid with a diameter of approximately 10 km. An impact of this sort would result in dust being injected into the atmosphere briefly, thereby suppressing photosynthesis and causing a temporary collapse in the food chain. They also argued that the supernova hypothesis is less likely than a hypothesis invoking the impact of an extraterrestrial body originating in the solar system. The proportions of the two stable isotopes of iridium in their clay samples from Gubbio indicated an origin within the solar system; plutonium 244, none of which has been detected, would be expected along with the iridium if the material had originated in a supernova. They did not regard the absence of plutonium 244 as conclusive, however, because alterations during deposition of rock formation might have destroyed it.

Several variants of the hypothesis have been proposed but all maintain that the observed increase in iridium at the K-T boundary was caused by the impact of an extraterrestrial body which resulted in catastrophic extinctions. According to Kyte et al.[8] the siderophilic element concentrations are too high to be understood in terms of the impact of a chondritic asteroid; either the projectile was a metal-sulphide core or the infalling material (probably weak cometary matter) was slowed down during atmospheric passage. Smit & Hertogen[9] reasoned that the impact of a large meteorite may have provided the required amounts of iridium and osmium with which the moment of extinction was coupled. Hsü[10] presented evidence indicating that the extinction of large terrestrial animals was caused by atmospheric heating during a cometary impact and that the extinction of calcareous marine plankton was a consequence of poisoning by cyanide released by the fallen comet and of a catastrophic rise in calcite-compensation depth in the oceans after the detoxification of the cyanide.

Evidence for worldwide fire

To learn more about the nature of the meteorite which deposited the layer of iridium and other meteoritic elements, Wolbach, Lewis & Anders[11] looked for noble gases in clay from the K-T boundary. Though the major part of the meteorite undoubtedly vapourized on impact, a small amount may have survived, and might be recognized or even identified by its primordial noble gas pattern. The authors did not find those gases; what they did find was pure graphitic carbon, mainly as fluffy aggregates of 0,1 to 0,5 micrometres - apparently a worldwide layer of soot. It may have been produced by wildfires triggered by a giant meteorite. This carbon, corresponding to a global abundance of 0,021 ± 0,0006 gram per square centimetre, could have greatly enhanced the darkening and cooling of the earth by rock dust, which has been suggested as a cause of mass extinctions.

Until now, it was thought that the dust kicked up by the impact of the meteorite would have blotted out the sun, triggering a deep chill lasting months. The idea led to the hypothesis that a nuclear exchange might do the same, creating a so-called nuclear winter. According to Wolbach et al. the surprisingly large amount of soot (10 per cent of the present biomass of the earth) implies either that much of the earth's vegetation burned down or that substantial amounts of fossil fuels were ignited too. They now believe that it was primarily soot from these fires created by the impact of a meteorite that plunged the earth into darkness. The impact, even if the meteorite had hit the ocean, ignited a fireball that spawned fires in the soil and vegetation at least 1000 km away. These burned over several continents and the soot blocked out the sun and cooled the earth. Carbon monoxide from the holocaust could have reached 50 parts per million in the atmosphere, well above toxic levels. With other pyrotoxins it would have killed animals outright. The particle-size distribution of the soot is similar to that assumed for the smoke cloud of "nuclear winter", but the global distribution is more uniform and the amounts are much greater, suggesting that soot production by large wildfires is about 10 times more efficient than has been assumed for a nuclear winter. Thus cooling would be more pervasive and lasting.

The K-T carbon, if dispersed in the atmosphere, would contribute to three or four proposed extinction mechanisms. First, it would absorb sunlight far more efficiently than does rock dust, which alone has been considered thus far.[6] An atmospheric load of 0,021 g of carbon per square centimetre, with an absorption coefficient typical of smoke (1 to

$6m^2/g$) would give an optical depth of 200 to 1200, thus absorbing virtually all the light and blocking photosynthesis. Second, the pyrotoxins formed during combustion would harm most land life. Carbon monoxide alone, if produced in the same amount as soot, would reach 50 ppm in the atmosphere, well above toxic levels. Third, the soot would cool the earth by the "nuclear winter" mechanism until most of the carbon had settled out of the atmosphere. The soot in the K-T clay thus is an ancient analog of the smoke cloud predicted for nuclear war.[11]

Periodic extinctions and impacts

Raup & Sepkoski[12] took the matter of mass extinction events a stage further. They investigated statistically the temporal distribution of the major extinctions over the past 250 million years, using various forms of time series analysis. The analyzed record is based on variation in extinction intensity for fossil families of marine vertebrates, invertebrates and protozoans, and contains 12 extinction events. The 12 events show a statistically significant periodicity with a mean interval between events of 26 million years. Two of the events coincide with extinctions that have been linked to extraterrestrail impacts (terminal Cretaceous and late Eocene). Though they do not commit themselves to any particular interpretation they favour an extraterrestrial cause because of the regularity of the cyclicity.

Whitmore & Jackson[13] and Davis et al.[14] have independently put forward a model in which the extinction cycle is associated with the orbital period of an unseen solar companion star. When near the perihelion the star is brought into the dense inner region of a comet cloud and by perturbing the cometary orbits initiated an intense comet shower, leading to a series of terrestrial impacts lasting up to a million years. Schwartz & James[15] and Rampino & Stothers[16] instead point out a possible correlation between the 26-Myr extinction period and the sun's oscillation about the galactic plane. They speculate that long-term changes in cosmic radiation flux due to this oscillation have provoked sufficient alterations of the biosphere to cause mass extinctions. Rampino & Stothers' reanalysis of Raup & Sepkoski's data leads them to suggest an extinction cyclicity of approximately 30 Myr, which correlates strongly with a galactic cycle.

Extinctions might have been caused when the earth passed through interstellar gas or dust clouds, or intercepted a cometary shower. To test a prediction implicit in the cyclicity model Alvarez & Muller[17] examined records of large impact craters on the earth and came to the conclusion that the craters occur in a 28,4-Myr cycle; within measurement errors, this period and its phase are the same as those found in fossil mass extinctions. Because only 13 craters met their rigious criteria, however, their conclusion must be viewed with caution.[3]

TERRESTRIAL CAUSES OF MASS EXTINCTIONS

Several recent articles have expressed grave doubts on various aspects of the impact theories. Those aspects include the contemporaneity of the iridium anomalies at different places, their correlation with an extraterrestrial event, the suddenness and contemporaneity of the K-T extinctions, and likewise their correlation with a single catastrophe.[18]

Hypotheses involving terrestrial causes for Cretaceous-Tertiary extinctions vary from catastrophic to noncatastrophic. A catastrophic theory in this class is the so-called Arctic spill-over theory:[19] The Arctic ocean was isolated from other oceans as a result of regression and tectonic activity and become brackish or fresh. Subsequent continental rifting, some 65 million years ago, broke the interoceanic barriers and allowed saline water from the Atlantic to pour into the Arctic Ocean and lighter, less saline water from the Arctic Ocean to spread as a surficial layer over all the oceans. At the surface, planktonic forms unable to withstand the decline in salinity were killed, while beneath the surface, oxygen depletion decimated other organisms. On land, organisms were most directly affected by the lowering of temperature and the drop in precipitation that would have resulted.

Climatic factors and extinction

The most important factor limiting the geographic distribution of animal species in the ocean is water temperature. An episode of climatic cooling could extinguish any species that was not adapted to the new, cooler temperatures and that lack a warmer refuge to which it could migrate.

Stanley[20] presents evidence pointing to climatic cooling as the primary culprit behind most of the known marine crises. Even the disappearance at the end of the Cretaceous of dinosaurs along with many marine animal species now appears to have been gradual. That is Stanley's main argument against attributing the entire Cretaceous crisis to an asteroid impact. Since the environmental effects of an impact would have been relatively short-lived, it cannot completely account for a crisis that probably lasted for at least two million years.

During the latter part of the Cretaceous shallow seas flooded large continental areas that are now exposed, and a belt of tropical oceans - the Tethyan Seaway - spread across southeastern Asia, the Mediterranean region and the Gulf of Mexico. Among marine organisms it was Tethyan faunas that suffered the most in the terminal Cretaceous event. Many groups of minute floating algae were decimated and planktonic foraminiferans also endured heavy casualties. The disappearing from the Tethyan Seaway of the reef-building rudists (bivalve mollusks similar to corals with cone-shaped skeletons) was particularly dramatic. So successful were these animals during the Cretaceous period that they seem to have pushed corals into a subordinate role on tropical reefs. Were it not for the sudden extinction of the rudists, they rather than corals would undoubtedly dominate the reefs in the shallow tropical seas of the modern world. Elsewhere on the Tethyan Seaway floor other groups of bivalves and gastropods also vanished, as did families of large bottom-dwelling foraminiferans. The ammonoids are one group whose elimination did not reflect the general tropical bias of the terminal Cretaceous crisis; nontropical as well as tropical species were lost. The Cretaceous crisis, therefore, was not a single brief event, but groups of organisms declined and became extinct at different times, over a period of at least two million years; there is ample evidence linking the crisis to climatic cooling. Various explanations have been suggested in making a case for the connection between climatic change and marine crises, but it may never be possible to understand fully the reasons for changes which occurred millions of years ago.[20]

Climatic factors could also have played a significant role on land. Some authors are of the opinion that there are sufficient evidence to support the argument that biotic changes across the K-T boundary were gradual and cumulative. Sloan et al.[21] present information reinforcing previous data showing that dinosaur extinction was a gradual process, lasting at least seven million years, and rapidly accelerating in the final 0,3 million years of the Cretaceous Period, during the interval of apparent competition from rapidly evolving immigrating ungulates in the Hell Creek formation of the USA. This interval involves rapid reduction in both diversity and population density of dinosaurs. Of the 30 dinosaur genera present in the area eight million years before the end of the Cretaceous, a maximum of 12 were present just before the K-T boundary event, and between 7 and 11 genera survived into the Palaeocene. Depending on the precise level of the K-T boundary with respect to these faunas, all that can be ascribed to the asteroid impact is the extinction of from one to three genera. The remaining genera either became extinct significantly earlier or later. If dinosaur extinction is not solely due to an asteroid impact the authors suggest a concurrence of several factors: global temperature lowering over the last 15 million years of the Cretaceous, lowering of sea level during the late Maastrichtian (= last epoch of the Cretaceous) and consequent increase in seasonality, major deterioration of the flora as the result of these two causes, and diffuse competition from new mammalian herbivores most likely introduced to North America from Asia.

Sloan and his colleagues also report finding dinosaur teeth in sediments laid down 40 000 years after the asteroid impact that allegedly ended the Cretaceous period and caused mass extinction of ocean life. Some authors, however, question the methods used to date the supposedly post-Cretaceous teeth, and others believe that Sloan's data do not justify the claim that dinosaur diversity was declining for seven million years before the end of the Cretaceous.[22] Deducing what actually happened to life on land 65 million years ago is a problem because the solution relies on analyses of rare terrestrial sediments. Marine sediments are easier to analyse because they are deposited slowly, predictably, and continuously over long intervals, leaving a fairly clear fossil record. Sloan agrees that the asteroid impact probably caused catastrophic extinctions in the oceans because marine animals depend heavily on phytoplankton, which would have died quickly after an impact; land plants would have survived longer and that is why an impact affects land life differently from sea life.

Kaufman[23] maintains that the terminal Cretaceous extinction event was not caused by the extraterrestrial meteorite falling on the earth's oceanic surface, but that it could have been "the straw that broke the camel's back". Detailed biological evidence, which shows that most of the terminal Cretaceous extinction was over by the time of the final catastrophe, "strongly suggests the latter". Kaufman actually favours the comet theory of Hsü, because there is not impact crater, no deposit reflecting very high global tidal waves which would have been generated by such an impact into the ocean, and no widespread mass mortality event among shallow marine organisms or among land plants that would have been shaded out by a global dust cloud. Diverse evidence suggests that terminal Cretaceous extinction was graded over[24] one to five million years in the marine realm and was primarily the result of "massive environmental deterioration resulting from relatively rapid, large-scale superimposed changes in sea level, water chemistry (especially oxygen), ocean temperature, circulation, climate, niche size and diversity, and resultant biologic effects of increased competition and broad destructuring of ecological units". The extinction was enhanced by some extraterrestrial event near the terminal phase of biotic decline.

The temporal overlap of many large-scale environmental factors is necessary for major extinction (affecting diverse organisms with varying ecological plans) to take place; many of these environmental factors are interrelated, others are chance occurrences.[23]

The view that dinosaurs attained an evolutionary acme late in the Cretaceous after which they gradually declined in taxonomic diversity over 7-10 Myr to their extinction, is questioned by Russel.[25] He assessed a possible terminal Cretaceous decline in diversity through a compilation of all the known families and genera of North American dinosaurs. The postulated decline is usually supported by comparing diversity levels in 78 Myr-old and 66 Myr-old dinosaurian assemblages. The resulting differences in diversity have never been compared, however, with those observed between older dinosaurian assemblages when their extinction was not imminent. Russel shows that, taken as a whole, the known fossil record of North American dinosaurs shows no evidence of a decline in taxonomic diversity lasting several million years or more before their extinction.

Activities of the earth and the sea

Some authors see no need to invoke an asteroid impact to explain even the iridium peak, let alone the death of the dinosaurs or any other animal group. They conclude that worldwide mass extinctions are closely related to changes in the geophysical activity of the earth. Sharp declines in the number and variety of species alternate with rapid radiations, and there are occasional major extinctions. Increased volcanic activity would also explain a worldwide deposition of iridium-rich dust.[26] The pattern of these declines and radiations exactly matches the changing rate of sea-floor spreading in the Atlantic and Pacific Oceans. Today, the Atlantic is widening at a rate of about two centimetres a year, but in the past there have been times when the spreading rates were several times greater. Just such a period of enhanced tectonic activity lasted from 73 to 65 million years ago, coinciding with the great extinction, including the death of the dinosaurs.[22] Other extinctions are also significantly correlated with the changing rate of tectonic activity. Peak rates of sea-floor spreading may coincide with enhanced volcanic and other activity, producing environmental changes which have a direct detrimental effect on life on earth.

A rival explanation to climatic cooling causing mass extinctions attaches primary importance to changes in the sea level: the area of the shallow sea floor decreases when sea level falls because portions of the continental shelf are exposed. The hypothesis assumes that vast areas of shallow sea floor are needed to sustain a diverse population of bottom-dwelling animals not adapted to conditions of the deep sea. This turns out not to be the case.[20] A quite narrow continental shelf can harbour an enormous diversity of bottom-dwelling organisms. In recent years knowledge of sea-level changes in the distant past has improved considerably, and this new evidence shows that socalled biotic crowding brought on by sea level lowering cannot possibly have caused most of the known mass extinctions in the ocean. Much of the evidence comes from the application of seismic stratigraphy techniques. By bouncing sound waves off ancient sediment layers under modern continental shelves it is often possible to detect discontinuities between the superimposed layers, which differ in density and therefore refract the sound waves in characteristic ways. A discontinuity may reveal the boundary between mud deposited in deep water and alluvial sands that accumulated on a coastal plain at a later time, after the sea has receded to a level lower than its present level. Analysis of rocks exposed on land reveals other times when the sea level was higher. Stanley[20] maintains that studies have demonstrated that during many mass extinctions sea level was no lower than it is now. Conversely, when the sea level has fallen, there has often been no biotic crisis.

Biotic factors

Purely biological factors, such as disease or accumulation of lethal genes, could play a role in background extinction but they are not likely to affect in concert a whole assemblage of organisms. An influx of immigrants can decimate a native fauna in a brief span of time - as happened, for example, when placental mammals were introduced into South America during the Pleistocene - but in such cases, the sequence of events leading to mass extinction is usually evident in the geologic record.[27] Van Valen & Sloane[28] are inclined to the view that something like this may have occurred at the end of the Cretaceous. The passing of the ammonites and dinosaurs at the close of the Mesosoic calls to mind the similar snuffings out of dominant higher categories at several levels in the Phanerosoic. Characteristically, these extinction events were followed by the loss of overall diversity, a reduction in provinciality, and the elimination of the most specialized groups.[27] Each of these events involved different geographic and climatic conditions, and each was, in this sense, unique.

One of the most important groups of marine invertebrates to be extinguished at the end of the Cretaceous period was the chambered cephalopods known as ammonites. The fossil record suggests that the extinction of the ammonites was a consequence not of a catastrophy caused by an extraterrestrial body, but of sweeping changes in the late Cretaceous marine ecosystem.[29,30] Any hypothesis about the fate of the ammonites must take into account the question why even the long-lived ammonite species should have died out when their near relatives, the nautiloids, survived? Ward's[29] guess is that the reproductive strategy or perhaps some aspect of the ecology of the adults saved them. From their shell structure it seems that most ammonites lived in comparatively shallow water. They would have imploded at the depths to which nautilus now penetrates. Juvenile ammonites, hatched from small eggs, with shells no larger than two millimetres in diameter, may have spent their first days or weeks as members of the plankton. And plankton had the highest rate of extinction of any group of marine organisms at the end of the Cretaceous; 90 per cent of all plankton species were extinguished. The juveniles of nautiloids from the Mesozoic onward, on the other hand, seem, on the basis of the form of their shells, to have hatched at a much larger size (from 5-25 mm). Quite possibly the ammonites had a survival strategy based on semelparous reproduction, with a lot of small eggs like most modern cephalopods, in sharp contrast to the iteroparous (repeated spawning), big-egg strategy of **Nautilus**. Juvenile nautiloids probably spent no time as members of the pankton and immediately assumed the near-bottom deep-water foraging mode of life characteristic of the adults. The ammonites may thus have been caught up in the collapse of the plankton ecosystem either as juveniles or as adults feeding lower down on the food chain than the nautiloids. Changes in the shells of these animals at the end of their long history suggest they were fighting a losing battle against more mobile, shell-crushing predators. They were especially unable to compete with the jawed, neutrally buoyant teleosts that began to arrive on the scene in Mesozoic times. Nautilus survived because it was already a relatively deep-water animal, able to retreat beyond the range of more dangerous fish, and it was presumably already specialising as a scavenger with sensitive chemical senses.

Valentine & Jablonski[31] also maintain that the patterns of marine larval extinction associated with the K-T extinction do not conform to most bolide impact scenarios; most versions of the bolide impact hypothesis of mass extinction propose occlusion of the sun by dust or smoke and severance of planktonic food chains for months or a few years, and this should select preferentially against planktotrophs (which feed on suspended food items). The K-T extinction factors cannot have completely severed the planktonic marine food chains or greatly destabilized the productivity regimes, or planktotrophs would have been preferentially extinguished. Valentine & Jablonski reason that among planktotrophs, taxa with short generation times should have suffered most heavily, and long-lived taxa should have been least subject to extinction. None of these predictions are met. For instance, among fossil prosobranch gastropods, planktotrophs survived the end-Cretaceous extinction equally as well as non-planktotrophs (which do not feed but are supplied with nutrients - yolk- parentally).[31] It does not seem plausible that the mechanisms linking bolide impacts with extinctions through catastrophic plankton mortality were responsible for the K-T extinctions of marine benthos. More complex models involving somewhat less extreme and more prolonged perturbations or other causal mechanisms entirely are evidently required.

CONCLUSIONS

As interest in mass extinctions has increased over the past few years, detailed documentation has become apparent for all but a few extinction events. One important unresolved question is whether apparently catastrophic events like the one at the end of the Cretaceous was different qualitatively as well as quantitatively from the more numerous smaller-scale events which have been studied far less. For instance, according to Benton[32] the present evidence regarding non-marine tetrapods does not support the view that mass extinctions are statistically distinguishable from background extinctions. Hallam[33] suggests that finer-grained analyses than those of Raup & Sepkoski[12] are required, down to species level where possible, at the maximum stratigraphic precision available. There should also be thorough documentation of changes in the stratal sequence in different regions in the hope of detecting correlations with biotic change that may lead to the inference of causal relationships. Too many of the theories that consider Cretaceous-Tertiary terrestrial extinctions, particularly dinosaur extinction, suggest causation based on generalized data but do not attempt to corroborate theory with documentation from fossiliferous sequences that transgress this boundary; unfortunately these sequences are extremely rare.[1]

Jablonski[34] is of the opinion that the hypothesis that geochemical and other geological anomalies at the end of the Cretaceous are the signature of an extraterrestrial impact have weathered an intensive round of testing.[35,36,37,38] Inconsistencies and uncertainties remain, but no conclusive falsification has been forthcoming. New evidence suggests that externally forced mass extinctions are "frequent, apparently periodic, and constitute a qualitative change in the rules of extinction and survival from those that prevail during times of background extinction." An expanded role for mass extinctions in evolutionary theory is probably necessary regardless of the ultimate fate of impact or periodicity hypotheses, but a 26-Myr forcing period - brief relative to the rates of macroevolutionary change during background times - drives this issue home with great force."[34]

No one has delivered a knockout punch to the idea that comet showers have caused periodic extinctions but the hypothesis is falling somewhat back under increasing criticism.[39] The absence of evidence for iridium maximums spanning one to three million years at the predicted times is strong evidence against the occurrence of comet showers. Kyte & Wasson[38] maintain that this confirms other arguments disputing their existence and casts doubt on the existence of periodicities. Everyone, however, agrees that statistical analyses will never decide the question. The search is still on for a solar companion, and geochemists have been searching for several years for new layers of iridium-rich sediments that might mark other major impacts besides the one now generally accepted to have occurred 65 million years ago; the search has not been all that productive, so far.

With solid geological evidence scarce and hard to interpret, the debate over what killed the dinosaurs and other groups seems sure to continue. Although the problem of mass extinctions is still unsolved, researchers are learning how to ask questions. One of the more puzzling aspects of the macroevolutionary pattern of mass extinction events is their selectivity.[40,41,42,43] The causes of mass extinctions possibly lie in the chance coincidence of multiple factors such as the area of habitat and the climate and chemistry of the atmosphere and ocean. The odds seem slim that someone will soon uncover any evidence as convincing as an iridium-covered dinosaur graveyard, or the remains of a sabre-toothed tiger making a meal of a dinosaur.[22] As far as hypotheses are concerned, the simplest one is not necessarily the best, and a single explanation may not even cover one mass extinction. It is, however, a certainty that the terminal Cretaceous event will remain a challenging and exciting area of research for many years to come.

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