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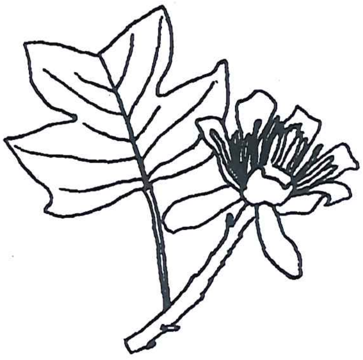

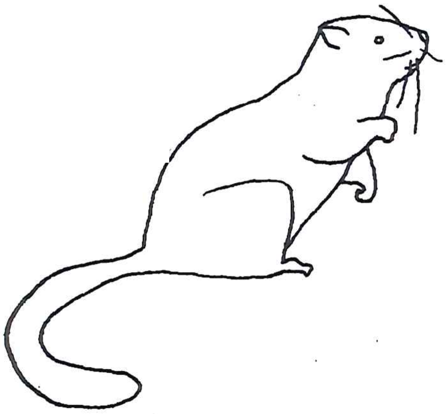

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GLOBAL EXTINCTIONS, RECOVERIES AND EVOLUTIONARY CONSEQUENCES

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ABSTRACT

The evidence pertaining to widespread, historic extinctions - usually described as global in scope - is examined. In recent years, it has become customary to evaluate the significance of such extinctions by attempting to sum the losses at the family or generic level based on information from the entire marine fossil record. However, it has been demonstrated that this record as a whole is not dependable to the extent that it can be used for such purposes. Consequently, the severity of widespread extinctions must be gauged from evidence provided by people who have done research on individual groups of organisms. Utilizing such information, it appears that seven widespread extinctions have taken place in the marine environment.

Historical extinctions should not be termed global unless they can be shown to have been effective in both the terrestrial and marine environments. The Permian/Triassic event is apparently the only time at which there was a drastic diversity decrease in both environments. The other six extinctions appear to have had only minor, if any, effects on the terrestrial and freshwater biotas. Even the Cretaceous/Tertiary extinction, which resulted in the demise of the large dinosaurs, had little effect on the other terrestrial groups.

The conventional assumption that extinction episodes have been advantageous in terms of general evolutionary progress, is difficult to justify. Severe extinction events appear to preferentially eliminate tropical organisms creating an ecological vacuum. The vacated area is then reoccupied by older, less derived taxa from higher latitudes or other refuges. This process has the effect of setting back the evolutionary clock to an earlier time. The evidence for this sequence is good for the marine environment and suggestive for the terrestrial habitat. Such information, plus that pertaining to the loss of evolutionary innovations during the extinctions, leads to the conclusion that the historic extinctions were disastrous interruptions to evolutionary progress.

The hypothesis that extinctions took place in a periodic manner approximately every 26 m.y., aroused great interest and stimulated much research. But, judging from the seven extinctions now recognized, their erratic chronology makes it difficult to discern any periodicity. As far as causes are concerned, sea-level regressions seem to have been a factor in all but one of the extinctions. The one exception may have been due in part to a sea-level rise that brought anoxic water to the continental shelf. Certainly, other factors came into play, some as the consequences of sea-level change and others coincidental. Tectonic plate movement, volcanism, polar glaciation, and possibly even extraterrestrial impacts, may have been important at certain times.

It is suggested that terms such as "mass extinction", "mass killing", or "catastrophic event" are inappropriate when used to describe extinction episodes in the geologic record. These were not sudden events but gradual deteriorations in biotic diversity that developed over periods of one to several million years. The time required for the recovery of diversity was usually much longer. Extinctions and their subsequent recoveries took place not on a contemporary, but on an evolutionary time scale.

> Species extinction in general, and mass extinction of species in particular, is a factor that cannot be neglected in any serious attempt to understand the present shape and past history of the biosphere.
>
> Antoni Hoffman, Arguments on Evolution, 1989

INTRODUCTION

Ever since the discovery of the fossil remains of a variety of huge dinosaurs in the northwestern interior of North America, discussions about the causes of their disappearance have been the focus of great scientific and public interest. The long-term fascination with this subject received a new impetus in 1980 when Luis Alvarez et al. published their theory about the Cretaceous/Tertiary extinction being caused by the impact of a giant asteroid hitting the earth. What a spectacular story--the earth hit by an extraterrestrial body which killed off the dinosaurs, the largest land animals that ever existed! No wonder it caused great excitement.

Soon after the hubbub created by the Alvarez theory, David Raup and John Sepkoski announced their "periodic hypothesis" which suggested that a great extinction had taken place about every 26 million years. This created a new wave of excitement and encouraged scientists to take another look at the evidence for extinction events in other parts of the stratigraphic record. Many people, representing a wide variety of disciplines, became involved. Astronomers and astrophysicists speculated about the causes of the supposed periodicity, sediments laid down during extinctions were examined by physicists and geochemists, and appropriate fossils were evaluated by the multitude of paleontologists specializing in various groups of plants and animals.

The result of increased interest in historic extinctions has been a flood of published material. Most of it has appeared in the form of articles in scientific journals but much of it, particularly on the popular subject of the demise of the dinosaurs, was printed in general magazines and newspapers. Almost all of the scientific material is devoted to events that occurred in one time frame, data on one group of plant or animal fossils, or theories about the history of one particular biotic group. A few accounts have dealt with the severity of extinctions in a given environment. Almost all of these contributions are important to an ultimate understanding of the causes and consequences of historic extinctions. However, there has been no comprehensive attempt to analyze this information with respect to the theories that started all of the excitement in the first place. In a large number of articles, the data has been discussed in terms of global extinctions, yet almost all of them pertain to either the marine or the terrestrial environment, very seldom both. If historical extinctions are to be discussed in a global context, evidence from both main components of the biosphere needs to be considered.

Despite all that has been published so far, many questions about historical extinctions still lie before us. Some of the more important are: (1) are the theories put forth by Alvarez and by Raup and Sepkoski still viable? (2) how many of the recorded extinctions are truly global in scope? (3) do these extinctions have common causes? (4) what were the evolutionary consequences of the major extinctions? and (5) did the extinctions actually represent "catastrophes" or "mass" die offs or did they occur on a more gradual or evolutionary time scale?

The following analysis is an attempt to evaluate the historic extinctions from a global (marine and terrestrial) standpoint with particular attention to the foregoing questions. The conclusions reached herein may change as more information becomes available from the many research projects that are still underway.

EARLY VIEWS

In the early 19th Century, the famous French anatomist and paleontologist Georges Cuvier became convinced that the Earth had undergone a series of great catastrophes, the most recent being the biblical Deluge. After each catastrophe, the Earth was repopulated by remnants that had somehow survived the crisis. The new species that subsequently appeared were supposed to have come from parts of the world previously unknown. Cuvier, like Carolus Linnaeus, believed that species once created did not evolve but remained fixed through time. The theory of catastrophism finally succumbed to the concept of uniformitarianism introduced by James Hutton and effectively championed by Charles Lyell and Charles Darwin.

Charles Lyell viewed life as a continuous fluctuation of living populations which expanded or contracted their boundaries as geological agents altered local topography and climates (Browne, 1983). Wallace (1855) observed that new species gradually arose to take the place of those that had become extinct. Darwin (1859) emphasized the imperfection of the geological record and noted that the sudden appearance or disappearance of fossil species was probably due to the fragmentary nature of that record. By the 20th Century, paleontologists had recognized two important times of change in the history of life, one at the end of the Permian and one at the end of the Cretaceous. But these changes were not, for many years, considered to be sudden catastrophes. For example, Dunbar (1960) described the Permian/Triassic change as "orderly and gradual, not cataclysmic."

More recently, changes in viewpoint about the rapidity of extinction began to be expressed, particularly in regard to the Cretaceous/Tertiary (K/T) boundary. Schindewolf (1962) announced his concept of "neocatastrophism" in reference to an essentially synchronous annihilation of major groups of Mesozoic organisms. Bramlette (1965) described "massive extinctions" in biota at the end of Mesozoic time, Newell (1967) referred to the boundary as marking a "mass extinction," and Percival and Fischer (1977) discussed a "Cretaceous-Tertiary biotic crisis." These more dramatic terms, plus continued speculation in popular science articles about the fate of the dinosaurs, apparently set the stage for acceptance of theories involving catastrophic events.

Before 1980, a wide variety of hypotheses were proposed in order to account for extinctions, most of them considered to be gradual in their effect. In regard to the demise of the dinosaurs, Woodford (1965) noted such factors as a colder climate, the sucking of reptilian eggs by little mammals, deterioration related to giantism, and virulent micro-organisms. Lipps (1970) reviewed extinction theories that involved racial senescence, sea-level fluctuations, cosmic radiation, nutrient depletion, changes in the composition of sea water, and biological interactions. Kauffman (1979) listed the supposed effects of radiation due to a solar explosion or a supernova, disruption of the O_2/CO_2 balance in the atmosphere and oceans, breakdown of oceanic circulation, increase in lethal trace elements, and spillover of the Arctic Ocean.

PALEOZOIC EXTINCTIONS

When organisms evolved the ability to secrete calcareous skeletons, they began building mounds on the sea floor. Calcareous cyanobacteria first appeared in the Tommotian Stage of the Lower Cambrian, about 570 million years ago (m.y.a.). Archaeocyathids, primitive sponge-grade animals, then evolved and invaded the cyanobacterial mounds (Rowland and Gangloff, 1988). The archaeocyathids, which may have contained photosynthesizing symbionts, produced skeletons of calcium carbonate.

The reefs built by these organisms became widespread through the course of the early Cambrian. A rapid rise in archaeocyathid diversity approximately coincided with the rise of the olenellid trilobites. For a period of about 10-15 m.y., the reefs were built and dominated by the archaeocyathids while the level bottoms were dominated by the olenellids (Fagerstrom, 1987). During the Elankian Stage, the archaeocyathid reefs underwent an abrupt decline, although the animals themselves persisted in level bottom communities until the late Cambrian. Very few reef structures have been found in Middle Cambrian to early Ordovician deposits.

Sepkoski and Miller (1985) recognized the Cambrian fauna as being the first of the three great evolutionary faunas of the Phanerozoic. It consisted largely of trilobites, inarticulate brachiopods, monoplacophorans, hyolithids, and eocrinoids. The Cambrian-Ordovician boundary is sometimes recognized as the time of a major extinction event. In their review of the fossil record of the arthropods, Briggs et al. (1988) concluded that the boundary did not represent a major extinction event for trilobites at the family level. There was apparently a high generic turnover, but taxonomic pseudoextinctions were considered to be a problem. The recognition of "biomere" boundaries within the Cambrian, as major extinctions, were viewed to have similar difficulties. Palmer (1984), in discussing trilobite communities of the middle and late Cambrian, referred to three disasters and recoveries. During each extinction, it was the shelf trilobite communities that suffered the most. The subsequent radiations originated from deep water or high latitude groups that had survived the extinctions (Stanley, 1989). With the advent of the Ordovician, the Cambrian fauna began to undergo a gradual decline and its communities became restricted to offshore environments. The nearshore habitats were occupied by the Ordovician brachiopod community (Sepkoski and Sheehan, 1983). Considering the fact that most of our information about diversity changes in the late Cambrian is based on trilobite material, and that this group does not demonstrate a clearly defined boundary effect, the close of the Cambrian is not recognized as a major extinction.

Ashgillian Stage

Over a period of about one to two m.y. near the end of the Ordovician, many taxa belonging to complex benthic and pelagic communities became extinct (Brenchley, 1989, 1990). There may have been two peaks of extinction. There were either two sea-level regressions or possibly one regression with the second extinction being caused by a transgression, which might have introduced anoxic conditions to the continental shelves. It has been suggested that the regression(s) were accompanied by climatic cooling which restricted the tropics and had a detrimental effect on diversity (Sheehan, 1982; Stanley, 1989).

Recent opinions differ in regard to the severity of the extinction. McLaren (1983) considered it to be neither sudden nor catastrophic, Stanley (1989) described it as one of the most severe ever to strike life in the oceans, while Brenchley (1989) termed it less severe than the end-Permian and end-Cretaceous events. Stanley stated that the tropical reef community was devastated but Fagerstrom (1987) had indicated that there was a far greater impact on the structure of the level bottom and pelagic communities than on the reef communities. The following groups apparently lost most of their genera: trilobites, conodonts, graptolites, primitive echinoderms, and corals (Brenchley, 1990). Eight echinoderm families disappeared (Paul, 1988).

The patterns of extinction and survivorship among the Ordovician trilobites were studied by Chatterton and Speyer (1989). They found that all taxa with pelagic adults had become extinct by the end of the Ordovician. Similarly, most of those with entirely pelagic larvae had also disappeared. They concluded that the preferential loss of certain life-history categories provided some information as to the causes of the Ashgillian extinction. In their opinion, this event was most likely the result of several factors including environmental perturbations, ecosystem breakdown, and biogeographic restriction. These changes are consistent with an extinction model involving global cooling and sea-level regression caused by glaciation.

Frasnian Stage

The other mid-Paleozoic extinction took place in the Frasnian Stage of the late Devonian. Fagerstrom (1987) described the extinction as extensive. It meant the end of virtually all the stromatoporoids, almost all the corals, many of the major brachiopod groups (Ager, 1988), and the tentaculitids. There was a substantial reduction in trilobite diversity and a high taxonomic turnover among the ammonoids. The higher taxa involved were generally important members of the level bottom, pelagic, and reef communities. Frasnian reefs were large and widespread but those of the next stage (Famennian) are relatively rare. Both rugose and tabulate corals were decimated (Scrutton, 1988). Pedder (1982), in discussing the rugose coral record across the boundary, noted that only 4% of the shallow (warm) water species survived compared to 40% of the deepwater species. Anstey (1987), who worked on the Paleozoic bryozoans, found that the morphologically complex taxa underwent a much greater rate of extinction during times of crisis. The tropical taxa were the most severely affected while, in contrast, the polar communities were largely unaffected (Stanley, 1989).

The first major foraminiferid radiation occurred in the Middle Devonian and culminated in the Frasnian Stage (Brasier, 1988). The extinction event eliminated forms of relatively advanced architecture while those of primitive or intermediate architecture survived. Supposedly, the foraminiferan extinctions were caused by a rapid transgressive pulse which caused anoxia on the continental shelves and a 'drowning' of reef-associated fauna. Among the cephalopods, major groups of nautiloids and ammonoids disappeared. However, it should be noted that the cephalopods have always been very sensitive to environmental changes, with a total of eight extinctions and recoveries being recorded for the mid-Paleozoic (House, 1988). The trilobite evidence suggests a protracted decline in diversity throughout the Devonian with the final demise of only a few clades at the end of the Frasnian (Briggs et al., 1988).

The general marine invertebrate data pertaining to the Frasnian extinction were reviewed by McGhee (1988, 1989, 1990). Instead of a single peak in the extinction rate, he found multiple periods of high extinction spanning an interval of two to four m.y. There was a sharp net loss in species diversity at the very end of the Frasnian but this appeared to be mainly attributable to a decline in species originations. Goodfellow et al. (1989) suggested that a sudden turnover of anoxic waters after a period of ocean stagnation was responsible for a "mass killing" at the boundary. They observed further that such a catastrophic mixing of bottom and surface waters could have been caused by the ocean impact of a large extraterrestrial body. This narrative appears to be speculative in view of the fact that there is, so far, no unequivocal evidence showing such a sudden extinction event. There is no doubt that the late Devonian extinctions constituted a series of disastrous events for many animal groups. As noted by Hallam (1989), anoxia appears to have been an important factor but it is unclear whether this condition was associated with sea-level transgression or regression. Global cooling has also been suggested (Stanley, 1989). The sea-level chart of Hallam (1984) shows a dramatic drop at about the end of the Frasnian Stage.

From an evolutionary standpoint, the data on differential survival, reviewed by McGhee (1989, 1990), appear to be of unusual significance. There was a latitudinal effect in that the stromatoporoids, brachiopods, and foraminiferans that survived the extinction were mainly high latitude forms adapted to relatively cool water. In the brachiopods, 91% of the primarily tropical families perished but only 21% of the families containing cool water species. In the Foraminifera, the high latitude species showed a better survival and, as the tropical species receded, expanded their ranges into the low latitudes.

There was also a differential survival in a bathymetric sense (McGhee, 1989, 1990). Among the rugose cnidariams, 96% of the shallow-water species were lost in the crisis compared to 60% of the deep-water species. At the Frasnian-Famennian boundary in eastern North America, many shallow-water sponges became extinct. Simultaneously, the hyalosponges (glass sponges) migrated from deep-water regions into the shallows and underwent a burst of diversification. Modern glass sponges are generally found at water depths in excess of 200 m.

PERMIAN/TRIASSIC BOUNDARY

Although the Permian/Triassic (P/T) boundary had been recognized for many years as a time of severe extinction, the probable magnitude of this event was emphasized when Raup (1979) estimated that as many as 96% of all marine species may have died out. His procedure was to determine the percent of extinction for the higher taxonomic groups by reference to the general fossil record. Then, using the rarefaction curve technique, he calculated the percent of species extinction that must have been responsible for the disappearance of the higher groups. It has since been shown that the fossil record as a whole cannot be used for broad analyses that attempt to define extinction events in the marine environment (Smith and Patterson, 1988, also see p. 27). However, this does not detract from the fact that the P/T boundary marks a major, probably the greatest, extinction episode. Work on individual animal groups by a multitude of investigators provides evidence of a severe global reduction in diversity.

Kanmera and Nakazawa (1973) noted that the great predominance of bivalve molluscs in the earliest Triassic was presumably the result of their adaptation to newly-vacated niches left by the abrupt extinction of the Permian brachiopods. But Ager (1988) detected a gradual decline in the brachiopods rather than a mass exit. Wiedmann (1973), in discussing ammonoid evolution at the boundary, found no evidence of abrupt change. Instead, he described the gradual disappearance of an antique fauna followed by a diversification of the new elements. Among the fishes, Schaeffer (1973) called attention to the appearance of six advanced chondrostean families at the beginning of the Triassic. Later, in the Middle Triassic, six advanced holostean families arrived on the scene. However, Schaeffer also noted that most of the Permian families continued into the Triassic.

In the late Permian, reefs of imposing size existed (Fagerstrom, 1987). They were constructed primarily by skeletal and non-skeletal algae of various types, calcareous sponges, bryozoans, and some brachiopods. These reefs supported a high diversity of animals. The Capitan Limestone reefs of the southwestern United States were found to contain about 350 species of reef dwellers. The end-Permian extinction event affected all of the reef-building higher taxa and resulted in the complete collapse of the structure of all existing reef communities. The annihilation was so extensive that it took eight m.y. before reef communities began to be reestablished. There are almost no early Triassic records of any skeletal, colonial reef-builders such as algae, poriferans, corals, or bryozoans. About 76 percent of the existing bryozoan families became extinct in the late Permian (McKinney, 1985). In regard to the foraminiferans, Brasier (1988) noted evidence of a prolonged decline with preferential extinction of specialized forms and the survival of simpler ones.

For the marine invertebrate fauna in general, the end of the Permian apparently constituted the greatest crisis in the whole of the Phanerozoic. High extinction rates began in the final three stages of the Permian (Vermeij, 1987) and culminated with the complete eradication of major groups such as the blastoid echinoderms, trilobites, eurypterids, rugosan corals, fusulinacean foraminiferans, rostroconch molluscs, and all crinoid subclasses except the ancestors of modern forms. Other groups, including the echinoids, ammonoids, ostracodes, and articulate brachiopods were reduced to a handful of surviving species. In common with the extinctions of the late Ordovician and late Devonian, the end-Permian event had its most devastating effect on the reef-building and other tropical marine groups (Stanley, 1989). Van Valen (1984b) observed that the probability of extinction had gradually decreased throughout the Paleozoic but this trend was interrupted by the late Permian extinction. That extinction was so drastic that it apparently reset the clock of community evolution so it resumed at a faster rate.

In the terrestrial environment, contrasting plant assemblages have been described from southern continent Permian and Triassic deposits (Schopf, 1973). A Glossopteris flora was dominant in the Permian but was replaced by a Dicroidium flora in the Triassic. In his work on patterns of extinction in vascular plants, Knoll (1984) pointed out that in some geographic areas the floristic transition from paleophytic to mesophytic appears to have been rapid. However, wherever fossiliferous sequences are complete enough, these assemblages are separated by intermediate floras that contain elements of both groups. In the Sydney Basin of Australia, for example, the Glossopteris and Dicroidium floras were found to be separated by a distinctive intermediate assemblage characterized by "Thinnfeldia" calipteroides (Retallack, 1977).

For the terrestrial vertebrates, Padian and Clemens (1985) and Colbert (1986) noted that the most conspicuous change took place in the therapsids or mammal-like reptiles. This group dominated late Permian history but, with the transition from Paleozoic to Mesozoic times, suffered a drastic reduction. Benton (1988) observed that 15 of the 20 families that existed in the final stage of the Permian died out. Among the true reptiles, more than one-half the families and over two-thirds of the genera disappeared (Olson, 1989). The beginning of the Triassic was marked by the rise of the archosaurs, the reptiles that were to dominate the Mesozoic. Colbert (1986) and Charig (1984) suggested that the origin of this new and vigorous group may have had something to do with the decline of the therapsids. Certainly, the archosaurs introduced a new and very successful suite of skeletal adaptations that greatly increased their agility. Padian and Clemens (1985) could find no definite causal relationship between changes in the marine and terrestrial environments.

Another important vertebrate group is the labyrinthodont amphibians. They were among the first of the tetrapods and for a long time in late Paleozoic history they dominated the land (Colbert, 1986). During Permian times, their dominance was challenged by the early reptiles but the labyrinthodonts continued on through the Triassic and Jurassic as a diminishing group occupying ecological niches that had not been fully exploited by the reptiles. They disappeared from most of the world by the late Jurassic but a labyrinthodont apparently persisted in Australia until the early Cretaceous (Rich and Rich, 1989). A similar history, Paleozoic origin and survival in decreasing numbers through part of the Mesozoic, is shown by the primitive cotylosaurs and protorosaurians.

Padian and Clemens (1985) called attention to Pitrat's (1973) original work on the family diversity of marine and freshwater fishes leading up to and through the P/T boundary. The marine families underwent a sharp decline at the boundary but the freshwater (and euryhaline) group did not. In fact, the latter had undergone a less severe decline some 15 to 20 m.y. earlier and, at the boundary, were in the process of increasing their diversity, a trend that continued on into the mid-Triassic. Consequently, one might observe that the terrestrial and freshwater (vertebrate) biota underwent considerable evolutionary change but the changes were apparently gradual with Paleozoic groups slowly dying out and being replaced by new groups in the Triassic.

MID-MESOZOIC EXTINCTIONS

Late Triassic

Major extinction events took place toward the close of the Triassic and possibly at others times in that Period. In the marine reef habitat, losses among the algae were minor but the calcareous sponges suffered greatly (Fagerstrom, 1987). The sphinctozoans, which had been major reef-builders, ceased to become important in this activity. By the late Norian Stage, scleractinian corals had replaced the sphinctozoans and inozoans as the dominant reef-builders. The Norian extinction represented a setback for the scleractinians and reef construction did not get underway again until the Pliensbachian Stage of the early Jurassic, some 15 m.y. later. For five of the nine bivalve orders, the generic extinction rate ranged between 40 and 62 percent (Hallam and Miller, 1988). The families and genera of ammonoid cephalopods showed a steep decline toward the end of the Triassic (House, 1988). The main invertebrate groups affected by the extinctions were the cephalopods, gastropods, brachiopods, bivalves, and sponges (Benton, 1990). In the fishes, the older paleopterygians decreased in diversity due to decreasing origination rates but the overall diversity in the early Jurassic was about the same as it had been throughout most of the Triassic (McCune and Schaeffer, 1986).

Although the Norian is often referred to as the Stage in which the greatest Triassic extinctions took place, Johnson and Sims (1989) found evidence of heavy marine invertebrate extinctions in the Carnian. Most recently, Benton (1990) concluded that there were three separate extinctions, none clearly larger than the other two. The first occurred during the Scythian Epoch over a period of 5-6 m.y., the second from the

Scythian to the end of the Carnian Stage (15-19 m.y.)., and the third during the Norian (12-17 m.y.). Thus there may have been three protracted extinctions which, together, occupied most of the Triassic.

In the terrestrial environment, an analysis of the fossil plants was published by Ash (1986). He concluded that neither megafossils nor palynomorphs showed a significant change across the Triassic-Jurassic boundary. In general, the fossils indicated that plants were slowly evolving with one assemblage gradually giving way to another and that the floras were gradually becoming more modern. The palynological data presented by Boulter et al. (1988) show a considerable drop in diversity beginning in the Rhaetian Stage, but the decrease may be mainly due to a cessation of species formation instead of species extinction.

The first positive dinosaur remains are found in the Carnian Stage of the Triassic (Padian, 1986). At its beginning, the Triassic was populated mainly by vertebrate groups that had evolved in the Paleozoic and had survived the extinction at the end of the Permian. The therapsids were the largest and most diverse tetrapod group at the beginning of the period. Their prominence decreased during the Triassic until only a couple of lineages survived at the end of that time. Other Paleozoic holdovers included various amphibian groups, the Procolophonia, and some small diapsids. According to present knowledge, some 19 groups of tetrapods, recognized as distinct families or higher taxa, are endemic to Triassic strata. It seems as if these groups ecologically replaced the early Triassic therapsid faunas just as they were, in turn, replaced by the dinosaurian faunas at the end of the Triassic.

Toward the end of the Triassic, several new groups of vertebrates began to appear. These included crocodylomorphs, pterosaurs, lepidosaurs, two orders of dinosaurs, and several groups of therapsid synapsids, including the morganucodontids, generally considered the first true mammals. Also, the first "salamander-like" lissamphibians showed up. It has been observed that evolution of these new groups marked the origin of the modern vertebrate fauna (Padian, 1986). Charig (1984) emphasized that, at the beginning of the Triassic, the large land vertebrates were nearly all therapsids but, by the end of that period, they were nearly all archosaurs (dinosaurs and their kin). He suggested that the competitive success of the latter was due to locomotor improvements and a great increase in size. Colbert (1986) noted that the tetrapod extinctions that took place at or near the end of the Triassic could be placed in three categories: (1) disappearances of long-established groups, (2) displacement of ancestors by their descendants, and (3) extinctions of small "holdovers" by newly arisen competitors. Altogether, about 22 percent of the tetrapod families disappeared (Benton, 1988). Shoemaker and Wolfe (1986) estimated that the extinction was distributed somewhere within an 18 m.y. interval. Olsen et al. (1987), suggested that a rapid or catastrophic change took place at the boundary but Padian (1988) felt that this conclusion was not justified.

Pleinsbachian Stage

Although the Pleinsbachian has been recognized as a minor, global marine extinction (Sepkoski, 1986), Hallam (1986) pointed out that this event was focused in western Europe. Here the seas retreated and black muds accumulated under conditions of reduced oxygen concentrations. About 80% of the bivalve species in that area were eliminated. In regard to reef communities (Fagerstrom, 1987) noted that the Pleinsbachian and Toracian were recovery periods for the reef-building corals that had been damaged in the Norian extinction. In the tetrapods, there appears to have been about a 30% reduction in family diversity at the end of the Lower Jurassic (Colbert, 1986). This may or may not have been concurrent with a possible extinction in the marine environment. None of the orders to which the eliminated tetrapod families belonged became extinct at the time.

Tithonian Stage

As with the Pleinsbachian event, Hallam (1986) determined that this was a regional rather than a global extinction. Five bivalve families became extinct but all were small, containing only a few genera (Hallam and Miller, 1988). Most of the extinctions took place among the ammonoids and to a lesser extent, bivalves and corals. Fagerstrom (1987) called attention to a remarkable change in the composition and structure of the reef-building guilds. The cyanophytes became considerably less important. Numerous sponge taxa became extinct so that, after the Jurassic, neither the hexactillinids nor the demosponges remained important reef-builders. The Inozoa and the Stromatoporoidea also decreased and thereafter did little reef-building.

According to Colbert (1986), there was a significant extinction of tetrapod families at the end of the Jurassic amounting to about 36% of the fauna. But the compilation of Benton (1988), based on more recent data, does not indicate a significant decrease. One may conclude that the end-Tithonian event was not a great disaster in terms of the loss of major evolutionary lines. Bakker (1978) detected a change in dinosaur feeding behavior at the beginning of the Cretaceous. About this time, a radiation of big, low-browsing ornithischian dinosaurs took place. This was also the time that the radiation of angiosperm plants got underway. It is possible that the new availability of low, fast-growing plants had an important effect on dinosaur evolution.

Cenomanian Stage

The Cenomanian Stage of the mid-Cretaceous has only recently become recognized as the time of an extinction event. Fagerstrom (1987) obtained an estimate from E. G. Kauffman indicating that 35% of the molluscan genera, 70% of the molluscan species, and 70% of the planktonic foraminiferan species became extinct at or near the end of the Cenomanian. Fagerstrom also noted that, by this time, the rudists had replaced the scleractinians as the chief reef-builders. Besides the foraminiferans, the taxa most affected were the ammonoids, bivalves, echinoids, dinoflagellates, malacostracans, and ostracodes. In contrast to the previous extinctions, which appear to have taken place during sea level regressions, the Cenomanian event correlates with a major sea level rise, perhaps to its highest point in the Cretaceous (Hallam, 1989). The benthic fauna was apparently impoverished by a progressive penetration of the oxygen minimum zone into the epicontinental seas (Jarvis et al., 1988).

On land, the tetrapod families lost very little of their diversity (Benton, 1988). As with the Tithonian event, it was apparently not a disaster in the terrestrial environment. Shoemaker and Wolfe (1986) referred to the Cenomanian as a stepwise extinction that probably spanned about 2.5 m.y.

CRETACEOUS/TERTIARY BOUNDARY

A new era of speculation about historic extinctions began in 1979 when Luis Alvarez and his coworkers discovered a level of enriched iridium in the clay of the K/T boundary. At first, Alvarez et al. (1979a) suggested that a supernova had been responsible for the excess iridium and the biotic extinctions. They soon decided that the supernova idea was not feasible and proposed an extraterrestrial, solar system source (Alvarez et al., 1979b). In the meantime, Napier and Clube (1979) suggested that the earth had been struck by an asteroid. This was followed by two other papers supporting an impact hypothesis (Hsu, 1980; Smit and Hertogen, 1980). Alvarez et al. (1980) then published their definitive paper in Science which called for an asteroid strike on the earth's surface about 65 m.y.a.

The idea that the earth had been struck by an asteroid or comet, followed by a cosmic winter lasting several years, and resulting in a biotic catastrophe, startled the scientific world and received extensive coverage in the popular press. New research was proposed, meetings were held, and speculative articles were published. The supermarket tabloids carried such headlines as "Missiles from Space Killed the Dinosaurs." So, the view of a series of gradual extinctions over a period of several million years became quickly overshadowed by the excitement generated over the impact hypothesis. For the first time since Cuvier's day, the concept of a sudden disaster to account for worldwide extinctions became popular.

Several paleontologists, who had worked with fossils from the K/T boundary era, protested the widespread assumption that the extinctions came about with catastrophic suddenness (Kauffman, 1979; Clemens et al., 1981; Hickey, 1981; Archibald and Clemens, 1982). But they were paid little heed and Alvarez (1983) expressed his frustration at his inability to convince them that an asteroid had done the job. General acceptance of the impact theory was aided by the fact that there seemed to be no other reasonable explanation for the iridium enrichment in the boundary clay.

When the K/T boundary sediments were examined by additional people, further evidence, that appeared to support the impact hypothesis, was published (see references in Hallam, 1987). Microspherules found in the boundary clay were supposed to be altered pieces of microtektites formed by the cooling droplets of impact melt. The boundary clay itself was considered to be formed by the fallout of material from an earth-embracing dust cloud produced by the impact. The occurrence of soot in some of the boundary clay was proposed to be the result of impact-caused wildfires on a spectacular scale which had a devastating effect on the global environment. Shocked quartz grains were found with features held to be characteristic of impact deformation. Bourgeois et al. (1988) found evidence that a tsunami had occurred at the K/T boundary on the Texas Gulf coast. They suggested that the most likely source for such a tsunami was a bolide-water impact. But Keller (1988) found that the tsunami disturbance apparently occurred earlier than the iridium anomaly.

Amid the mass of publications on historic extinctions that appeared from 1980 to 1990, were several that provided important summaries of progress or shed new light on those phenomena. Van Valen (1984a) reviewed the various theories that had been presented to that time and pointed out that most of the publications dealt with either the marine or the terrestrial environment and tended to ignore the other class. He also pointed out that the entire freshwater community, which is well represented in fluviatile deposits, passed unscathed through the K/T boundary.

Marine Environment

Kauffman (1979, 1984), in studies of Cretaceous extinctions in the marine realm, concluded that the terminal Cretaceous extinction was graded over a period of one to five m.y. and was primarily the result of massive environmental deterioration. The principal causes listed were relatively rapid changes in sea level, water chemistry (especially oxygen), ocean temperature, circulation, and climate. He also felt that the extinction was enhanced by some extraterrestrial event near the terminal phase of biotic decline. However, Kauffman warned that, despite the general acceptance of a catastrophic terminal Cretaceous extinction, this event had been poorly documented. In the marine environment, over 90% of exposed boundary sequences have major disconformities, paraconformities or intercalations of nonmarine sediments. Part or all of the late Maastrichtian and Danian are commonly missing in continental shelf sites, and more in cratonic interior sites. The bigger the marine stratigraphic gap across the boundary, the greater the observed discontinuity between Cretaceous and Paleocene biotas, and the greater the apparent boundary catastrophe.

The most continuous stratigraphic record may be found in deep sea cores but, even there, the record is often disturbed. Burrowing benthic animals can cause a vertical mixing of sediment particles. As a result, a given biological or chemical event may be spread out so that the timing may be accurate only within a few centimeters (which could represent several thousand years depending on the sedimentation rate) of bottom sediment accumulation. The cores taken by the Deep Sea Drilling Project (DSDP) have yielded information critical to our understanding of events near the K/T boundary. Research by Boersma (1984) showed increased bottom temperatures immediately prior to the boundary. This occurrence, combined with the decreasing surface temperature of the late Maastrichtian, produced a decrease in the thermal gradients. At about the same time, the Calcite Compensation Depth (CCD) showed a drop, then a rise. A significant drop in carbon isotope ratios at the boundary was interpreted to mean a drop in nutrient supplies (inorganic phosphorus and inorganic fixed nitrogen).

Hsu et al. (1982) concluded that the K/T "catastrophe" had the most drastic effect on the organisms living in the surface currents of the Tethyan realm. The extinction of these tropical species then made room for invasions by surviving species that had been more widespread or had been living at higher latitudes. They observed also that the sudden reduction in productivity probably led to an increase in atmospheric CO_2 which, in turn, caused a global increase in temperature. Benson et al. (1985) reported an important crash event in the Ostracoda at 65 m.y.a. Johansen (1989) described a mass extinction in the brachiopod fauna of northwest Europe which eliminated more than 70% of the species. Williams et al. (1985), working with DSDP core material, found that ^{13}C and calcium carbonate records suggested a significant reduction in primary productivity possibly accompanied by a rapid shoaling of the CCD. Zachos and Arthur (1986) noted a relatively stable water temperature but a major decrease in surface productivity that lasted at least one m.y. beyond the K/T boundary.

In regard to the pelagic realm, Fischer and Arthur (1977) concluded that times of maximum species diversity (polytaxic intervals) coincided with higher and more uniform oceanic temperatures and eustatic sea-level rises. Conversely, lower temperatures and marine regressions were associated with low species diversity (oligotaxic intervals). But Lipps (1986) reached just the opposite conclusion, that species diversity dropped as oceanic temperatures rose and circulation slowed. Fischer and Arthur also noted that the unit-area productivity of the open seas is probably highest during oligotaxic intervals. This idea was reinforced by Bralower and Thierstein (1984) who found that, in the warm mid-Cretaceous oceans, low organic productivity coincided with a slow deep-water circulation.

Hallock (1987) proposed a model called the "Trophic Resource Continuum." She noted that reduced rates of ocean turnover bring up fewer nutrients and produce oligotrophic conditions, while increased turnover produces more nutrients and eutrophic conditions. It is the oligotrophic condition that, over time, will produce the greater diversity (species richness) and longer food chains. Conversely, the availability of more nutrients will result in less diversity and shorter food chains. An important point is that it takes millions of years of slow ocean turnover to produce a substantial increase in diversity. But the complicated, high-diversity systems are very vulnerable and can be destroyed by a sudden change to more eutrophic conditions.

The Cretaceous Period was a time of extensive inland, epicontinental seas. Nutrients, carried down by the rivers, were deposited in the shallow seas where they were recycled by wind-driven currents. This permitted a sustained, high productivity on the continental shelves. There, a eutrophic environment was created with short food chains and low species diversity. At the same time, in the open ocean the surface temperatures were warm and there was very little thermohaline circulation. This meant that few nutrients were being carried upward from deeper waters. Thus, in the pelagic environment, oligotrophic conditions prevailed with extensive food chains and high species diversity.

In regard to the planktonic foraminiferans, Gerstel et al. (1986) reported that in the extinction the warm-water species suffered the most and that cool-adapted species then migrated to low latitudes. Brasier (1988) referred to a rapid ecological breakdown and catastrophic extinction. Jiang and Gartner (1987) found evidence of a sudden reduction in the calcareous nannoplankton at the K/T boundary and that the final demise of some species took place in the early Paleocene. In his history of reef communities, Fagerstrom (1987) emphasized that the Maastrichtian reefs were dominated by rudists and that these bivalves had attained their maximum family and generic diversity at that time. But their disappearance was not instantaneous for, as Kauffman (1979) noted, their major extinction had taken place prior to the K/T boundary. None of the rudists survived into the Paleocene. The late Cretaceous was also a time of maximum diversity in the scleractinian corals. Two of the families and perhaps 60% of the genera disappeared. In general, Fagerstrom noted that Tethyan (tropical) taxa suffered the highest extinction rates.

In a comprehensive review of global Cretaceous bio-events, Kauffman (1986) reached some conclusions that will be helpful in obtaining a better grasp of the changes that took place in the marine environment. He found the K/T boundary extinctions to be stepwise in nature with the tropical, temperature-sensitive taxa becoming extinct earlier, and at higher levels of magnitude, than those of temperate areas. These extinctions apparently spanned a 2.5-2.75 m.y. interval beginning near the Middle-Upper Maastrichtian boundary and extending into the lowest Paleocene. By the time of the actual K/T boundary, many marine groups were already decimated but the calcareous and siliceous plankton were still abundant and underwent a catastrophic extinction. Kauffman felt that this event, and the final demise of other groups, was due to the atmospheric dust cloud produced by an asteroid (bolide) impact. Kauffman's conclusions about the gradual rather than precipitous decline of most of the marine biota were reinforced by Wiedmann (1986), who found a gradual decline, in most of the macro-invertebrate groups, toward the K/T boundary.

There now appears to be some doubt that the planktonic groups underwent an abrupt, catastrophic extinction. Zachos et al. (1989) suggested that the plankton extinction occured over a period of less than 10,000 years. However, Keller (1988) found that the extinction of planktonic foraminiferans took place over a period of .8 to 1 m.y. She (Keller, 1989) then described a stepped pattern of species extinctions which suggested a progressively stressed ecosystem related to sea level regression and global cooling. One may conclude that the demise of the plankton, while not instantaneous, was certainly more rapid than that of the biota in other habitats. In contrast, Widmark and Malmgren (1988) found that benthic foraminiferans in the deep sea were scarcely affected by the boundary crisis. Some 75 to 90% of the species from the middle and lower slopes of the Central Pacific and South Atlantic survived the boundary.

Terrestrial Environment

Ever since the late 19th Century, when the great fossil discoveries of O.C. Marsh and E.D. Cope were made, dinosaurs have been the object of special public interest. As Jeffe (1944) said, "Frightening, nightmarish gigantic animals set men, women, and children all over America gaping, and made the world of the strange dinosaurs the table talk of millions." In recent years, with additional fossil discoveries and popularization by means of books, children's toys, and movies, dinosaurs have become an important part of 20th century culture. This has made "What happened to the dinosaurs?" a question of almost continuous speculation. It has, in turn, focused attention on the K/T boundary, the time when the great dinosaur lineages presumably came to a sudden end.

In regard to dinosaur diversity, Russell (1984a and 1984b) objected to earlier observations that there had been a gradual decline prior to the K/T boundary. But Clemens (1986), in his review of the terrestrial vertebrate fauna during the boundary transition, said that in the northwestern interior of North America, ornithischian dinosaurs (the largest group) appear to have undergone a decrease in diversity and a southward shift in geographic range before their apparent demise at the end of the Cretaceous. He stated that it is unwarranted to assert that the dinosaurs were a stable group that became extinct without warning. In their investigation of the Hell Creek Formation (Montana, Dakotas, Wyoming), Sloan et al. (1986) found dinosaur extinction to be a gradual process that began 7 m.y. before the end of the Cretaceous and accelerated rapidly in the final 0.3 m.y. Also, they observed that the final period apparently involved competition from rapidly evolving ungulates. As Van Valen (1988a) pointed out in his review, there have been reports, from several parts of the world, that dinosaurs persisted into the Paleocene. The evidence appears to be reasonably good for North America (Rigby et al., 1987) and suggestive for India (Sahni, 1984) and South America. Coe et al. (1987) suggested that the family diversity of herbivorous dinosaurs in North America was increasing when the group was suddenly terminated at the end of the Cretaceous. But, according to Padian (personal communication) only one group, the Ceratopsia, had been increasing; all others had declined well before the boundary. It now appears that only about 12 species of dinosaurs survived until the K/T boundary (Halstead, 1990).

One may conclude, in general, that the large dinosaurs had almost all died off before the K/T boundary. It is possible that, in some areas at least, they may have survived into the Paleocene Epoch. Certainly, they did not all become extinct at the same time. For the other vertebrate animals, Clemens (1986) noted that all the families and genera of Cretaceous fishes passed through the boundary and have been found in Paleocene or later deposits. All but one of the amphibian families and most of the genera did the same; as did all 10 lizard families and most of their genera, both snake genera, and three of the four crocodilian genera.

The data base for mammals across the K/T boundary is poor. Western North America is the only place where a continuous succession of fossil bearing strata have been found. Savage (1988) compared the generic diversity in the three major mammalian groups: in the latest Cretaceous there were 10 genera of the primitive multituberculates and 10 also appear in the earliest Paleocene, five marsupial genera decreased to one across the boundary, and seven placental genera increased to 22. It is only the marsupials that appear to have been overstressed (Van Valen, 1984a). It should be noted that 11 marsupial genera have been reported from the late Cretaceous of South America (Marshall and de Muizon, 1988). It has been suggested that these genera were actually Paleocene (Van Valen, 1988b). The survival of 11 marsupial genera in South America compared to one in North America may reflect significant ecological differences between the two continents. As Clemens (1986) concluded, the demise of the large dinosaurs was eventually complete but gradual while the other vertebrate groups were not severely affected.

Sullivan (1987) conducted a reassessment of reptilian diversity across the K/T boundary. He concluded that there was no isochronous mass extinction and that numerous species successfully crossed the boundary. The flying reptiles (pterosaurs) apparently did not survive the end of the Cretaceous but this was not considered to be a catastrophic extinction because by then there were only a few remaining members. The pterosaurs had been gradually diminishing in numbers throughout the Cretaceous (Carroll, 1987). In the meantime, another vertebrate group had developed feathers and the ability to fly. The fossils of Archaeopteryx from the Upper Jurassic of southern Germany indicate that it was very similar to other small coelurosaurian dinosaurs. The only significant difference was the presence of feathers. From an anatomical viewpoint, the dinosaurs are still with us in great variety, but we call them birds. Unwin (1988) has shown that as bird diversity rose, that of the pterosaurs steadily declined. Altogether, the tetrapods lost only about 14 percent of their familial diversity (Benton, 1988).

In regard to insects, Whalley (1987) observed that the lack of evolutionary change in insects across the boundary argued against abrupt or catastrophic change. Briggs et al. (1988) found that there was no evidence of a major insect extinction at the end of the Cretaceous.

There are some differences of opinion about the effects of the K/T boundary events on the terrestrial flora. Hickey (1984), in describing the angiosperm flora across the boundary, noted that the change was relatively minor and geographically variable on a world-wide scale. Similarly, Tschudy (1984) concluded that no prominent world-wide extinction could be predicted from examination of the pollen and spore record. However, more recently, Tschudy et al. (1984) examined the boundary clay on top of the iridium-rich layer. They noted an abrupt disappearance of certain pollen species and a great increase in fern spores relative to angiosperm pollen. They attributed these changes to a continent-wide (North America) destruction of the terrestrial ecosystem probably caused by a catastrophic event. However, in Australia, White (1990) could find no evidence of any mass extinction in plants.

Upchurch and Wolfe (1987) concluded, upon examination of K/T boundary leaf megafossils and dispersed cuticles, that their findings corroborated palynological interpretations of mass-kill and recolonization. But, more recently, Upchurch (1989) emphasized that extinction by a catastrophic event was not the only agent affecting the survival of vascular plants across the K/T boundary. Some clades became extinct in the Tertiary after declining in abundance at the boundary. Others had shown notable declines during the Maastrichtian, indicating some kind of gradual environmental change. Also, the leaf megafossil record suggests, at least in North America, a differential survival related to latitude in which the lower latitude species suffered the greater extinction. In the southern Rocky Mountains, the decline was as high as 75% while in central Alberta it was only about 25%.

Crane (1987) noted that estimates of extinction based on megafossils varied from 40% to 75%. Coe et al. (1987) noted the great increase in the relative abundance of fern spores and that this had been interpreted as evidence of recolonization of devastated mid-continental regions by wind-dispersed ferns. They observed that a vegetational simplification of this order would have produced a great reduction in the biomass of large vertebrate herbivores, which would probably have produced a great reduction in the biomass of large vertebrate carnivores, and would probably have been accompanied by extinctions. A fern-dominated landscape has been described following a modern volcanic eruption in Mexico (Spicer et al., 1985). Upon reviewing the evidence from megafossils, pollen, and spores, Boulter et al. (1988) concluded that an ecological trauma had occurred followed by a steady recovery over the ensuing 1.5 m.y.

Volcanism Effects

Most books on climatology do not consider volcanism to be an agent of climatic change, probably because the effects are considered to be short-lived. However, climatic changes of only a few years duration can have such drastic effects on living organisms that evolution in major phyletic lines can be profoundly disturbed or even terminated. It was not until the first quarter of the 20th century that scientific evidence about the influence of volcanic dust on surface temperature was published. Abbot and Towle (1913) measured the direct radiation of the sun following the eruption of Mt. Katmai in Alaska in 1912. Radiation was reduced by nearly 20% at two localities, Mt. Wilson in California and Bassour, Algeria. In the same year, Humphreys (1913) also called attention to the correlation between major volcanic eruptions and global temperature decrease. Similar early observations have been noted by Budyko et al. (1988).

In 1970, Kennett and Watkins observed that maximum volcanic activity seemed to occur when the geomagnetic polarity changed. They suggested that the coincidences of faunal extinction and polarity change, that had been previously observed, may be explained as the result of volcanically induced climatic change. Vogt (1972) noted that volume estimates and age dating of igneous deposits suggested synchronous discharge from many hot spots. He noted further that extinction crises in faunal evolution may reflect trace metal pollution occurring during intervals of intense volcanism.

Axelrod (1981) wrote a comprehensive review of the role of volcanism in climate and evolution. By this time, considerable literature had been published showing that material ejected from a large eruption can encircle the earth for several years. Also, deep-sea cores had shown relatively short periods of high volcanic activity that occurred at the same times as significant temperature decreases. The effects of an eruption by a single volcano have been described by Sigurdsson and Carey (1988). In 1815, the eruption of Tambora on the East Indian island of Sumbawa injected volcanic debris about 30 miles up into the atmosphere. This material included approximately 400 million tons of volcanic aerosols, which absorbed solar radiation and reflected it out into space. About 150 million tons of volcanic acids rained down over the next four years. The summer of 1816 was so cold that widespread crop failure and famine resulted. It was called "the year without a summer."

McLean (1982, 1985) called attention to the Deccan volcanism as an important agent of extinction at the K/T boundary. Previously, Kaneoka and Haramura (1973) had written about the great increase of volcanic activity in India. This involved massive vertical movements of mantle material to the earth's surface forming a basaltic flood called the Deccan Traps. The basalt spread over an area of more than 500,000 km^2 with an estimated volume of 500,000 to 1,000,000 km^3. The major episode apparently took place from 60 to 65 m.y.a. More recently, Besse et al. (1986) suggested that the Deccan Traps eruptions took place over a period of less than one m.y. and judged them to be contemporaneous with the K/T boundary. Two new estimates of the age of the Deccan basalts have been made (Duncan and Pyle, 1988; Courtillot et al., 1988). The first predicted 66.6-68.5 m.y. and the second 65-69 m.y.

Officer and Drake (1985) examined a series of deep-sea cores and found evidence that a number of phenomena, previously attributed to the effects of an asteroid impact, could have been caused by volcanic action. Perhaps most important, they found the iridium enrichment at the K/T boundary was not confined to a single "spike" but was present as a flux extending over an interval of 10,000 to 100,000 years (although the flux could possibly be due to postdepositional migration). They also found, in association with the iridium, arsenic and antimony far in excess of what would be expected from an asteroid or meteoritic source. Furthermore, they observed that the microspherules of the boundary clay existed at other levels and were probably of volcanic origin. The boundary clay did not prove to be mineralogically distinct from clays above and below the boundary, soot or charcoal also occurred at other places in the stratigraphic record, and enriched iridium particles had been produced by a recent eruption of the Kilauea volcano in Hawaii. It has subsequently been maintained that the microspherules are of algal origin (Hansen et al., 1986).

The question of the possible occurrence of high amounts of iridium at other boundaries in the geologic record is obviously important. Orth et al. (1985) were unable to find any meaningful anomalies of iridium abundance in rocks older than the K/T boundary. Kyte (1988) reported on the results of investigations of seven horizons that appeared to show mineralogical evidence of extraterrestrial impact. All but one (Precambrian) were in the Cenozoic. Of these, only one, the K/T boundary, indicated a global distribution of high iridium concentration. This marks the K/T boundary as the time of a unique event. It is perhaps significant that the sediments of the Deccan Traps contain no iridium anomalies, but it has been suggested that the iridium could have been outgassed from the magma (Rocchia et al., 1988).

The subject of the relationship of volcanic activity and the periodicity of magnetic field reversals was reviewed by Loper and McCartney (1986). They theorized that the thermal boundary layer surrounding the earth's core becomes gradually thickened by heat diffusion. It then becomes dynamically unstable and hot material erupts from it. The now thinner boundary layer extracts heat from the core at a greater rate, increasing the energy supply, and reversing the dynamo. The material erupted from the boundary layer rises via mantle plumes to form volcanos that affect the climate and the biota. Such hotspot volcanism will expel gaseous iridium together with other materials.

The occurrence of peculiar shocked quartz grains from K/T boundary clay in several parts of the world has been presented as evidence in confirmation of an extraterrestrial body impact (Bohor et al., 1987). But, as noted by Hallam (1987), quantities of shocked quartz could only have come from an impact on land or continental shelf. The soft sediments of the ocean floor contain very little quartz. A land impact would have produced a huge crater with a diameter of 150 to 200 km. A crater of this size is unlikely to have been completely buried or erased by erosion. Chatterjee (1990) suggested that an impact at the India-Seychelles boundary resulted in the basaltic flood of the Deccan Traps and the formation of new sea floor. Bohor and Seitz (1990) proposed that an impact took place south of the western half of Cuba and that the Isle of Pines might represent a central uplift feature. However, the outline of a crater is not clearly discernable in either location.

In his review of the causes of the K/T extinctions, Hallam (1987) indicated essential agreement with Officer and Drake (1985). Hallam also noted that, in addition to volcanism on an enormous scale in India, there was substantial volcanic activity in an extensive region from the South Atlantic to the Antarctic. Eruptions that produce large lava flows may also inject sulphate aerosols into the atmosphere. These substances, in sufficient quantity, would produce acid rain, resulting in a reduction of the ocean surface pH, global atmospheric cooling, and ozone-layer depletion. Finally, Hallam noted that increased mantle-plume activity has the potential for causing uplift of extensive sectors of continents and hence regression of epicontinental seas. Another review, which reiterated support for a volcanism cause of the sudden extinctions at the end of the Cretaceous, was that of Officer et al. (1987).

Global surface temperature responses to major volcanic eruptions were analyzed by Sear et al. (1987). They found that significant surface cooling occurs over the northern hemisphere following eruptions in that hemisphere but that the southern hemisphere was little affected. However, southern hemisphere eruptions affected both hemispheres after a lag of six months to a year. Courtillot and Besse (1987) noted that, toward the end of the Cretaceous, magnetic field reversals resumed following a long quiet period and suggested, as did Loper and MacCartney (1986), that volcanism and biotic extinctions followed. Loper et al. (1988) then presented a refined model involving magnetic reversals, climate, and mass extinctions. They also observed that the dust veil and aerosols produced by volcanism would produce a short-term cooling but, in the long term, the increased CO_2 vented into the atmosphere would produce a climatic warming.

CENOZOIC EXTINCTIONS

Priabonian Stage

At about the close of the Eocene, an extinction event has become recognized. Among the scleractinian corals, 18 families were present in the Eocene and four had became extinct by the end of that time. But six Eocene families increased in generic diversity in the Oligocene and one new family appeared. Despite these fluctuations, the reef-building process was generally continuous throughout the Cenozoic (Fagerstrom, 1987). Earlier, Lipps (1970) had shown sharp declines in species diversity of several planktonic groups, including the calcareous nannoplankton, dinoflagellates, silicoflagellates, and ebridians. Lipps (1970, 1986) and Lipps and Mitchell (1976) emphasized that the end-Eocene (and K/T extinctions) were caused by a global warming phase during which horizontal and vertical circulation became less intense. The slowdown in circulation supposedly removed boundaries to distribution and caused a decline in species diversity of the planktonic organisms. The decline in upwelling was said to have resulted in the extinction of the archaeocete whales.

Contrary to Lipps et al. (1970, 1976, 1986), most authors have attributed the terminal Eocene extinctions in the marine environment to factors such as a sudden regression due to Antarctic ice accumulation, global cooling, decrease in the calcite compensation depth (CCD), and a stronger deep ocean circulation. Van Couvering et al. (1981) described a major glacio-eustatic regression with a duration of about .5 m.y. and a change in oceanic circulation to a psychrosphere state. Cavelier (1981) and Herman (1981) also referred to a major regression and suggested that tektite showers may have contributed to atmospheric cooling. Alvarez et al. (1982), Asaro (1982), and Ganapathy (1982) found enriched iridium layers and attributed the extinctions to extraterrestrial impacts. However, Kyte (1984) showed that none of the E/O iridium layers is significantly above background level. Previously, Keller (1983) and Keller, et al. (1983) observed multiple microtektite horizons and suggested that microtektite and iridium anomalies are subject to calcium carbonate dissolution and are concentrated at dissolution levels. They also observed five foraminiferan faunal assemblages that turned over coincident with paleoclimatic cooling episodes.

Aubrey (1983) noted a stepwise extinction in the calcareous nannoplankton that affected the tropical species and caused an equatorward migration of species from higher latitudes. Dockery (1984) described pulses of extinction in molluscs due to episodes of climatic cooling and increased water turbidity. Keller (1986a and 1986b), working with the dominant planktonic foraminiferan species, gave evidence for four stepwise extinctions, each of which was minor. However, the total result was a replacement of two-thirds of the species. This led to the conclusion that there was not a single massive extinction. Causes were said to be steeper latitudinal and vertical temperature gradients, cooling, and lower sea levels. Planktonic species that continued across the E/O boundary were cool-water forms that lived at high latitudes or at the deepest levels (Brasier, 1988). Hansen (1987) found a stepwise extinction pattern in molluscs and suggested temperature drops as the primary cause. Shackleton (1986) noted that the most dramatic Paleogene cooling event took place just after the Eocene/Oligocene boundary, at about 35.8 m.y.a., when deep ocean temperature cooled by several degrees, probably in response to glaciation in Antarctica.

In the terrestrial environment, Prothero (1986) gave a detailed description of changes that took place in the mammalian fauna. That significant changes had taken place at the end of the Eocene has been recognized by mammalogists for many years. The "Grande Coupure" of Stehlin (1909) took place in Europe at about this time. Prothero's article made it apparent that this was not a single catastrophic event. The majority of archaic groups were gone by about 42 m.y.a., well before the E/O boundary. In regard to the tetrapod families as a whole, the E/O decline amounted to only about 8% (Benton, 1988). Recently, in a comprehensive review of both marine and terrestrial events, Prothero (1989) provided evidence that the extinctions took place in five steps spaced out over a period of 10 m.y. The extinctions are reflected, in varying degrees, by changes in the pelagic, shallow marine, and terrestrial animals and plants. Climatic changes including severe cooling, glaciation, and changes in oceanographic circulation, were considered to be the proximal causes.

Miocene and Pliocene

Although the marine invertebrate record at the generic level appears to show two comparatively low extinction peaks in the Neogene (Sepkoski, 1986), they may not be real since the data base is suspect (p. 27). A mid-Miocene extinction supposedly shows a sharp decline among the foraminiferans but Stanley (1987) asserted that there was no real crisis in that group. The Messinian salinity crisis took place at the end of the Miocene. Although this was a catastrophic event for the Mediterranean biota (Benson, 1984), it apparently had little effect elsewhere. Toward the end of the Pliocene, the molluscan faunas of the tropical western Atlantic began to undergo a notable extinction (Stanley, 1986). In the bivalve group, only about 20% of the modern fauna is composed of mid-Pliocene species. Contrarily, along the coasts of California and Japan, about 70-75% of the modern fauna extends back that far. The data indicate that this bivalve extinction began after about 3.5 m.y.a. and ended before the last interglacial interval of the Pleistocene.

By the Miocene, mammal faunas were well known in both North America and Europe (Savage, 1988). There were successive changes with high rates of disappearance and appearance but no large extinction episode. A radiation among the birds took place beginning in the Lower Miocene and peaking in the Middle Miocene (Unwin, 1988). A number of passerine families are first known from this period. A sharp increase in the extinction rate began in Upper Miocene. For the larger groups of tetrapods, and amniotes in general, a marked decline in family diversity took place in the late Miocene (Benton, 1988). This was considerably later than the supposed mid-Miocene extinction among marine animals. Benton observed that such family data do not support a model of periodic extinction events.

DISCUSSION

P/T Boundary

Although the end result of the P/T extinctions was a great biotic turnover, there is very little indication that the process was a sudden one. In the trilobites, for example, a plot of their generic diversity (Eldredge, 1977) shows a drop beginning in the Ordovician, a low point in the Carboniferous-Permian, and the final demise at the end of the Permian. For the invertebrate fauna in general, Vermeij (1987) noted that high extinction rates began in the final three stages of the Permian. So, the losses and replacements in the marine environment may have occurred more rapidly than on land, but the time scale was still on the order of several m.y.

In the latter part of the Paleozoic Era, the tectonic plates bearing Gondwana and seven other continental blocks slowly converged to form a single Pangaea by about 240 m.y.a. (Howarth, 1981). When the formation of Pangaea was completed, plate movement ceased and the ocean basin became relatively quiet. The hot mantle material, which had been extruded in the form of spreading ridges, began to cool and contract. As a result, the ocean basin became deeper and the sea level fell. Most of the regression, in which the sea level may have fallen as much as 280 m (Hallam, 1989), took place during the final stage of the Permian, a period lasting about five m.y. (Holser et al., 1986). The formation of ice sheets also has a direct effect on sea level, but the P/T crisis apparently occurred after the Permian glaciations were over (Fischer, 1984). However, Stanley (1988) found some evidence of polar glaciation in the late Permian and has emphasized the possible role of temperature reduction in this as well as the Ashgillian and Frasnian events. Maxwell (1989) also emphasized the possible effect of temperature reduction by referring to "a period of global refrigeration". But evidence for a global-scale, temperature drop, at the end of the Permian appears to be lacking (Erwin, 1990).

In analyzing the marine fossil record, Sepkoski and Miller (1985), identified a dominant Paleozoic fauna that declined in the late Permian and in the Triassic. At the same time, they demonstrated an expansion of the modern Mesozoic-Cenozoic fauna to become the dominant group. Most of the change-over took place during an interval of about 60 m.y. This analysis, and that of Jablonski (1986), show that the rise of the modern fauna was already underway and may have taken place even in the absence of the end-Permian and end-Triassic extinctions. In the terrestrial environment, the big therapsids dominated the late Permian and were still dominant at the beginning of the Triassic. However, during the latter period they slowly gave way to the archosaurs. Charig (1984) felt that this was a competitive replacement.

As the continents of the early Permian closed with one another, they brought together terrestrial faunas which had developed in isolation for many millions of years. The resulting competition probably resulted in an extensive loss of species (Briggs, 1987). The accompanying climatic changes must have been severe. Pangaea was evidently dominated by a highly seasonal, monsoonal circulation (Parrish, 1987). This condition strongly affected the zonal circulation in both hemispheres. The result was a large dry region that included equatorial latitudes and the subtropics. For much of the world, this meant a sharp contrast to the previous moist, maritime climate. The changes in the flora and fauna must have been extensive. About 49 percent of the tetrapod families disappeared (Benton, 1988).

In the marine environment, the continental amalgamation resulted in a significant reduction of the world shoreline and, consequently, a loss of marine provinces (Schopf, 1980). This, combined with the loss of shelf area due to sea level regression, probably had a drastic effect on shallow water diversity. Beurlen (1956) proposed that the late Permian crisis was caused by a marked reduction in oceanic salinity. This theory was further elaborated by Fischer (1964) and Flessa (1980). Supposedly, as the Permian seas withdrew, large shallow basins were left. Evaporation in the basins produced large amounts of brine which drained into the oceanic abyss and stagnated. This led to a great reduction of salinity in the circulating part of the ocean, resulting in an extinction of stenohaline organisms. Stevens (1977) estimated that the accumulation of salt deposits during the Permian was equal to at least 10% of the volume of salt now in the oceans. But Benson (1984) maintained that this salinity reduction was not enough to cause a general reduction of the normal marine faunas.

Although a dominant role for temperature has been advocated (Stanley, 1984, 1987) in mass extinctions, its involvement at the P/T boundary seems problematical. The earth was apparently in a warming phase following the mid-Permian glaciation. Volcanism was probably at a low level (Fischer, 1984). Considering the magnitude of the drop in sea level, it is likely that the rivers began depositing their sediments, together with phosphates, nitrates, and other nutrients, directly into the deep sea. This would vastly decrease primary productivity in shallow waters. Gruszczynski et al. (1989) suggested that an additional cause of extinction was a decrease in atmospheric oxygen caused by the oceanic burial and oxidation of large amounts of organic material. The disappearance of the continental shelves, plus a reduction in shallow-water marine provinces from 14 to 8 (Schopf, 1980), could go a long way toward explaining the gradual but enormous loss in diversity toward the end of the Permian. A salinity reduction effect should not be discounted, for great salt deposits did take place toward the latter part of the Permian (Stevens, 1977). As Schafer and Fois-Erickson (1986) suggested, the primary causes of extinction were probably the final accretion of the continents, climatic extremes, and marine regression.

K/T Boundary

The Cretaceous was a period in which greenhouse conditions existed. The divergence of tectonic plates in the ocean causes the development of mid-ocean ridges. As the ridges become enlarged vertically and horizontally, they displace water from the oceanic basins to form epicontinental seas. Consequently, the area of land to which the atmosphere loses CO_2 by weathering is decreased, and with it the rate at which CO_2 is removed from the air and returned to the lithosphere. The net effect of these two processes is that, during times of increasing plate movement, the level of CO_2 in the atmosphere-hydrosphere must rise (Fischer, 1984; Marshall et al., 1988). To these must be added the effect of increased volcanism, which also contributes CO_2 to the atmosphere-hydrosphere system. The rise in atmospheric CO_2 causes retention of much of the heat now lost to space by radiation, so the average surface temperature of the globe will rise.

The extensive inland seas, the moist tropical climate, and the high CO_2 level produced a luxuriant growth of plant life. This great primary production on land and in the epicontinental seas provided fodder for a large mass of herbivores which, in turn, permitted the evolution of a variety of carnivores. The greenhouse condition of the Cretaceous lasted more than 60 m.y., allowing time for the evolution of ecosystems dependent on a high level of primary production.

In the sea, the epicontinental flooding allowed the rivers to deposit their loads of sediments and nutrients in the shallow waters of the continental shelves. This permitted the nutrients to be recycled by vertical, wind-driven currents and caused the production of phytoplankton at a continuously high rate. The evolution of coccolithophorids in the Triassic and diatoms in the early Cretaceous may have increased the, per unit of area, primary production of shelf waters about eight times (Walsh, 1988). Considering that, during the middle and late Cretaceous, extensive continental seas covered the interior of North America, southern Europe, and large portions of Australia, Africa, and South America, primary production in the shallow sea may have been several times that which exists today. By the mid-Cretaceous, the phytoplankton supported a huge mass of zooplankton, which was, in turn, fed upon by many large carnivores.

On land, the high primary production resulted in a diverse fauna of large herbivorous dinosaurs that were preyed upon by large carnivorous dinosaurs. Coexisting were other food chains supporting much smaller animals (mammals, reptiles, amphibians, insects and other invertebrates). The predominant food chain in the sea was longer, due to the fact that the primary producers were mostly small, one-celled organisms. They were eaten by zooplankters which were then consumed by fishes and larger invertebrates. Both primary and secondary carnivores were eaten by very large fishes and marine reptiles. While other, more complicated food webs existed in both environments, the main flow of energy through the systems was by means of short food chains that supported many large-size animals.

In the late Cretaceous, the sea level reached its maximum height, flooding nearly 40% of the continental area (Howarth, 1981). This left as land only 18% of the earth's surface, compared to 28% today. This phase eventually came to a close, for the end of the Cretaceous was marked by a significant global fall of sea level (Hallam, 1987). The regression may have been caused by a reduction of plate movement and collapse of the spreading ridges or from continental uplift or both. Formation of ice sheets, a factor in other regressions, could not have been involved for the climate was too warm. At approximately the same time, the major volcanism episode of the Deccan Traps took place in India.

Judging from the volume of basaltic material produced, the Deccan eruptions may have been among the most violent in Phanerozoic history. The resulting aerosol and dust veils must have caused global temperature drops that may have each lasted for several years. These short-term cooling events were followed by a longer-term warming due to the volcanically produced CO_2, which could be removed only by the slow weathering process. Hsu (1986a) estimated that the warming phase lasted 30-50,000 years. The sulfate aerosols ejected by large-scale eruptions probably produced acid rains which affected the surface of the land and sea.

The sea level regression and volcanic induced events produced important changes in both marine and terrestrial environments. In the oceans, as the sea level receded toward the edges of the continental shelves, the nutrient materials brought in by the rivers began to be transported to the deep sea, the nutrient recycling process became less efficient, and epicontinental primary production probably dropped. The decrease in ocean-surface temperature had its most devastating effect on the tropical biota, which is more stenothermic than that of the higher latitudes. In addition to having a direct effect on the tropical biota, the temperature decrease stimulated the oceanic thermohaline circulation which increased the nutrient supply to the surface. As predicted by the Hallock (1987) model, this probably had a detrimental effect on organic diversity. Primary production in the offshore environments must have increased but probably not on the continental shelves. The intricate reef ecosystems and other tropical communities suffered great damage. They had to rebuild over the next several million years from surviving remnants and from eurythermic organisms which invaded from cooler waters to the north and south.

As Kauffman (1986) emphasized, most of the marine extinctions were stepwise (incremental) in nature, occurring over a period of 2.5-2.75 m.y. But the final step, the disappearance of the pelagic calcareous and siliceous plankton, was relatively sudden. It is likely that these populations were directly affected by the acid rains which lowered the pH of the ocean surface. The DSDP cores showed an approach of the CCD toward the surface which indicated the onset of acid conditions at the K/T boundary. The advent of acid rains must have been devastating. Because the surface waters became almost devoid of phytoplankton, the oxygen-minimum zone in the oceans expanded, and in many places the sea bottom became anoxic. The zooplankton, which depended on the primary producers, became scarce, while the big secondary and tertiary carnivores such as the plesiosaurs and mosasaurs became extinct.

In the terrestrial environment, with regression of the sea, a much greater land area was exposed and the continents stood higher. Both of these factors affected the prevailing weather patterns. Large continental masses, with high elevations relative to sea level, tend to develop dry seasonal climates over much of their central areas. Sometimes, depending on latitudinal position and prevailing winds, extensive deserts will form. In general, one may predict a drier climate with greater seasonal temperature extremes. This gradual climatic change, when combined with the short-term temperature drop and acid rain produced by volcanic activity, must have curtailed plant growth to the extent that primary production fell to a fraction of its former level.

In the flora, it appears that many of the major changes were gradual and evolutionary in nature as angiosperms replaced gymnosperms over the tropical and temperate parts of the globe. The former are better adapted to drier habitats so that the end-Cretaceous climatic change probably aided the evolutionary transformation. In North America there is evidence of a sudden, widespread destruction of the higher plant life over a small time interval at the K/T boundary. This may have been the direct result of acid rains produced by volcanic activity. Evidently, sufficient vegetation survived to support the small vertebrates and invertebrates but not the great dinosaurs.

In several sites in Europe and New Zealand, the boundary clays were found to be enriched in elemental carbon, mainly soot (Wolback et al., 1985, 1988). Since the soot layer coincided with the iridium layer, it was suggested that the source was a single global fire started by a meteorite impact. But Hansen et al. (1987) found that the carbon associated with iridium had a different isotop value than charcoal or soot derived from forest fires. They suggested that the iridium-bearing carbon black was generated during subaerial volcanic eruptions.

The large dinosaurs began to decline several million years prior to the K/T boundary so that, by the end of the Maastrichtian, only about a dozen species remained. A few may even have survived into the Paleocene in perhaps two or three places in the world. In contrast, a major group of their smaller relatives did not disappear at all but managed to develop feathers and evolve into birds. They did this in the late Jurassic and eventually began to replace the pterosaurs. The primitive birds may have been mostly shore birds or insect eaters and able to survive into the Tertiary because their food source was not severely affected.

Among the other vertebrate animals, it also seems clear that there was no mass-extinction event. The Cretaceous fishes, amphibians, lizards, snakes, and crocodiles passed through the K/T boundary almost unaffected. Among the mammals, most of the early multituberculates survived into the Paleocene but the marsupials suffered a decline (at least in North America). The great majority of the genera and families of placental mammals survived the boundary.

One may conclude that, at the K/T boundary, there were some relatively sudden changes probably caused by acid rains. These probably came during the approximate 10,000 to 100,000 year interval of greatest volcanic activity. In the sea and on land, acid rains adversely affected primary production, which was already in a state of decline. The most drastic result was elimination of the large animals that had been supported by the extensive base of the food pyramid. The smaller animals, with individually small demands on primary production, suffered very little. In a geological sense, the disappearance of the very large land and sea animals was relatively sudden but not so sudden that an asteroid impact event would be needed to explain it. For the great majority of the earth's biota, the changes occurring near the K/T transition were gradual and evolutionary.

E/O Boundary

In considering the Phanerozoic record of major and minor extinctions, the farther one goes back in time, the less dependable the information. There are difficulties with the continuity of the stratigraphic record, the precise dating of events, the condition of the fossils, and the dependability of the data on concurrent changes in the physical and chemical environment. Although the Eocene/Oligocene (E/O) boundary event was not as severe as several others, it happened a relatively short time ago (33-43 m.y.), so that the chances of unraveling the causes may be better.

Although plate tectonic events are seldom mentioned in connection with historic extinctions, they are likely to be of fundamental importance. Williams (1986) noted that, about 36 m.y.a., spreading activity took place along the newly formed Reykjanes Ridge separating Greenland from Norway. The shallow passage from the Arctic Ocean to the North Atlantic, which had existed since the early Eocene, opened wider and, near the E/O boundary, it became deep enough for cold, saline Arctic water to migrate south, forming the Atlantic bottom water. At the same time, a cooling and subsidence of the Walvis/Rio Grande Rise in the south Atlantic took place. Herman (1981) suggested that a general collapse of spreading ridges took place. The sea level fell approximately 150 m to almost its present position (Hallam, 1984). The Turgai Sea, which had separated Europe and Asia since the mid-Jurassic, dried up, and the narrow Beringian connection between North America and Asia became a broad migratory avenue.

Just after the E/O boundary, about 35.8 m.y.a., a dramatic cooling event took place in the deep sea (Shackleton, 1986). This was the beginning of the modern era of cold water in the ocean basins, often called the psychrosphere. Shackleton suggested that this was associated with a temporary glaciation in the Antarctic region. Earlier, Van Couvering et al. (1981) had referred to a major glacio-eustatic regression as the result of the formation of a large Antarctic ice cap. Stanley (1987) concluded that the introduction of the E/O cold climate was due to the isolation of Antarctica as part of the final fragmentation of Gondwanaland. But, at this time, a full circum-Antartic current had not developed, since the shallow Shackleton Fracture Zone extended between South America and Antarctica (Barker and Burrell, 1977). Most likely, the regression was caused by both a reduction of plate movement and by some glacier formation. The formation of the psychrosphere was caused by both the extrusion of Arctic Basin water and by polar climatic deterioration which enhanced the thermohaline circulation.

In summation, it seems that the physical and chemical events of the E/O boundary included a reduction of tectonic plate movement, subsidence of oceanic ridges, sea-level regression, and colder high latitude climate. The biological events need to be separated in two parts, marine and terrestrial. In the marine environment, the changes were dramatic but they took place in sequential stages rather than all at once. In general, the marine biota is much more sensitive to temperature change than its terrestrial counterpart. Global temperature changes affect not only the surface but also the deep water. Polar temperature drops can result in a chain of events. A suddenly greater thermohaline circulation will cause increased upwelling. The availability of increased nutrients would lower species diversity by creating shorter food chains. At the same time, the increased flow of cold, oxygenated water to the deep sea would make more of that habitat available to multicellular animals. Considering the cyclic nature of climatological change, it is likely that the E/O global temperature decrease did not take place all at once. A series of cold years with intermediate recoveries could help account for the stepwise extinction stages found in the marine environment.

In the terrestrial environment, changes in the northern hemisphere fauna and flora indicate that temperature deterioration began to have its effect several million years prior to the boundary. The desiccation of the Turgai Sea resulted in a flood of new mammal taxa from Asia into Europe. With the greater emergence of Beringia, many new families of mammals invaded North America from Asia (Webb, 1985). In mammals at least, it appears that many of the archaic forms had begun to disappear before the E/O boundary. In the tetrapod fauna as a whole, there was a loss of only about 8% of the families. In regard to both land and sea, it now appears evident that the E/O extinctions took place in a series of steps that occurred over a period of about 10 m.y. The proximal causes seem to have been climatic changes which most severely affected the marine biota.

THE PERIODICITY HYPOTHESIS

Soon after the publication of the Alvarez (1980) hypothesis about the asteroid impact cause of the K/T extinctions, a national conference was organized. This meeting, called "Geological Implications of Impacts of Large Asteroids and Comets on the Earth," was held at Snowbird, Utah, in October, 1981. It was sponsored by the Lunar and Planetary Institute and the National Academy of Science. This was the first of many meetings and conferences on the subject.

The Snowbird Conference, and other publicity surrounding the impact hypothesis, stimulated people to begin looking at other extinction events in the geological record. Previously, Fischer and Arthur (1977) had suggested that there was evidence for the existence of a 32 m.y. cycle of extinctions. At that time, this observation was not given much credibility (Raup, 1986), but the possibility of an astronomical cause for the K/T crisis raised the question anew. Many astronomical events are cyclic in nature. If an impact event was responsible for one extinction, what about the others?

In the spring of 1983, David Raup and John Sepkoski started work using a computerized version of Sepkoski's "Compendium of Fossil Marine Families" (1982). Their results, which provided evidence for a 26 m.y. cycle in global extinction events, were presented by Raup at the Dahlem Conference in Berlin in May, 1983. In August of the same year, a "Dynamics of Extinction" conference was held in Flagstaff, Arizona. The proceedings of that conference, which were published in 1986, contained a more detailed analysis of the 26 m.y. hypothesis (Sepkoski and Raup, 1986). This meeting engendered considerable publicity, with articles about the 26 m.y. cycle in various newspapers, Science, and Science News.

Early in 1984, with no scientific account of their periodic theory having yet appeared (except for news articles based on oral presentations), Raup and Sepkoski (1984) published their results in the Proceedings of the National Academy of Science. This exposure immediately stimulated considerable interest among astronomers and astrophysicists. An immediate result was the appearance in Nature, in April 1984, of five papers giving astrophysical interpretations of the 26 m.y. periodicity. These were soon followed by other publications on the same theme.

The astronomical mechanisms proposed are of four different types: The first deals with the effects of the transit of the solar system through the spiral arms of the Milky Way Galaxy. Clube and Napier (1984) argued that planetesimals are captured by the sun during these transits and that this capture could increase asteroid bombardment of the earth at the appropriate intervals. Shoemaker (1984) suggested that tidal forces resulting from the higher density of the spiral arms might perturb the comet cloud surrounding the solar system and increase the flux of comets in the earth's direction.

The second astronomical mechanism involves an oscillation about the galactic plane. As the solar system orbits the Galaxy, it oscillates vertically through the galactic plane. The passage through the plane takes place about every 33 m.y. Rampino and Stothers (1984) suggested that tidal forces from intermediate-size molecular clouds concentrated near the galactic plane, might perturb the cometery cloud as the solar system approached the plane. This could theoretically produce comet showers of up to several m.y. duration during which one large and several smaller comets might impact the earth.

The third mechanism involves a mysterious tenth planet, sometimes called "Planet X", which possibly lies beyond the orbit of Pluto, within the solar system. According to Whitman and Matese (1985), such a planet could produce periodic showers if its orbit was on a track to disturb the comet cloud at the necessary intervals. The fourth and most intriguing astronomical hypothesis is the proposal that the sun is a part of a binary star system with an undetected companion of low mass and luminosity. Davis et al. (1984) and Whitmire and Jackson (1984) speculated that this may be the case. If the sun's companion, which Davis et al. called "Nemesis," had the correct orbital periodicity, it could disturb the inner comet reservoir and produce comet showers. The Nemesis idea caught the public imagination, and it became the subject of newspaper stories, a cover article in Time Magazine, and even a dinosaur book for children. These events have been narrated by Raup in his book, "The Nemesis Affair" (1986). Shoemaker and Wolfe (1986), in considering the extinction events of the last 250 m.y., provided some indication of a 31 m.y. periodicity. They suggested that mild comet showers, that appear to be recorded in the earth's impact history, have probably been produced by the nearly random close passage of stars through the sun's comet cloud.

The periodicity theory was challenged on the basis of its statistical procedure (Hoffman, 1985), but the theory was then strengthened by refining the data and utilizing information on generic as well as family extinctions (Sepkoski, 1986). Another such challenge was issued by Stigler and Wagner (1987). These and other criticisms were answered by Sepkoski (1989) in a detailed defense of the theory. However, the most serious criticisms have to do, not with the statistics, but with the dependability of the data base itself.

Patterson and Smith (1987) and Smith and Patterson (1988) conducted an examination of the fossil record in their areas of expertise (echinoderms and fishes). They found that, at first, their subset of the record appeared to show the same extinction peaks that Raup and Sepkoski had discovered for the whole. However, when the evidence for each extinction was reviewed, an incredible amount of error and misleading data were found. Only 25% of the entries represented correctly dated last occurrences of monophyletic groups, which constituted valid extinction data. The other 75% comprised entries that for various reasons could be considered as noise. These were monophyletic groups whose last occurrences were wrongly dated, monotypic families, exclusively freshwater fishes, and nonmonophyletic groups.

Smith and Patterson (1988) pointed out that the nonmonophyletic groups were taxonomic artefacts that did not represent real phyletic lines. Therefore, their disappearance from the fossil record constituted pseudoextinctions. When they constructed a plot of all last occurrences of fish and echinoderm monophyletic families and genera, they found no statistically significant peaks of mass extinction since the start of the Triassic. They concluded that there was no unambiguous evidence that either fishes or echinoderms were affected by periods of mass extinction on the scale currently envisaged for the marine biota during the Mesozoic and Tertiary.

If the fish and echinoderm data are representative of the fossil record as a whole, and there is no reason to think they are not, the periodicity hypothesis becomes nonviable. It also means that the paleontological record, in its present state, cannot be used for broad analyses that attempt to define global events in the marine environment. It suggests that, for some years in the future, information about widespread extinctions and their evolutionary consequences should come from detailed studies of individual groups where the histories of discrete phyletic lines have been determined.

EVOLUTIONARY CONSEQUENCES

There has been, in recent years, considerable speculation about the evolutionary effects of extinction episodes. These provide a consistent message which gives the impression that a "wiping out of the old forms to make way for the new" has long-term evolutionary benefits. Gould (1984) suggested that extinctions might be the primary and indispensable seed of major changes and shifts in life's history; that if environments did not undergo such changes, evolution might well grind to a virtual halt. Raup (1986) referred to the common belief that, during an extinction event, the better adapted types would survive and that this would lead to an improvement in the entire biota.

Eldredge (1987) expressed the firm belief that, without extinctions to free up the ecological niches, life would still be confined to a primitive state somewhere on the sea bottom. Stanley (1987) stated, "Had the dinosaurs survived, there is no question that we would not walk the earth today. Mammals would still remain small and unobtrusive, not unlike the rodents of the modern world." The idea that major extinctions convey evolutionary benefits has been developed into a new theory of evolution by Hsu (1986). He would substitute the concept of evolution by means of global extinctions for Darwin's mechanism of natural selection. In this "new catastrophism" evolutionary advances would take place as the survivors adapt to spaces created by extinction events. In his view, "it is time to awaken to the absurdity of the idea of natural selection".

The available data on the widespread extinction patterns do not support the common assumption of evolutionary benefits. A number of authors have observed that, in the groups they studied, the warm-water or tropical marine organisms have been more prone to extinction during crises than those in cold or deep waters (Hsu et al. 1982; Aubrey, 1983; Gerstel et al., 1986; Anstey, 1987; Fagerstrom, 1987; Brasier, 1988). Vermeij (1987) noted that this pattern has been found in late Cambrian trilobites, late Ordovician and early Silurian brachiopods, late Devonian brachiopods and corals, late Cretaceous gastropods and planktonic foraminiferans. In regard to all large extinctions, Jablonski (1986) stated that low latitude taxa, particularly in reef communities, were invariably more severely affected than temperate, polar, and cosmopolitan taxa.

Gerstel et al. (1986) found, in regard to the K/T crisis, that cool-adapted species of planktonic foraminiferans migrated to low latitudes replacing warm-adapted species that had become extinct. Lipps (1986) called attention to the fact that several groups of the pelagic plankton exhibit a much simpler structure in cooler, higher latitude waters and, following the K/T and E/O extinctions, it was these species that survived while the more complex tropical forms became extinct. It seems probable that preferential removal of the complex tropical species by extinction episodes and their replacement by simpler forms would ordinarily involve movement by the latter from higher to lower latitudes. Relatively primitive taxa of many groups also tend to inhabit deeper, cooler waters or special refuges such as caves and the interstitial environment. It is possible that some of the replacement forms could have come from such places as well as from higher latitudes.

For some groups of marine animals that possess good fossil records, such as the hermatypic corals (Stehli and Wells, 1971), bivalve molluscs (Hecht and Agan, 1972), and benthic Foraminifera (Durazzi and Stehli, 1973), the younger more advanced genera are found in the tropics while, the higher the latitude, the more ancient they become. In other groups, whose fossil history is not as well known, the higher-latitude representatives often have a simpler, more primitive morphology.

Many, if not most, geographically widespread families and higher taxa of shallow-water marine organisms demonstrate their greatest diversity in tropical waters. Recent systematic work has shown that the tropics, and especially certain centers of origin within them, tend to be inhabited by the youngest and most specialized genera and species (Briggs, 1984). As such taxa slowly disperse to higher latitudes, they become older, thus accounting for the patterns of increasing age with increasing latitude (Kafanov, 1987). In the meantime, still younger and more advanced species continue to evolve in the tropics. This general process may be the rule in times of non-crisis or background evolution. When a widespread tropical or circumtropical extinction occurs it has its most drastic effect on the youngest, most advanced taxa.

It is apparent that most, perhaps all, of the great extinctions preferentially eliminated the tropical shelf and epipelagic organisms. This created an ecological vacuum which was gradually reoccupied by simpler, eurythermic organisms from higher latitudes, and possibly from deeper water and other refuges. I suggest that this process of succession by older, more primitive forms sets back the evolutionary clock to an earlier time. Furthermore, the damage to the tropical centers of origin must have interrupted, for some time, the production of successful new species and genera.

There is another way in which extinctions caused evolutionary setbacks. Jablonski (1986) has related how the shell-drilling habit in gastropods first appeared in the late Triassic, only to be lost in the end-Triassic extinction. It took another 120 m.y. for it to re-originate. Bivalves first developed the ability to bore into rocks in the late Ordovician, but this adaptation was lost in the Ashgillian extinction. Such bivalves did not reappear until more than 100 m.y. later. If these evolutionary innovations had persisted and developed through time, what would our molluscan assemblages look like today?

There are data that indicate, in general, the amount of time that it takes a community to recover from a severe extinction. In the P/T event, all of the existing reef communities completely collapsed (Fagerstrom, 1987). It took approximately eight m.y. until such communities began to reestablish themselves. The Norian extinction affected the scleractinian corals so severely that reef construction was halted and did not get underway again until some 15 m.y. later. Hansen (1988) studied the long-term effects of the K/T extinction on marine molluscs. Along the Gulf Coast of the United States, the extinction reduced the diversity from about 500 species to a few over 100. Afterward, the diversity slowly returned in a series of steps to about 400 species in the mid-Eocene. So it took nearly 25 m.y. for the diversity to build back to almost its late Cretaceous level. Hansen estimated that, for bivalves and gastropods as a whole, it takes about 10 m.y. for a doubling of species diversity.

As part of their argument for the evolutionary advantage of extinctions, Gould and Calloway (1980) gave the example of the brachiopods versus the pelecypods. They felt that the pelecypods gained the advantage because the brachiopods were hit harder by the P/T extinction. But this idea overlooks the fact that the pelecypods are clearly the superior competitors. Pelecypods can actively move about instead of being attached to the substrate, they pump water through their gills far more efficiently, and they grow faster (Vermeij, 1987). The present dominance of pelecypods in the warm, shallow habitats of the world, compared to brachiopods, which are mainly relegated to colder and deeper waters, is a tribute to the superior competitive ability of the former.

Similar evolutionary replacements have taken place in other groups. The stalked crinoids, once common on the continental shelves, became restricted after the Jurassic to waters deeper than 100 m (Meyer and Macurda, 1977). Their shelf habitat was taken over by their relatives, the mobile, active feather stars. Glypheoid crustaceans, once widespread in shallow waters during the early Mesozoic, are now represented by a single deep-water species (Forest et al., 1976). Its modern descendants, the lobsters and crabs, now occupy the shallow waters. There are many other examples. These represent gradual replacements that have taken place over very long periods of time. It would be difficult to find a positive role for sudden extinction episodes in these processes.

In the terrestrial environment, the large-scale changes in plant communities (Fig. 1) have been summarized by Niklas (1986). The gymnosperms began their development in the mid-Paleozoic and, for about 100 m.y., increased their diversity along with the pteridophytes. In the latter part of the Paleozoic, gymnosperms became somewhat the more diverse. Both groups suffered about equally in the P/T extinction but afterward the gymnosperms continued their expansion while the pteridophytes played an increasingly minor role. The angiosperms arose in the beginning of the Cretaceous and quickly developed into the dominant plant group. In each case, the more primitive group that was succeeded continued to do well for about 100 m.y. beyond the time of origin of its successor. Both pteridophytes and gymnosperms eventually began to decline, but these changes had become evident prior to the P/T and K/T boundaries, respectively. The angiosperm increase continued despite a brief interruption at the K/T boundary.

The biogeographic consequences of the changes in the major plant groups are that the angiosperms now dominate the tropical and warm-temperate zones of the terrestrial world where edaphic and rainfall conditions are favorable. Angiosperms, in the form of sea grasses, have also invaded the warm, shallow marine waters and make an important contribution to primary production in that habitat. In contrast, the gymnosperms predominate at higher latitudes and in less favorable locations, while the pteridophytes tend to be interspersed in marginal habitats. Neither the origination of the major plant groups nor the relative decline of two of them is clearly attributable to large-scale extinction events.

The popular belief that the evolutionary success of the mammals was due to the extinction of the large reptiles at the K/T boundary is still prevalent (Stanley, 1987). The general view among vertebrate paleontologists is that the large dinosaurs

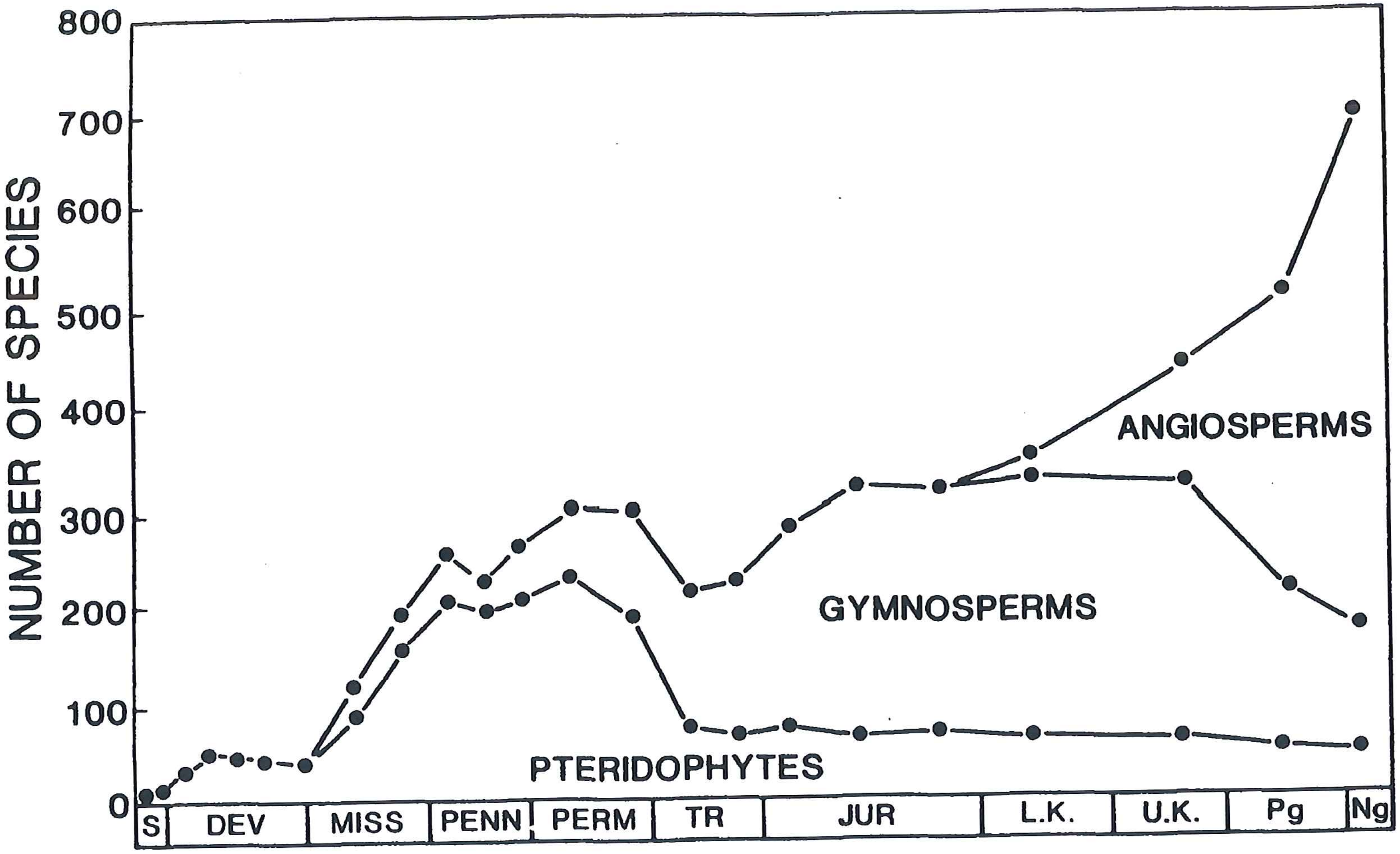

Figure 1. Historical changes in the species diversity of the major groups of vascular plants during the Phanerozoic. After Niklas (1986).

had been declining in diversity for several m.y. prior to the boundary (Sloan et al., 1986). Of greater importance is the fact that mammalian evolution did make considerable progress in the late Cretaceous when the large dinosaurs were still prevalent. In northwestern North America, there existed ten genera of multituberculates, five genera of marsupials, and seven genera of placentals (Savage, 1988). These data provide evidence that a mammalian radiation was already well underway before the large dinosaurs had left the scene. Sloan et al. (1986) described fossils from the Hell Creek Formation which suggested to them that dinosaur extinction and ungulate (hooved mammal) radiation were simultaneous events. This may imply that a competition existed in that region.

As in the case of the flora, the great evolutionary replacements among the major groups of terrestrial vertebrate animals do not seem to have been caused by or greatly affected by extinction episodes. As Colbert (1986) has shown, several orders of tetrapods continued from the Paleozoic well into the Mesozoic. They were gradually replaced by newer orders beginning in the Triassic. In most cases, there was an extended overlap lasting several m.y. in which the older group coexisted with its newer counterpart. Much of this temporal overlap occurred during the late Triassic. Feathered dinosaurs (birds) came on the scene in the late Jurassic, but the older pterosaurs were able to carry on, in diminishing diversity, for another 70-80 m.y. These exceedingly slow, evolutionary replacements of major groups appear to be the almost invariable rule in both the terrestrial and marine environments.

In the terrestrial environment, when one compares the biota of the high-latitude versus the low-latitude parts of the world, it becomes at once apparent that the former usually contains the older and more primitive organisms (Briggs, 1987). In this habitat also, it is probable that the tropical organisms were more vulnerable to extinction episodes. Higher latitude forms are better adapted to extremes of temperature and humidity. Unusual fluctuations in these physical factors are likely to have taken place in conjunction with regressions of the sea and consequent formation of larger and higher continents. With higher rates of extinction in the tropics, we might expect an invasion of more primitive forms from higher latitudes. The end result would be a setting back of the evolutionary clock on land as well as in the sea.

Data that might indicate a setback to evolution on land are scarce because fossil localities are few and widely scattered so that it is almost impossible to correlate extinction events on a global scale. The bed of the ocean, on the other hand, is a great fossil repository which can be sampled in many places and often correlated chronologically. At the present state of our knowledge, it seems worthwhile to hypothesize that the great historical extinctions were disasters which interfered with rather than enhanced the course of evolution.

COMMON CAUSES

There were nine episodes in Phanerozoic history at which the rate of extinction might have been extraordinarily high. In chronological order, they are the late Ordovician (Ashgillian), late Devonian (Frasnian), Permian-Triassic (P/T), late Triassic (Norian), early Jurassic (Pleinsbachian), late Jurassic (Tithonian), mid-Cretaceous (Cenomanian), Cretaceous-Tertiary (K/T), and the late Eocene (Priabonian). If we eliminate, on the basis of their apparent regional rather than global significance, the Pleinsbachian and Tithonian events, this leaves seven possibly significant extinctions. An important question is, are these apparent evolutionary setbacks attributable to a single common cause or a combination of causes?

When one compares the extinction events with the eustatic curve of sea-level change (Hallam, 1984), it is apparent that the extinctions generally coincide with notable regressions (Fig. 2). This was first pointed out by Newell (1967). As observed earlier, such regressions affect both the marine and terrestrial environments. In the sea, they reduce the continental shelf area where most of the marine biota lives and they probably decrease primary production in such areas. On land, the enlargement and higher stand of the continents produces dryness and

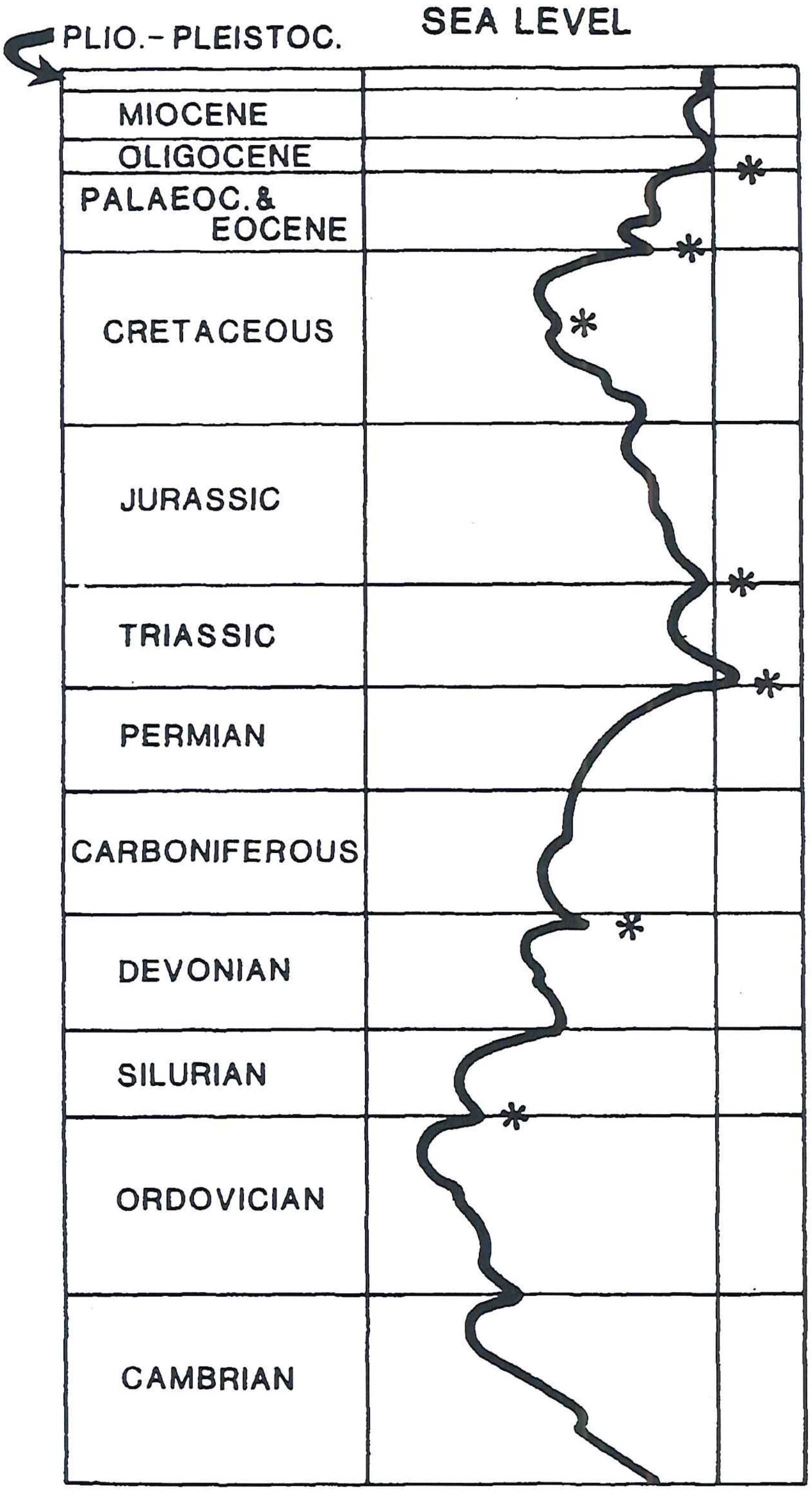

Figure 2. The Phanerozoic eustatic curve with asterisks denoting the seven major extinction episodes. Redrawn after Hallam (1984).

seasonally more severe weather patterns. These changes, in turn, have a detrimental effect on primary production. In winter, the offshore movement of air masses from enlarged mid- or high-latitude continents will in some areas lower the sea-surface temperature and the diversity of the marine biota.

It has been argued that regression should not have much effect on diversity in the sea because small areas such as oceanic islands often have rich biotas (Stanley, 1987). There is little doubt that, on land, the size of the geographic area has an important effect on species diversity (richness). This has been reviewed for terrestrial island populations by Williamson (1981) and for larger areas by Darlington (1959) and Preston (1962). For the marine environment, Flessa and Sepkoski (1978) felt that the species-area relationship would be a productive tool in the evaluation of fossil diversity but its use is limited by the lack of documentation about the nature of species-area effects in the recent marine benthos. Abele (1982) compared the number of crustacean species in the four great tropical shelf regions of the world and plotted those numbers against the area of continental shelf in each region. The result showed an almost linear relationship. Briggs (1985) accumulated data on the echinoderms (crinoids, asteroids, ophiuroids, echinoids), molluscs, crustaceans (brachyurans, stomatopods), hermatypic corals, and fishes. These were the groups that had been subjected to the most thorough systematic work. The total number of species for each region was tabulated and then compared to the area of continental shelf. The result showed an almost linear relationship among the tropical eastern Pacific, western Atlantic, and Indo-West Pacific. The diversity of the eastern Atlantic proved to be markedly lower. It was suggested that its relative poverty was due to the lowered sea-surface temperature during the Pleistocene glaciations, which had a more severe effect on the eastern Atlantic than on other parts of the tropics.

The general result of these works indicates that the species-area relationship is indeed applicable to large areas of the continental shelf. It means that a significant reduction in shelf area will be followed by a reduction in species diversity. In the case of the P/T regression, where the sea level dropped about 280 m and probably exposed all of the continental shelf, this factor alone could have been responsible for the elimination of most of the neritic biota.

There are evidently three important causes of sea-level regression. First, plate-tectonic movement may slow down, permitting the mid-ocean ridges to cool and shrink. Second, ice accumulation in the form of ice sheets or glaciers removes water from the hydrological cycle and prevents it from reentering the sea. Third, increased volcanic activity or continental collision may cause the uplift of sections of continents and hence provide more space in the ocean basins.

Another possible common cause of extinctions is temperature change. Marine organisms are, in general, very sensitive to the temperature of their environment. The oceans can be divided into four latitudinal temperature zones, each with its own characteristic biota (Briggs, 1974). The same zones can be recognized in the terrestrial habitat but the separations are not as sharp because that biota is physiologically acclimated to large excursions in diurnal and seasonal temperatures. Also, many terrestrial animals are endothermic, making them even more independent of environmental temperature.

In the late Ordovician, there was evidently some glaciation in North Africa which, at that time, was situated over the South Pole (Stanley, 1987) and brachiopod distribution (Sheehan, 1982) may indicate that a temperature decline accompanied the sea-level regression. For the late Devonian extinction, there seems to be no direct evidence of glaciation and global cooling. However, the reef and other shallow-water communities were hit very hard and this may indirectly indicate that a temperature drop was involved.

In regard to the P/T extinction, it would be difficult to involve a temperature decrease as a major factor. The earth was apparently in a warming phase following a mid-Permian glaciation. As already mentioned, the huge drop in sea level, the loss of marine shoreline due to continental amalgamation, and a possible reduction in salinity would all have severe effects on marine diversity. While there may have been some ice formation toward the poles (Stanley, 1987), it probably did not have much effect on the rest of the world. In a like manner, there seems to be no direct evidence of a temperature decline during the late Triassic and mid-Cretaceous extinctions but the losses were high among the major reef-building organisms and this may be an indication of a temperature effect.

In the K/T extinction, the climate was generally warm with no indication of ice formation at the poles. However, it seems likely that the intense volcanic activity at that time produced a global drop in temperature (or a series of them) for possibly several years. This may have been followed by a sustained temperature rise due to excess atmospheric CO_2. There is little doubt that the late Eocene extinction took place at a time of polar cooling when there was glaciation in the Antarctic and possibly in the North Pole area. This introduced the modern era of cold water in the deep ocean basins.

The most powerful argument for temperature reduction, as an effective agent in extinction episodes in the sea, is that in each case, it was the tropical or Tethyan organisms that appear to have suffered the greatest losses. We know, from the study of living forms, that they are the most stenothermic of all marine organisms. In discussing extinction causes, there has been a tendency to use the historic occurrence of polar ice formation as an indication of global temperature deterioration which would then account for the destruction of tropical organisms (Stanley, 1987). The difficulty with this approach is that the world can stand a lot of polar glaciation and still maintain extensive low latitude regions that remain warm enough to support a tropical biota. Even during the most recent Pleistocene glaciation, the tropical regions, although reduced in size, maintained their integrity.

Crowley and North (1988), in their review of the effects of abrupt climate change on extinction events in earth history, suggested that terrestrially induced climate instability was a viable mechanism for causing rapid environmental change and biotic turnover. They observed that sometimes abrupt transitions can occur in climate models involving atmospheric circulation, general ocean circulation, and thermohaline deep-water circulation. They concluded that such transitions cause climatic changes which affect the biotas. The best examples of abrupt transitions involved changes between polar-ice and ice-free conditions.

Volcanic aerosols and dust reflect sunlight and can markedly reduce the surface temperature. If a major eruption occurs at a low latitude, it will probably affect the major parts of both hemispheres. The same effect could be caused by the impact of a large comet or asteroid, which may inject fine debris into the upper atmosphere. As noted, one effect of regression is cooler continental temperatures but these alone would probably not eliminate large segments of the tropical marine biota. Another point is that polar cooling will stimulate the oceanic thermohaline circulation. The increased upwelling may bring up excess nutrients that would have a destructive effect upon the shallow oligotrophic system in the tropics (Hallock, 1987). There is some information which suggests that the nutrient supply to major parts of the low- and mid-latitude oceans is controlled by upwelling (Sarnthein and Winn, 1988). This means that the eutrophication caused by increased upwelling may be the primary cause of species extinction over large areas.

It seems that the only readily identifiable common cause for most extinctions is sea-level regression. And, it is perhaps significant that the greatest regression, at the P/T boundary, occurred at the time of the greatest extinction. There is also some evidence that sea-level transgressions, when they introduce anoxic water to epicontinental seas, may cause significant extinctions in the marine environment. This may have been the primary cause of the Cenomanian extinction (Hallam, 1989). Judging from the differential effects on the marine biota, it seems likely that a temperature decrease was also involved. Other factors, such as acid rains, a drop in oceanic salinity, the competition engendered by the coming together of previously separated continents, and the loss of shoreline habitat, were probably important at particular times. These all come under the category of direct effects which had immediate consequences for the vulnerable populations. The extinction of the largest terrestrial and marine animals was probably due to the indirect effect of reduced primary productivity. Short food chains, with very large animals at the top, are the evolutionary result of high primary production that has been sustained for millions of years. When that production declines, the large animals are the first to go.

The question of common causes for historic extinctions still needs to be satisfactorily answered. There was probably not a single cause but a combination of events such as regression, transgression, global temperature decline, and others at particular times. It would help to know if other episodes, besides that of the K/T boundary, were closely associated with major volcanic eruptions. Shoemaker and Wolfe (1986) discovered some evidence that the formation of large impact craters in the past 250 m.y. appears to be periodic. They also noted that the cycles of crater ages match fairly closely the best-fit cycle obtained from the strongest extinctions. However, the authors warned that this apparent periodicity may also be due to chance. McLaren (1989) felt that mass killings were due to high-energy events such as bolide impacts and volcanism.

Despite the setbacks caused by the extinctions and the effects of their long recovery times, global species' diversity (richness) has apparently increased over time, with more than twice as many species occurring in the Cenozoic than in any other era (Signor, 1985). At present, however, this diversity is undergoing an exceedingly rapid decline due to the impact of human activities. If this continues, the world will undergo its first genuinely catastrophic extinction event.

SUMMARY

1. Two important extinction events took place in the Paleozoic. Both of these were times of crisis for the marine biota but apparently had little effect on the terrestrial habitat. The first took place over a period of about one m.y. in the late Ordovician at the end of the Ashgillian Epoch. The extinctions were concentrated on the level bottom and pelagic communities. The second event occurred in the Frasnian Stage of the late Devonian. This time, the extinction was more widespread, occurring in the reef communities as well as those of the level bottom and pelagic zone. Frasnian reefs were large and widespread, but became relatively rare by the next stage. This extinction occurred over an interval of about three m.y., with the total extinctions being somewhat greater than for the late Ordovician event.

2. Toward the end of the Permian, about 240 m.y.a., several separate continental blocks slowly converged to form a single Pangaea. As the plate movement slowed, the ocean basin became quiet. The mid-ocean ridges began to cool and contract, permitting the ocean basin to become deeper and the sea level to fall. Most of the regression, in which the sea level fell about 280 m, took place during the final five m.y. of the Permian. As the continents closed with one another, they brought into contact terrestrial and shallow-water marine biotas that had evolved in isolation for many millions of years. The resulting competition probably caused an extensive loss of species. The formation of Pangaea significantly reduced the marine shore line of the world. The formation of inland seas and their subsequent evaporation may have substantially reduced the salinity of the circulating part of the ocean. The Pangaean continental climate became drier and more seasonal. All of these factors were probably important in the gradual rise of extinctions as Pangaea was formed.

3. The P/T extinction episode was the most severe on record. The high extinction rates took place over the final three stages of the Permian, a period of about 10 m.y. By the end of that time, several major groups of marine animals had completely disappeared and, in many others, the diversity was greatly reduced. On land, the dominant therapsids and the reptiles were greatly reduced in diversity. The labrynthodont amphibians and other groups also suffered reductions but, in general, the

major groups survived into the Triassic. Among the terrestrial plants, the dominant Glossopteris flora was gradually replaced by more modern types.

4. In the mid-Mesozoic, there was one major extinction event and three minor ones. The major event occurred toward the end of the Triassic. Many genera of bivalve molluscs disappeared. The scleractinian corals were set back to the extent that reef construction did not get underway again until the Pliensbachian Stage of the early Jurassic, some 15 m.y. later. In the marine environment, there may have been as many as three extinctions over a period of some 40 m.y. On land, the first dinosaurs appeared in the mid-Triassic. At the beginning of the Triassic, the large land vertebrates were nearly all therapsids but, by the end of that period, they were nearly all dinosaurs. During the Triassic, many new groups of vertebrates appeared and many older ones died out, but these changes occurred throughout the Period and do not appear to be concentrated at the end of that time. The changes in the terrestrial flora were slow and evolutionary.

5. The three minor events of the mid-Mesozoic took place in the early Jurassic (Pleinsbachian Stage), end of the Jurassic (Tithonian Stage), and mid-Cretaceous (Cenomanian Stage). For the first two, there is evidence which suggests that those events may have been regional rather than global in scope. The mid-Cretaceous extinction seems to have been somewhat the larger. Losses among the molluscs and planktonic foraminiferan species were apparently high. On land, there was some reduction in tetrapod family diversity in the Pleinsbachian but very little in the other two stages. No significant losses in the flora have been detected.

6. It is the K/T event of about 66 m.y.a. that has received the most publicity in recent years. Most of the marine extinctions spanned a 2.5-2.75 m.y. interval. The calcareous and siliceous plankton disappeared more suddenly. But, even these groups may have been progressively stressed over a period of .8 to 1 m.y. On land, the large dinosaurs apparently began to decline several million years prior to the boundary. About a dozen species remained by the time of the K/T crisis and some of them may have managed to survive into the Paleocene. Other terrestrial vertebrates were affected very little. Angiosperm plants in North America underwent an abrupt decline near the boundary and were largely replaced by ferns. The comparatively sudden demise of shallow-water plankton and angiosperm plants greatly reduced primary productivity in the sea and on the land. Consequently, the largest animals, whose populations were dependent on a sustained high primary productivity, suffered the most.

7. In comparison to other extinction episodes, the K/T event appears to be unique in that a rather sudden extinction, over an interval of perhaps .8 to 1 m.y. took place on top of a gradual decline that had been going on for several million years. The chemical and physical evidence found in the boundary clay could have been caused by large volcanic eruptions. Such eruptions, among the greatest in Phanerozoic history, took place in India and resulted in the basaltic formation known as the Deccan Traps. Recent research suggests that the Deccan eruptions took place over a relatively brief period of two to four m.y. and were contemporaneous with the K/T boundary. The volcanic dust and sulfate aerosols probably reduced the global temperature by interfering with solar radiation and produced acid rains that destroyed plant life. This does not necessarily mean that an extraterrestrial impact did not occur. Such an impact is simply not required in order to explain the K/T boundary events.

8. The one major extinction event of the Cenozoic took place near the close of the Eocene (Priabonian Stage). Since this event occurred only about 33 to 43 m.y.a., the fossil information is more plentiful. In the marine environment, the extinctions apparently took place as a series of pulses spread over a period of up to 10 m.y. On land, many archaic groups of mammals died out by about 42 m.y.a., well before the E/O boundary. The actual boundary is marked more by the immigration of new taxa and diversification of local groups than by extinctions. In the mid-Oligocene, there was another wave of extinctions. New groups of mammals entered North America via the Bering Land Bridge and arrived in Europe from Asia following desiccation of the Turgai

Sea.

9. The biotic changes around the end of the Eocene took place during a time of important physical changes. The sea level fell approximately 150 m to almost its present position, the mean annual air temperature in North America fell about 10°C., the passage between Greenland and Norway became wider and deeper, allowing cold, saline Arctic water to migrate south, and glaciation took place in the Antarctic. A renewed thermohaline circulation markedly reduced the temperature of the deep sea. All of these changes had an effect on the global biota. The marine life changes were evidently more severe than the terrestrial but both took place gradually over a period of several million years. They may be described as evolutionary and distributional but not catastrophic.

10. Great interest was aroused by the hypothesis that the historic extinctions took place in a periodic manner occurring approximately every 26 m.y. Since this idea was published at the time that the impact theory was enjoying its greatest popularity, it became a leading topic in the scientific and popular press. Considerable speculation was devoted to the ways in which clouds of comets might be directed at the earth on a regular schedule. However, it has since been found that the general fossil record, in its present state, probably cannot be used for analyses that attempt to define global events in the marine environment. This means that the global marine extinction peaks, which have been previously identified, may be the products of a faulty data base. For now, and for some years in the future, information about widespread extinctions and their evolutionary consequences should depend on detailed studies of individual groups.

11. It has been conventionally assumed that extinction episodes have been advantageous events in terms of general evolutionary progress. However, when the global effects of the extinction episodes are examined, a much different scenario emerges. In the marine environment, the tropical, low-latitude taxa were almost invariably more severely affected than those of higher latitudes. In some families with good fossil records, the younger, more advanced genera are found in the tropics while, the higher the latitude, the more ancient they become. Such taxa continually form in tropical centers of origin and slowly disperse to higher latitudes as they become older. A severe extinction event will eliminate tropical organisms creating an ecological vacuum. The vacated area will be reoccupied by the older, more primitive forms from higher latitudes or other refuges. This process has the effect of setting back the evolutionary clock to an earlier time.

12. Not only will an evolutionary setback occur as the result of major extinctions, but new evolutionary innovations originating in the tropics are apt to be lost. In the gastropods, the shell-drilling habit first appeared in the late Triassic only to be lost in the end-Triassic extinction. It took another 120 m.y. for it to reoriginate. Bivalves first developed the ability to bore into rocks in the late Ordovician, but this adaptation was lost in the Ashgillian extinction. It did not reappear until more than 100 m.y. later. It takes an enormous amount of time for a community to recover from a severe extinction. After the P/T event, it took about eight m.y. before the reef communities began to rebuild. It took a molluscan community nearly 25 m.y. to recover its diversity after the K/T extinction.

13. In the terrestrial environment, when one compares the biota of the high-latitude versus the low-latitude parts of the world, it becomes apparent that the former usually contains the older, more primitive organisms. Here also, it is probable that the tropical biota was the most vulnerable to extinction episodes. The result would be a setting back of the evolutionary clock on land as well as in the sea. It appears that the modern mammalian radiation was well underway when the large dinosaurs were still on the scene. There seems to be no reason why it would not have continued had the dinosaurs not died out. Thus, in the long-run, even mammalian evolution may not have benefited from the K/T extinction.

14. The best candidate for a common cause of extinction appears to be sea- level

regression. The curve of eustatic sea level change shows that all but one of the extinction episodes coincide with regressions. It has been demonstrated that the species-area relationship is applicable to the marine environment of the continental shelf. Therefore, a reduction in continental shelf area will be followed by a reduction in species diversity. It may be significant that the greatest extinction, at the P/T boundary, occurred during the time of the greatest regression. Another factor is temperature reduction. A sudden onset of cold temperature can be very destructive to tropical organisms. A drop in temperature will also increase upwelling which results in extinctions due to eutrophication. So colder sea surface temperature will reduce low-latitude diversity both directly and indirectly. The K/T extinction occurred at a time of generally warm temperature but a decline was evidently caused by a major volcanic eruption or possibly an impact from a large comet or asteroid. Considering the evidence as a whole, the latter cause is less likely. Acid rains, as the result of volcanic activity, or changes in oceanic salinity may have been important. Anoxic conditions have sometimes been important.

CONCLUSIONS

The evidence now before us indicates that all of the major extinction events took place over extended periods of time ranging from about one m.y. to ten m.y. or more. Furthermore, it seems likely that all may have occurred in the form of a sequential series of minor episodes that, only collectively, comprise a significant extinction. Hoffman (1989) concluded that the major extinction peaks may in fact be clusters of separate events more or less accidentally aggregated in time. However, I would suggest that sea-level regression has almost always been a major factor. Regressions have direct and indirect effects detrimental to biotic diversity. Impacts by extraterrestrial bodies could have added to the magnitude of some of the extinctions. But, none of the major extinctions can possibly be attributed to a single impact event.

Of the seven episodes in Phanerozoic history which have been identified as times of great extinctions, only the P/T event deserves to be considered a truly global phenomenon. This is the only extinction in which there was a drastic diversity decrease in <u>both</u> the marine and terrestrial environments. For the K/T boundary, which has often been described as a global catastrophe, the overall effect on the terrestrial biota was small compared to the reduction of marine life. Certainly, a few large dinosaurs died out but the other vertebrate and invertebrate groups survived quite well. The angiosperm plants received only a temporary setback which had little effect on their long-term expanding diversity.

Terms such as "mass extinction", "mass killing" or "catastrophic event" are misleading when applied to extinction episodes in the geologic record. These were gradual deteriorations in biotic diversity which developed in response to environmental changes. The deliberate pace of the extinctions was, in reality, the antithesis of catastrophic.

It is proposed that, contrary to conventional wisdom, the historical extinction episodes were disastrous interruptions to evolutionary progress. They set back the clock of evolutionary time, destroyed communities that took millions of years to reassemble, and eliminated new ecological inventions that did not re-originate for 100 million years or more.

During the past ten years, two extraordinary theories have had a galvanizing effect on research pertaining to the extinction episodes. First came the extraterrestrial impact hypothesis which was primarily developed and defended by Alvarez et al. (1980). Then came the periodicity hypothesis of Raup and Sepkoski (1984). The fact that neither of these two ideas now appears to be entirely correct is of little importance. They were responsible for inspiring an enormous amount of thought and research. The real value of a hypothesis lies in its utility to scientific progress, not whether it turns out to be right or wrong.

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