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SYNOPSIS



Revolutions in the History of Life

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Paleontology's "... involvement in geology and inclusion in that science as well as in biology are primarily due to the fact that the history of organisms runs parallel with, is environmentally contained in, and continuously interacts with, the physical history of the earth. It is of less philosophical interest but of major operational importance that paleontology, when applicable, has the highest resolving power of any method yet discovered for determining the sequence of strictly geological events." (Simpson, 1963, p. 26).

Catastrophe Versus Uniformity

At the time of publication of Darwin's *Origin of Species*, in 1859, practically all paleontologists shared the belief of Georges Cuvier (1769-1832) and Alcide d'Orbigny (1802-1857) that the history of life on earth had been marked by a succession of catastrophic extinctions. The stratigraphic column, characterized by discontinuities and contrasting changes in lithologic type and fossil content, by its very heterogeneity, seemed to give support to nineteenth-century catastrophism. The rocks had been neatly classified in eras, systems, and stages outlining an arrangement still in general use today. Previous experience had convinced paleontologists that earth history fell naturally into books and chapters, each characterized by its organic remains and delimited by widespread interruptions in the sequence of fossils.

The usefulness of this method of classification has not been a matter of serious dispute, but many geologists, arguing that time and organic evolution are both continuous and uniform, have had reservations

with respect to the periodicity inherent in the standard scale of geologic time. The purpose of this essay is to demonstrate that the history of life on which our geologic time scale is based, has been episodic rather than uniform, and to show that modern paleontology must incorporate certain aspects of both catastrophism and uniformitarianism while rejecting others.

Today, the concept of change in geologic history is almost universally accepted. Organic evolution, the transmutation of chemical elements, endless changes in geography, atmosphere, climate, and other aspects of physical and biological environments are taken for granted; but many geologists, still influenced by Lyell's views on uniformitarianism, think of most of these changes as smooth and gradual rather than episodic, uniform and predictable rather than variable and stochastic.

The stratigraphic record supplies abundant evidence that physical and biological processes have fluctuated greatly in extent and rate in the past, at times certainly exceeding limits observed during the course of human history. Environments have changed unceasingly and biologic reactions to those environments likewise have varied. Present conditions have unique aspects of relief, climate, and biota, and therefore cannot be regarded as an average sample of geologic history. Hence the present resembles the past only in the special sense of the timelessness of many geologic and biologic processes. But conditions in space and time do change, and the same processes operating in a context of changing environments will, of course, produce varied results (Simpson, 1963; Kitts, 1963; Gould, 1965). The search for analogies between past and present must take these changes into account. On the other hand, the intuitive conclusion that many of the *basic principles* of biology, physics, and chemistry are unaffected by the passage of time gains some support from repeated direct observations and from experimentation.

Geologists generally agree that the present provides many keys to the past. But this concept should not be equated with the more limiting principle of strict uniformity. Geological uniformity, as was pointed out long ago (*e.g.*, by Kelvin, 1864; Huxley, 1869; Sollas, 1900), implied to many constancy instead of evolution and minimized the great secular and episodic changes—the revolutions—that highlight earth history. Lyell and Darwin did not believe in world revolutions.

In the development of geology, the concepts of catastrophe and

uniformity have both been useful. Formerly regarded as diametrically opposed, they have gradually become modified and blended together so that there is no longer a clearly defined distinction between them. If we overlook mystical and religious overtones, catastrophism rightly emphasized the episodic character of geologic history, the rapidity of some changes, and the difficulty of drawing exact analogies between past and present. Aside from the objectionable implications of constancy of rate, uniformitarianism (*actualism* of European writers) stressed the application of scientific principles to geologic history. Many modern geologists unconsciously embrace the best features of both points of view (Bülow, 1960). Uniformitarianism and catastrophism, however, no longer exist in their original form as separate doctrines. They have been replaced by the concept of an evolving universe in which erratic changes, conditioned by pre-existing states, take place at greatly fluctuating rates.

The cataclysmic working of certain natural processes was an aspect of, but not peculiar to, Cuvier's philosophy of catastrophic changes. For example, the pioneers of uniformitarianism, Mikhail Lomonosov (1711–1765), James Hutton (1726–1797), C. E. A. von Hoff (1771–1837), and Charles Lyell (1797–1875), all regarded floods, volcanic eruptions, and earthquakes as normal geologic phenomena. Herein lies the semantic confusion between the two philosophies. The most significant element in Cuvier's catastrophism was, however, not suddenness of change, but that observed conditions were considered to be inadequate to explain the history of the earth (Cuvier, 1812). This view was completely consistent with the belief generally held in his day that the earth was only a few thousand years old. He believed that sufficient time simply was not available to explain the earth by known processes. However, the supernaturalism and multiple creations envisioned by many catastrophists did not stem from Cuvier, who regarded new faunas as migrants from remote regions. He used uniformitarian methods of analogy when he drew detailed and accurate comparisons of anatomy in fossil and living animals.

I think that the evidence requires the conclusion that many significant episodes in geologic history took place during comparatively brief intervals of time and that some of these probably involved unusual conditions for which there are no modern close parallels. Growing acceptance of this view has been regarded by the Soviet geologists N. S. Shotski and D. L. Stepanov (Stepanov, 1959) as a trend toward

neo-catastrophism. This, however, like catastrophism, is a term with an emotional connotation that implies calamity and destruction, and as such it is not appropriate in any scientific context.

On a local or even regional scale, many sedimentary processes operate intermittently and at high rates; for example, the emplacement of deposits of turbidity currents, landslides, and stream floods. Estimates of the average rates of accumulation of any sequence of sediments undoubtedly fall far short of maximum rates.

Zangerl and Richardson (1963), in a monumental study of the paleoecology of certain Pennsylvanian rocks in Illinois, have shown that great fresh-water swamps were flooded by the sea within a few hours or days without a gradual transition in salinity (Fig. 1). This was deduced from known rates of aerobic decomposition of animal tissues from which the rate of burial of fish carcasses was computed at about 1 mm in 5 days. The character of the associated fossil communities also shows that the increase in salinity was abrupt. It is salutary to keep in mind the fact that many geologic processes today are highly uneven in their operation; there is no *a priori* reason to think that rates known today are representative for all of geologic history.

The Biostratigraphic System

Early in the nineteenth century, long before the publication of Darwin's great work, it had become apparent that the history of life was marked by great events. In 1841, John Phillips, nephew of William Smith, proposed a three-fold division of the stratigraphic column based on fossils rather than the character of the rocks. He termed these units Palaeozoic, Mesozoic, and Cainozoic. The wisdom of his choice is shown by the fact that fundamental paleontologic characters and differences among the three eras have been accentuated rather than diminished by continued investigations. Advances in knowledge have necessitated only minor adjustments of the boundaries separating these eras. Revolutionary changes in life occurred all over the world at the close of the Paleozoic and Mesozoic eras. These changes included mass extinctions of animals accompanied and followed by adaptive radiation of new groups (Newell, 1966).

In the same year that Phillips defined the eras, d'Orbigny (1841) named the first of his paleontological stages which were based on distinctive marine faunas. Ultimately he divided the stratigraphic

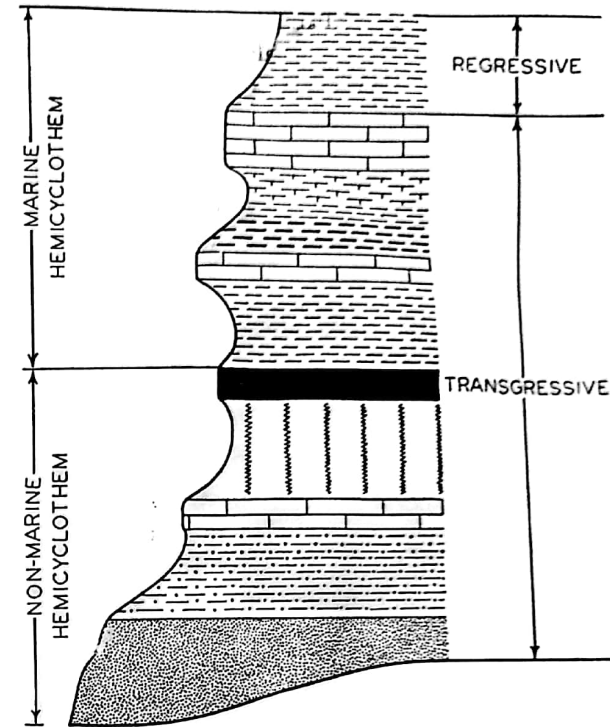


Figure 1. Idealized Mid-Century Pennsylvanian cyclothem. Fresh-water coal beds (black) commonly are succeeded abruptly by marine units without an intervening transition of the brackish-water deposits (after Weller, 1960, courtesy of Harper & Brothers, Inc.).

sequence into 27 stages, in addition to the modern fauna, and subdivided them into zones. Because he was a catastrophist, d'Orbigny thought that his faunal stages would prove to be worldwide. Now we know that many are more restricted, but it is remarkable how distinctive, widespread, and uniform some are, e.g., Norian, Toarcian, Coniacian. Most are recognized on more than one continent and some are known from all the continents. For others, however, correlations are not so refined; and the characteristic fauna of a given zone or stage may not be identifiable far from the type region. Particular evolu-

TABLE 1. AMMONOID ZONES OF THE DEVONIAN SYSTEM*

Zone	Germany	Great Britain	North Africa	United States	Western Canada
<i>Wocklumeria</i>	x	x	x
<i>Clymenia</i>		x	x
<i>Platyclymenia</i>	x	x	x	x	?
<i>Cheiloceras</i>	x	x	x	x	x
<i>Manticoceras</i>	x	x	x	x	x
<i>Maenioceras</i>	x	x	x	x	x
<i>Anarcestes</i>	x	x	x	x	x
<i>Mimosphinctes</i>	x	x	x	x	x

* After House, 1963

tionary development and position in the sequence permit recognition of these successive faunas from place to place (Tables 1-3) and indicate the high probability that they are about the same age wherever they occur.

The problem of temporal correlations between widely spaced localities is, of course, complicated by geographic and environmental variations in the faunas and floras, although in some cases variations are surprisingly small. Frequently, many elements of an older fauna were extinguished before the establishment of a younger fauna in the same region, so that many stages and zones are sharply differentiated and contain many distinguishing animal species or genera.

Sometimes it is said that geochronology by means of fossils involves circular reasoning. First the fossils are dated by the rocks in which they are found (for example, dinosaurs are limited to Mesozoic rocks); then the fossils are used as evidence for the geologic age of strata. This misrepresents the paleontologic method. Dinosaurs are not Mesozoic in age because they are found in Mesozoic rocks but because experience

TABLE 2. FUSULINID ZONES OF THE PENNSYLVANIAN AND PERMIAN SYSTEMS
Data from John W. Skinner (personal commun., 1963)

Zone	Pacific Northwest	Texas	Peru	Urals	Alps	Nanking	Japan
<i>Polydiexodina</i>	x	x
<i>Parafusulina</i>	x	x	x	x	x	x	x
<i>Schwagerina</i>	x	x	x	x	x	x	x
<i>Triticites</i>	?	x	?	x	x	x	x
<i>Fusulina</i>	..	x	..	x	..	x	x
<i>Fusulinella</i>	..	x	..	x	..	x	x
<i>Profusulinella</i>	x	x	x	x	..	x	x
<i>Millerella</i>	x	x	..	x	x

shows that they invariably lie in a particular part of the vertical succession of fossils. The rocks containing these fossils are said to be Mesozoic rocks because they contain Mesozoic fossils, not vice versa.

Admittedly, the geologic systems were established in a haphazard manner in Western Europe for various local sequences of rocks; and it was inevitable that some systems in the stratigraphic column were

TABLE 3. GRAPTOLITE ZONES OF THE ORDOVICIAN AND SILURIAN SYSTEMS
Data from Isles Strachan (personal commun., 1963)

Zones	Great Britain	Eastern North America	Australia	China
<i>Monograptus nilssoni</i>	x	x	x	x
<i>Monograptus testis</i>	x	..	x	..
<i>Cyrtograptus linnarssoni</i>	x	x
<i>Monograptus riccartonensis</i>	x	x
<i>Cyrtograptus murchisoni</i>	x	..	x	x
<i>Monograptus crenulatus</i>	x
<i>Monograptus greistoniensis</i>	x	x
<i>Monograptus crispus</i>	x	x	..	x
<i>Monograptus turriculatus</i>	x	x
<i>Monograptus sedgwicki</i>	x	..	x	x
<i>Monograptus gregarius</i>	x	..	x	x
<i>Orthograptus vesiculosus</i>	x
<i>Akidograptus acuminatus</i>	x	..	x	x
<i>Dicellograptus anceps</i>	x	?
<i>Dicellograptus complanatus</i>	x	x	x	..
<i>Pleurograptus linearis</i>	x	?	x	x
<i>Dicranograptus clingani</i>	x	x	x	x
<i>Nemograptus gracilis</i>	x	x	x	x
<i>Glyptograptus teretiusculus</i>	x	x	x	..
<i>Didymograptus murchisoni</i>	x	x
<i>Didymograptus bifidus</i>	x	x	..	x
<i>Didymograptus hirundo</i>	x	..	?	x
<i>Didymograptus extensus</i>	x	..	x	..
<i>Dictyonema "flabelliforme"</i>	x	x	x	x

at first chronologically overlapping while others were separated by gaps. These discrepancies gradually have been reduced or eliminated by the adjustment of systemic boundaries to agree with widely recognizable paleontologic horizons. Thus the geologic systems and their stratigraphic limits are recognized outside their type localities by their paleontological zones and stages (Newell, 1966).

Mass Extinctions

Rejecting catastrophism, Darwin (1859, p. 281) thought that the suddenness with which some major groups, such as the ammonites,

disappeared was more apparent than real and attributable to deficiencies in the record. Unconformities and barren sequences do enhance the sharpness of widespread faunal interruptions, but, the magnitude of a paleontologic discontinuity does not bear a simple relationship to the time represented by a barren interval or an unconformity.

Physical gaps in a sedimentary sequence range from insignificant diastems to breaks of enormous temporal value. In the more stable regions of the cratons, they commonly are bounded by parallel sequences of strata, sometimes loosely termed conformable because of the lack of conspicuous angularities. Physical gaps in the record result from geographic and climatic changes which may be sufficiently severe to alter greatly the character of organic communities through changing environments and migrations. Hence an unconformity of small temporal value may be marked by a great paleontologic change not directly attributable to evolution. Evolutionary changes are likely to be conspicuous only after an appreciable lapse of time—hundreds of thousands of years for rapidly evolving species and millions of years for rapidly evolving genera.

Can stratigraphic breaks of short duration be widely distributed? We lack the means to measure an hiatus accurately, but circumstantial evidence suggests that obscure paraconformities and compressed sequences marked by striking paleontologic discontinuities are abundant in the fossil record and may, indeed, be widespread and thus significant in terms of earth history. The meaning of these discontinuities constitutes a major problem for which many observational data are needed.

The boundaries at the base and top of the Mesozoic Era are in many places paraconformities where the reworking of sediments over very flat surfaces produced contacts that are now obscure (Newell, 1967).

Paleontologists are sometimes charged with inventing invisible unconformities of convenience, but in many circumstances the paleontologic and paleogeographic evidence taken together suggest at least short intervals of nondeposition or erosion without conspicuous channeling, leaching, or other unequivocal indications of exposure to subaerial agencies. Studies of the physical relationships at these contacts usually provide no basis for judging the significance of the stratigraphic interruption. Stratigraphic breaks, in any case, can be evalu-

ated only by reference to intermediate strata and transitional fossils preserved in contiguous areas.

Continued field studies show, however, that many persistent paleontological discontinuities are not being bridged by new discoveries. Consequently these breaks in the record are important both historically and stratigraphically. As in the days of Lyell and Darwin,

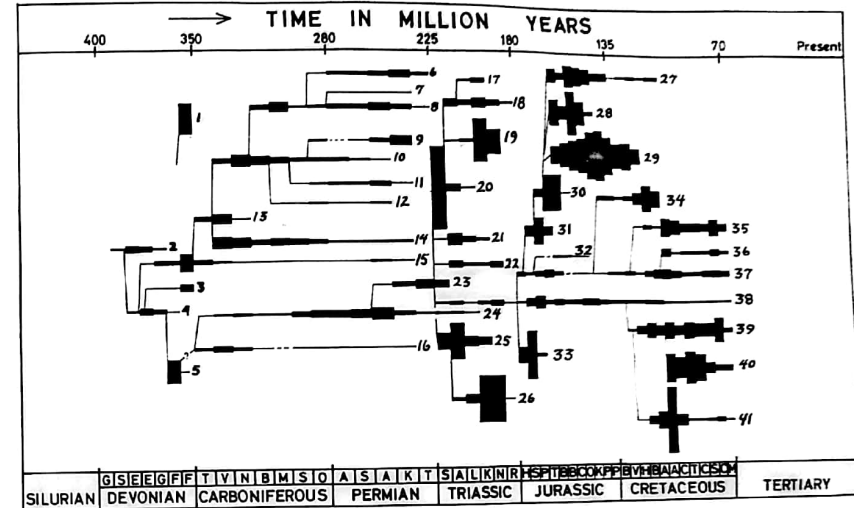


Figure 2. History of the 41 superfamilies of ammonoids showing mass extinctions at the close of the Devonian, Permian, Triassic, and Cretaceous periods. Height of the blocks is proportional to the number of genera known from each stage. Number 26 represents 48 genera (after House, 1963). Letters in boxes above the names of the periods are the initial letters of the standard stages.

they constitute a major problem in the history of life. Cuvier thought that mass extinctions of entire faunas took place quickly. Judging from the evidence, many of them did. In other cases they were simply the culminating phases of long declining trends, and we should focus attention on the trends as well as the final disappearance.

The history of the ammonoids is well known and may be taken as an illustration of the uneven course of a major group of animals (Fig. 2). They arose out of the nautiloids in the late Silurian, diversified slowly to a maximum of 10 superfamilies by mid-Permian time, then quickly

dropped to two superfamilies by the close of that period. One of these repopulated the Triassic seas and soon underwent explosive radiation, increasing in diversity until near the close of the period when the order suddenly was reduced again, this time to a single surviving superfamily. The early Jurassic was the scene of a third major evolutionary burst, followed by a recession in the early Cretaceous and a minor flowering again in the late Cretaceous. Finally, after a premonitory

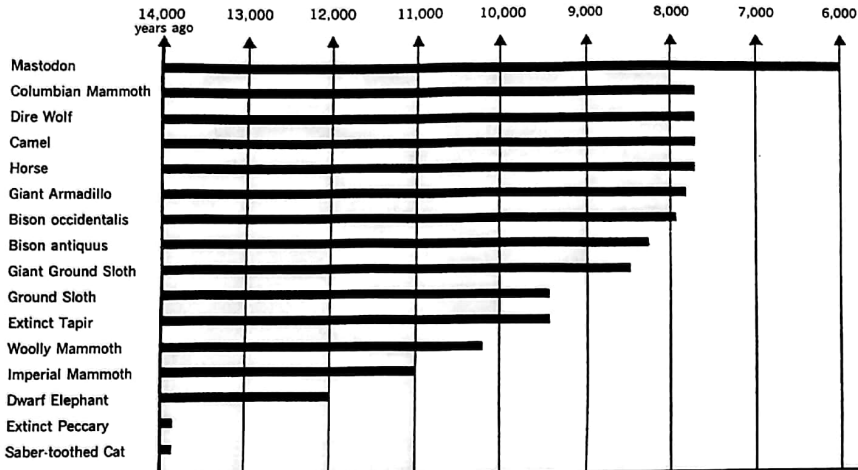


Figure 3. Late Quaternary extinctions of North American mammals based on radiocarbon dates (*from* MacGowan and Hester, 1962, courtesy of Doubleday and Company, Inc.)

dwindling of numbers of genera in the latest Cretaceous, the seven remaining superfamilies dropped out together, along with representatives of a host of other animals. As might be expected, the periods of mass extinction were relatively brief as compared to the expanding phases. It appears that these events took place within the time span of a single stage—say, 5 or 6 million years at most. This establishes the maximum interval within which the extinctions probably took place, but the time may have been much shorter.

A fascinating illustration of mass extinction was the disappearance outside of Africa of very many of the larger grazing and browsing mammals around the end of the Pleistocene epoch. In North America, for example, roughly three quarters of the larger herbivorous mammals died out within a very short time, geologically speaking (Fig. 3).

This event apparently was compressed mainly between the Wisconsin glacial maximum, some 11,000 years ago, and the close of the hypsithermal epoch, some 3000–4000 years ago. Much evidence remains to be collected and interpreted about this event, but the general facts now are clear (Martin, 1958). Many large mammals of quite diverse habitats were affected but there were very few extinctions among other animals or plants. The cause of this very recent event is unknown; doubtlessly it is significant that it corresponds in time to a marked drying of climate over much of the world and rapid advances in human technology.

The radiocarbon dates for the youngest known occurrences of the extinct species were collected from many sources by James Hester (1960). Obviously these do not correspond to the time of death of the last representatives of each species, but it is interesting that many dates fall between 7000 and 8000 years ago. Further collecting should reduce the apparent dates of extinction of many of the species. The data clearly show that many of the extinctions in North America took place within an interval so short that for practical purposes it was instantaneous.

The Fossil Record of Animal Revolutions

Notwithstanding the imperfections of the fossil record and the limitations of paleontologists, innumerable inductive conclusions have been confirmed so often that the chances of future contradictions seem small. That the probability of contradiction is, however, never zero, is shown by the recent discoveries of living coelacanths, monoplacophorans, and other surviving organisms long believed to have been extinct. It is, of course, possible, but not probable, that some ammonites and dinosaurs lived beyond the end of the Cretaceous Period. As in the physical sciences, conclusions in paleontology are statements of probability, not certainty. Everything is conditioned by the chance factors of evolution, circumstances of preservation, and the fortunes of discovery. But even if future discoveries show that a few stragglers persisted beyond the Cretaceous-Paleocene boundary, the image of a late Cretaceous crisis in the animal world would not be much affected. Experience suggests that such stragglers probably would show evolutionary differences from typical Cretaceous forms. The age of the enclosing rock would not be judged solely from the

TABLE 4. FIRST AND LAST KNOWN OCCURRENCES OF MAIN ANIMAL GROUPS

Series	Duration (million years)	Total Families	First Occurrence		Last Occurrence	
			Families in per cent	Families per million years	Families in per cent	Families per million years
Neogene	32.5	856	17	.52	10	.30
Paleogene	32.5	834	44	1.35	15	.46
Upper Cretaceous	35.0	629	26	.74	26	.74
Lower Cretaceous	35.0	520	35	1.00	11	.31
Upper Jurassic	15.0	377	15	1.00	11	.73
Middle Jurassic	15.0	346	14	.93	7	.47
Lower Jurassic	15.0	328	50	3.33	10	.66
Upper Triassic	16.6	278	19	1.14	35	2.11
Middle Triassic	16.6	254	25	1.50	10	.60
Lower Triassic	16.6	235	36	2.17	18	1.08
Upper Permian	25.0	303	21	.84	50	2.00
Lower Permian	25.0	330	15	.60	27	1.08
Upper Pennsylvanian	10.0	315	11	1.10	11	1.10
Middle Pennsylvanian	10.0	318	5	.50	5	.50
Lower Pennsylvanian	10.0	308	6	.60	3	.30
Upper Mississippian	17.5	318	8	.46	9	.51
Lower Mississippian	17.5	315	28	1.60	7	.40
Upper Devonian	20.0	327	14	.70	30	1.50
Middle Devonian	20.0	326	15	.75	13	.65
Lower Devonian	20.0	298	21	1.05	7	.35
Upper Silurian	6.6	272	8	1.21	13	1.96
Middle Silurian	6.6	265	13	1.96	5	.75
Lower Silurian	6.6	243	28	4.24	5	.75
Upper Ordovician	25.0	228	10	.40	24	.96
Middle Ordovician	25.0	221	33	1.32	7	.28
Lower Ordovician	25.0	192	76	3.04	23	.92
Upper Cambrian	33.3	97	34	1.02	52	1.56
Middle Cambrian	33.3	82	50	1.50	22	.66
Lower Cambrian	33.3	55	100	3.00	25	.75

presence or absence of ammonites and dinosaurs, but from the character of the entire biota.

It is consistent with the uniformitarian doctrine to interpret abrupt first and last appearances of fossil faunas in local sequences as the effects of migrations, hiatus, or contrasting depositional environments. As Schindewolf has pointed out however, where these abrupt changes occur in relatively complete sequences over a large part of the earth, they indicate episodes of greatly increased rate of extinction and evolution (Schindewolf, 1955).

Table 4 and the graphs of Figures 4-7 show fluctuating extinction rates in the main groups of fossil animals as inferred from available information on stratigraphic ranges. The plotted data represent not total extinctions but percentages of the families that drop out in each stratigraphic series.

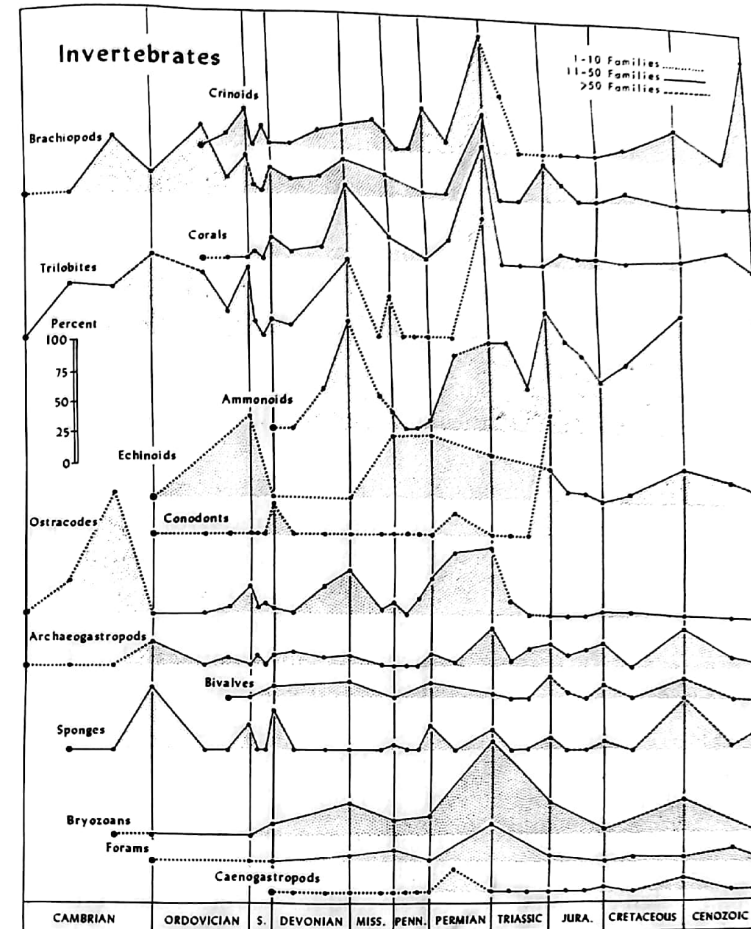


Figure 4. Percentage extinction of families of the chief groups of fossil invertebrates. There is strong correlation of extinction peaks near the end of the Devonian, Permian, Triassic, and Cretaceous periods.

There are, of course, two kinds of extinctions. Even though a family ceases to exist, it still may have contributed to the heredity of a descendant family. But a different kind of extinction is involved when a family dies without descendants. In paleontologic studies it frequently is difficult or impossible to distinguish between these two and no attempt has been made to do so in the present study.

Estimates of rates of change in fossils based on taxonomic groups are subject, of course, to many limitations and errors. Fossils provide only an incomplete and biased record of past life, limited mainly to the forms of shallow waters and lowlands. The reported stratigraphic ranges probably generally are less than the true ranges of the original organisms. Apparent ranges are affected by the intensity and extent of collecting, by environmental facies, accidents of preservation and discovery, and by taxonomic treatment, which may vary with different authors. For example, splitting tends to shorten ranges and lumping may extend them. Furthermore, the degree of stratigraphic precision in reporting ranges has much bearing on the result. These sources of error are recognized here, but certain over-all regularities within the data suggest that they are meaningful and allow some general conclusions.

In the first place, the data agree closely with the common knowledge that the era and certain other stratigraphic boundaries are sharply defined by mass extinctions. Secondly, there is an intriguing coincidence of peaks of extinction in quite unrelated groups. For example, marine invertebrates (Fig. 4) show accelerated extinction near the close of the Cambrian (trilobites, archaeogastropods, and sponges), late Ordovician (crinoids, brachiopods, trilobites, and echinoids), late Devonian (brachiopods, corals, trilobites, ammonoids, ostracodes, archaeogastropods, bryozoans, and foraminifers), late Triassic (brachiopods and ammonoids), and late Cretaceous (crinoids, ammonoids, echinoids, archaeogastropods, bivalves, sponges, and bryozoans). The lower vertebrates (Fig. 5) also show coincident peaks of extinction in the late Devonian, late Permian, late Triassic and late Cretaceous. There is an intriguing parallelism in extinction patterns of ammonites and reptiles (Fig. 6).

These relationships are even clearer if the data on all animal groups are synthesized. In Figure 7, the episodes of extinction are shown (solid line) for all the families (a total of some 2250) of the groups represented in the preceding figures. Taking all major fossil groups of animals into consideration, the most critical times of extinction occurred near the close of the periods, especially the late Cambrian (52 per cent extinction); late Devonian (30 per cent extinction), late Permian (50 per cent extinction), late Triassic (35 per cent extinction), and late Cretaceous (26 per cent extinction). During relatively short spans, one fourth to a half of all the families of animals of the world

disappeared. The average extinction rate for all the geologic series was about 17 per cent, and the minimum about 3 per cent. As might be anticipated from the involved history of classification of the geologic systems, the Silurian-Devonian boundary, the two boundaries of the Pennsylvanian, and the upper boundary of the Jurassic are not as well characterized paleontologically as are some of the others.

Times of accelerated extinction were followed by episodes of ex-

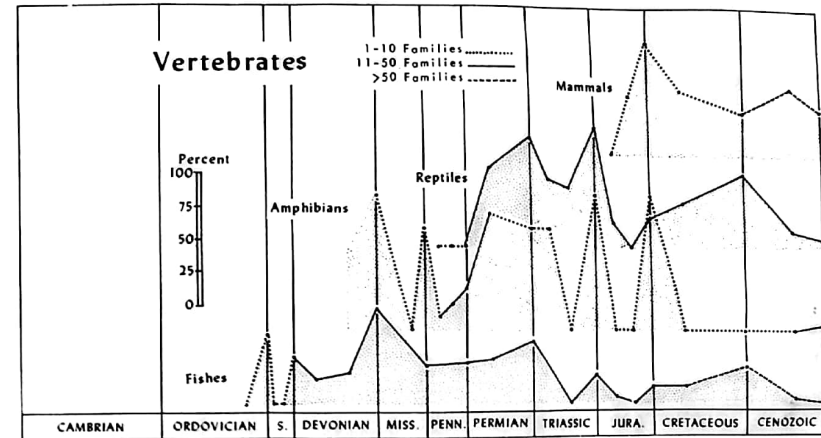


Figure 5. Percentage extinction of families of the chief groups of fossil vertebrates. There is strong correlation of extinction peaks near the end of the Devonian, Permian, Triassic, and Cretaceous periods.

ceptional radiation into vacated and new niches. It often has been noted that the pace of evolutionary diversification increases during and immediately after an episode of mass extinction (Fig. 7, broken line). This would appear to be an effect of the freeing of ecologic niches for reoccupancy by new forms added to the steady multiplication of new microhabitats consequent on the spread of life itself. Thus there appears to be a tendency for oscillations between times of accelerated extinction, which in many cases have been taken as the closing phases of chapters of geologic history, and episodes of radiation at the beginning of the subsequent intervals. This is true of many of the more distinctive series and stages, which provide subdivisions of the systems.

These tabulations were based on families of animals at the scale of stratigraphic series. More detailed tabulations of the fossils of separate

stages or zones certainly would also show sporadic replacement of faunas at the taxonomic level of species or genera. Seventy-five per cent or more replacement of species in successive faunas is not exceptional in the fossil record. This may occur at a bedding plane or above an interval of barren strata. The abrupt replacement of old by

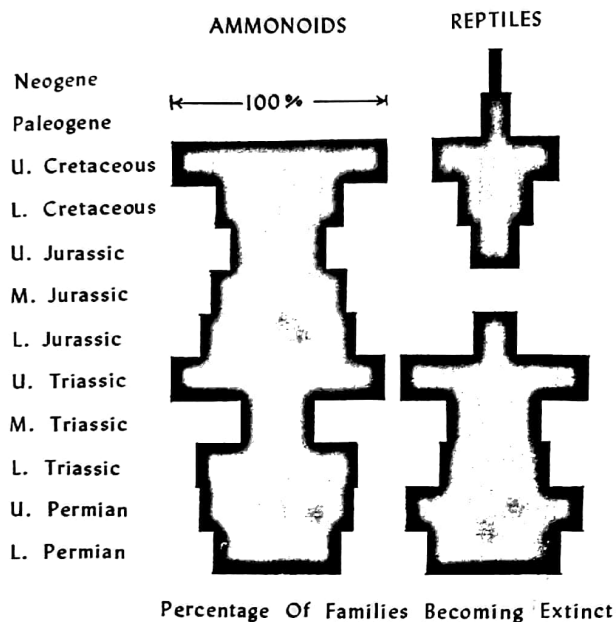


Figure 6. Parallelism in extinction of families of ammonoids and reptiles

new faunas is so common in the fossil record as to suggest general and recurring causes capable of simultaneously affecting diverse groups of animals.

The losses by extinction were quickly replaced and over-all diversity increased by continued evolution of surviving stocks (Fig. 8). There is some suggestion that their average increase was exponential at times since the early Cambrian. It seems probable that new organisms, by providing new microenvironments and new opportunities for further radiation, have stimulated evolution in a sort of ecological feed-back. A long pause occurred in this expansion during the Triassic period, as shown in Figure 8, and another may be taking place at the present as a

result of the late Quaternary and modern extinctions. Very probably there always has been at least brief reduction in diversity during an episode of mass extinction, but the stratigraphic column is not so narrowly zoned, nor our correlations so precise, that we can measure exactly the duration of episodes of decreasing or increasing diversity. The calculated trends represent a greatly generalized average.

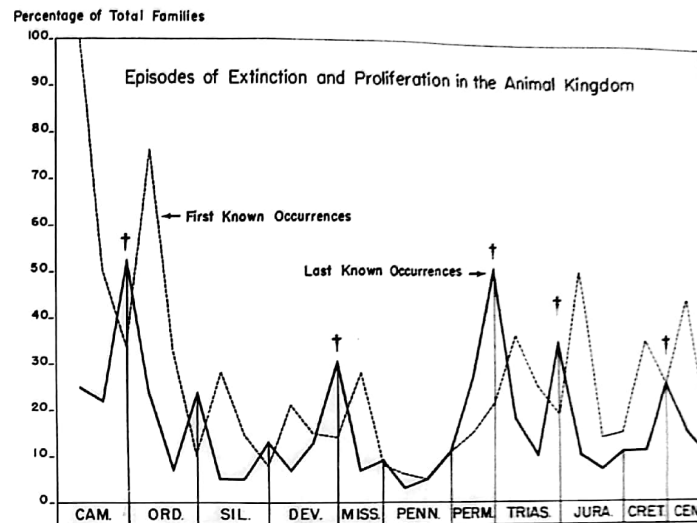


Figure 7. Percentage of first and last appearances of animal families through geologic time. Main episodes of extinction were near the close of the Cambrian, Devonian, Permian, Triassic, and Cretaceous periods.

The record of fossil plants is not nearly as well known as that of animals (Fig. 9). No detailed modern survey of the stratigraphic distribution of fossil plants is available; hence, we are unable to attempt correlations between the histories of animals and plants. Since animals are dependent on plants for food and shelter, there must have been many parallel developments in the two kingdoms. The spread of prairies and coincident adoption of the grazing habit by several groups of mammals in mid-Tertiary times may be cited as one example; the simultaneous deployment of pollinating insects and flowering plants during the Cretaceous period is another.

It seems that the greatest events in the plant kingdom were con-



Figure 8. Expansion of the animal kingdom during geologic time as expressed in numbers of known families of the main fossil groups. Heavy line indicates inferred fluctuations during most critical times of faunal revolution.

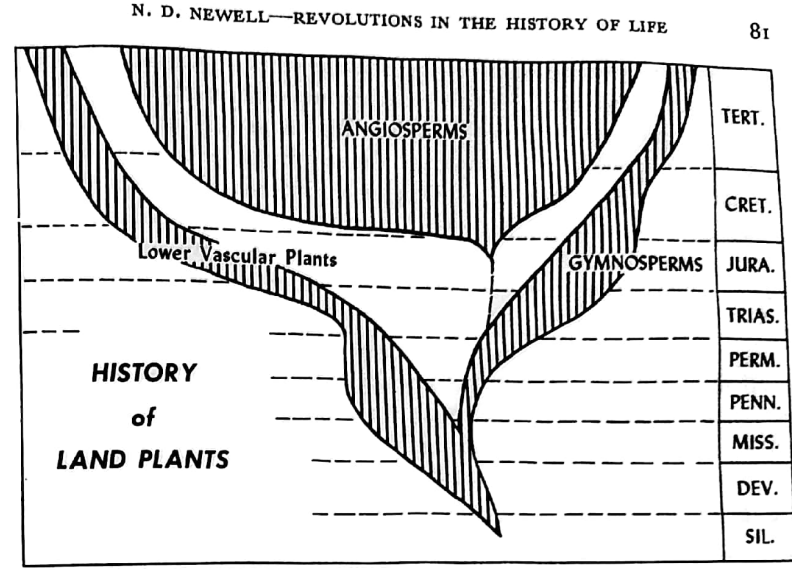


Figure 9. Trends in plant evolution (after Dorf, 1955). Apparently, none of the great events in plant history coincides with major revolutions in the animal kingdoms.

cerned with adaptive radiation and not with mass extinction, *e.g.*, the colonization of the lands by primitive vascular plants in the early and middle Paleozoic, the rise and spread of the gymnosperms in the Carboniferous, and the explosive radiation of the angiosperms in the early Cretaceous. It appears that the plants as a whole have been more conservative and ecologically more resilient than animals.

The Causes of Animal Revolutions

Hypotheses are necessary in scientific work because they guide the investigator to new observations in the search for truth. But explanations are really meaningful only if they can be tested. In paleontology, historical veracity—not reasonableness alone—is the main objective. Most of the many suggestions that have been made about the causes of past animal revolutions are of little use because they do not include satisfactory tests or analyses of corollaries. This is true of the hypothesis that mass extinctions and subsequent evolutionary deployment were caused by occasional bursts of cosmic or ultraviolet radiation from the

sun or supernovae (Wilser, 1931; Schindewolf, 1955; Uffen, 1963). The same objection applies to ideas of extinction based on fluctuations in the oxygen content of the atmosphere (Schatz, 1957), in the amounts of trace elements (Cloud, 1959), and the salinity of the ocean (Beurlen, 1956; Fischer, 1965); or, the failure in productivity of the sea (Bramlette, 1965). Furthermore, these suggestions are not general explanations and in some respects most are at variance with many of the known facts about the fossil record as I have discussed elsewhere (Newell, 1962; 1963; 1965).

Occasional writers with vague ideas about the methods and objectives of science, still turn uncritically to unrestrained imagination, sophism, and folklore in their interpretations of earth history with little or no thought to scientific implications and objective tests (*e.g.*, Velikovsky, 1955; Hapgood, 1958; Sanderson, 1960; *also see* Farrand, 1961; Larrabee, 1963, for contrasting viewpoints on the scientific methods of historical geology). The adage that "anything that can happen, will happen" cannot be construed to mean that anything that might happen, has indeed happened.

Most of the hypotheses of mass extinction were designed to explain only a single event, such as the Permian-Triassic episode and the extinction of the dinosaurs or the mammoths, and there is an implication that the simultaneous disappearance of ecologically unrelated groups such as the dinosaurs and ammonites were matters of chance coincidence. This would not be an unreasonable conclusion were it not for the fact that such coincidence happened many times and was not exceptional. Experience shows that several major cosmopolitan groups characteristically dropped out simultaneously in each of many of the episodes of mass extinction. In the present state of knowledge, it seems to me to be more fruitful to seek a general explanation adequate to embrace many examples of mass extinction rather than to attempt a unique explanation for each episode. This is in better accordance with the known facts and satisfies the principle of simplicity of hypothesis.

It has been shown in this paper that episodes of mass extinction commonly were followed by increased tempo in the appearance of new families. Thus a revolution characteristically consisted of two phases: an epoch of extinction and rapid decline by natural selection, accompanied or followed by an epoch of more gradual adaptive radiation and recovery. It is consistent with modern evolutionary theory to

conclude that the recovery phase represents an evolutionary stimulus that resulted from the new availability of an unusual number of vacant niches. The episodes of extinction prepared the way and in a sense were responsible for succeeding evolutionary bursts.

Mass extinctions may occur quickly, but there is no evidence that new faunas may suddenly spring into being, as postulated by the creationists or the macroevolutionists. Assuming high rates of extinction and evolution, it still must have required thousands to millions of years to complete the cycle of a typical revolution. They probably were not instantaneous in the sense of Cuvier, but as yet we do not have the means for measuring the time closely.

What can we say about the causes of mass extinctions of the past? Judging from the complexity of the interrelationships of living organisms with their environments, the causes of extinction are legion and it is doubtful that we shall ever be able to sort out all the responsible factors. Studies of living animals show that any species that is now successfully maintaining itself has achieved an approximate balance between the natural tendency to overpopulate its habitat and the many physical and biological factors of natural selection that oppose its spread. As Darwin pointed out, this balance between organisms and their environment is precarious and constantly in flux. Any disturbance of ecological equilibrium is likely to be deleterious to some species but may be advantageous to others. This is the selective factor in extinction.

If unfavorable environmental changes are continued throughout the range of a species, it will diminish in numbers and density until a threshold minimum is reached and then quickly disappear. This is now taking place on a world scale with many kinds of organisms as man's activities result in disturbance and continuous reduction of natural habitats. The last phase in the elimination of a species may be caused by disease, starvation, predation or some other ever-present hazard of life, but modification and loss of habitat are now probably the most important factors in the persistent decline of natural populations. Of course, man is a newcomer, but there is evidence that sweeping natural disturbances of environmental equilibrium have always been characteristic of geologic history. Herein lies the most promising explanation of animal revolutions.

With examples of modern life before us, fundamental biologic and geologic principles may be applied to the fossil record in the construc-

tion of a testable hypothesis of mass extinctions. This hypothesis postulates widespread, approximately synchronous, environmental disturbances and greatly increased selection pressure stemming primarily from three different sources. These usually are interrelated and combine to produce great stress on living populations. They are: (1) animal migrations, involving competition between better adapted immigrants and less adapted natives; (2) severe climatic changes manifested in modification of temperature and precipitation patterns; and (3) great and relatively rapid changes in distributions of land and sea.

TABLE 5. REPLACEMENT OF SOUTH AMERICAN MAMMALS BY IMMIGRANTS*

	Native Families	Introduced Families
Recent	17	10
Pleistocene	21	12
Late Pliocene	23	7
Mid-Pliocene	25	1

*After Simpson (1940)

The postulated mechanisms differ in important ways from those implied by classical catastrophism and uniformitarianism.

MIGRATIONS

The sequential replacement of old by new organisms was explained by Darwin as ordinarily a selective and continuous process resulting from unequal competition between more adapted and less adapted organisms. He also envisioned sporadic biologic changes that might periodically result from the elimination of natural barriers, such as the Isthmus of Panama, which separates two marine faunas. The elimination of such barriers and the mingling of established and invading organisms results in the decline and disappearance of members of the former group (Elton, 1958). A well-documented example of this from the fossil record was the decline of the South American mammalian fauna after the establishment of a land bridge between the Americas in the late Tertiary (Simpson, 1940). The wholesale replacement of long-established native families by North American immigrants was slow, spanning at least 4 or 5 million years; yet this was a short interval in comparison with all of Cenozoic history (Table 5).

Replacement resulting from competition is, of course, a gradual process and initially it probably always involves intimate mixing of two separate faunas. But very great changes have been recorded among living organism communities within only a few generations (Elton, 1958). If the transition is not preserved in the fossil record, the replacement of one fauna by another would appear to be very abrupt and there would be very little evidence of mixing. It is doubtful, however, that a worldwide, sharp, paleontologic boundary could originate solely by this means. Competitive replacement on a world scale would require appreciable time and transitional biotas should not be rare.

CLIMATE

Probably the most popular of all hypotheses to explain mass extinctions concerns postulated sharp changes in climate. There is no doubt that large-scale climatic changes have occurred in the past. But for the most part these must have been sufficiently gradual so that organisms have survived by evolving or by migrating into more favorable areas. It is curious that none of the ice ages of the past coincided with outstanding mass extinctions. In fact, few if any extinctions can be attributed directly to the glacial climates of the Pleistocene.¹

Nor has it been demonstrated that climatic oscillations were the main causes of mass extinctions before the Pleistocene. The fossil plants, good indicators of past climatic conditions, do not provide evidence of marked shifts in climate at the end of the Devonian, Permian, Triassic, and Cretaceous periods, or at other times of unusually rapid turnover in the animal kingdom.

Long-term variations in solar radiation or in the insulating character of the earth's atmosphere could affect climates over the earth, but temperature zones at intermediate latitudes would most probably simply shift laterally and their characteristic biotas would probably move with them without being eliminated. The shrinking of the trop-

¹ I have cited the early Recent mass extinctions of large mammals throughout the northern hemisphere and elsewhere. The episode corresponds closely in time with the warm and dry climatic optimum or hypsithermal interval and it is likely, but not yet demonstrated, that the floral patterns over much of the world were disturbed at this time more severely than they were during Glacial times. Certainly a protracted drought over the earth for some hundreds of years would adversely affect both floras and faunas that had become adapted to the moist conditions of the Pleistocene. The role played by early man in these extinctions is a moot question.

ical and subtropical belts from the Cretaceous period to the present illustrates this sort of change.

PALEOGEOGRAPHIC CHANGES

The main constituents of the fossil record are the remains of lowland and neritic organisms deposited in sedimentary basins. The most outstanding episodes of mass extinction among these corresponded to times of widespread emergence, whereas new faunas generally first appeared during times of submergence. There is a strong (but not perfect) correlation between the animal revolutions and extensive paleogeographic changes and these changes were largely diastrophic in origin as pointed out by Chamberlin, Schuchert, and others. The major geographic changes did not, however, originate in orogenies but in epeirogenies and eustatic changes in sea level. Mountain building probably had important local effects on climate and topography, but the great animal revolutions did not correspond closely in time with the most widespread orogenies (Henbest and others, 1952) which, in any case, were not as narrowly limited in time as we used to think (Gilluly, 1949). On the contrary, many great and small paleontologic discontinuities coincide with obscure paraconformities (Dunbar and Rodgers, 1957) within parallel sequences of strata deposited during times of crustal stability over the continents (Fig. 10).

The present relief of the continents is much greater and the land surface much more uneven than was usual through geologic history. Under more normal conditions of relief, minor epeirogenic movements or oscillations of sea level of a few feet probably would have produced vast geographic and climatic changes. That these changes were sufficient in extent and severity to be responsible for initiation of episodes of mass extinction is suggested by the common association of major paleontologic changes with obscure stratigraphic breaks (Newell, 1962; 1963). The frequency of this association is susceptible to investigation.

The idea of diastrophic control in evolution and extinction has fallen into disfavor because many geologists now believe that diastrophism is continuous and local rather than episodic and worldwide. In the past few decades much evidence has been cited in support of the idea that the earth's crust is inherently unstable and weak. Geographic relationships are continually modified by orogenic, epeirogenic, and eustatic movements, some of which must be mutually opposing and

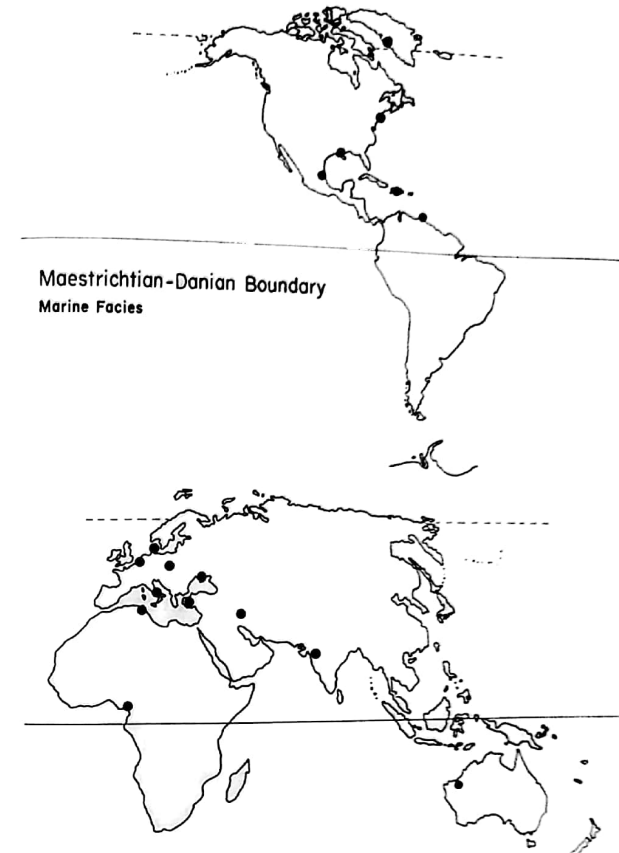


Figure 10. Location of some relatively complete sequences of parallel marine strata containing the Cretaceous-Tertiary boundary. The faunal changes at the boundary are great but the amount of time represented by these changes probably was small (data from W. A. Berggren, personal commun., 1961).

compensating. Mounting emphasis on instability has tended to discredit the simple eustatic controls of Eduard Suess and the idealized periodicity of T. C. Chamberlin (Chorley, 1963). Consequently, many unfamiliar with, or distrustful of, the fossil record are inclined to doubt the approximate synchronicity of marine transgressions or regressions over broad areas of the earth. In spite of the obscuring effects of local diastrophism, however, it is clear from the paleontologic evidence that

many episodes of submergence and emergence did, in fact, affect much of the known world within short spans of time.

Paleontologists generally agree that the continents were exceptionally emergent at the close of the Permian and Cretaceous periods, and that at other times they were widely flooded over as much as 40 per cent of the present land areas. The disturbance to marine and terrestrial ecosystems produced by these changes must have been enormous. We do not know the length of time involved in these changes, but given very flat, low land surfaces, the migration of the strand line may have been rapid and effectively "cataclysmic" in effect.

The fact that all the continents are now emergent is the best evidence that they are affected simultaneously by epeirogenesis or eustasy. Clearly the effects of global changes have more than compensated for local diastrophism. The continental areas now below sea level are small indeed compared with the situation during past intervals of flooding.

Mayr (1965) and Wace (1966) have demonstrated that a high correlation exists between biotic diversity and total area of habitat available for colonization. It may be inferred that rates of extinction are higher in small areas of habitat than in large ones. Hence, shrinkage of habitat is deleterious and probably is always lethal for those populations in delicate balance. It seems clear that rapid emergence of the continents would result in catastrophic changes in both terrestrial and marine habitats and such changes might well trigger mass extinctions among the most fragile species.

Conclusions

The fossil record shows that animal history has been marked by brief episodes of exceptionally high rates of extinction commonly accompanied and followed by somewhat more gradual evolutionary recovery. These revolutions were largely independent of the much more regular trends in plant history. The differences in the histories of animals and plants suggest that the latter were on the average more conservative and tolerant of environmental change than were animals.

All evidence indicates that episodes of mass extinction may occur within a few hundreds or thousands of years, while the development of a new replacing fauna probably requires hundreds of thousands or

millions of years. There is nothing in the record to give support to catastrophism, as Cuvier understood it, nor to the literal uniformity of Lyell which emphasized slow and uniform instead of episodic changes. Yet the record of past revolutions in the animal kingdom is understandable by application of basic principles of modern science. In this sense, the present is the key to the past.

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