[12] J. E. Burchard, "Resetting a Biological Clock," Ph.D. thesis, Princeton University, 1958.

[13] Cf. Pittendrigh and Bruce, *Rhythmic and Synthetic Processes in Growth*, p. 80; and Pittendrigh, *Perspectives in Marine Biology*. The latter paper has been in press since 1956 and will be out of date when it appears.

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# *TETRAPOD EXTINCTIONS AT THE END OF THE TRIASSIC PERIOD*

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The phenomenon of extinction has fascinated and vexed paleontologists for decades. It is a fascinating process because it has brought to an end many varied and seemingly successful lines of evolution during the successive periods of geologic time, and it is a perplexing one because it is so difficult to explain. Why should a group of animals or plants, evidently vigorous and well adapted to the environments around them, come to a relatively abrupt end at some particular stage in geologic history? Why should several groups of organisms die out almost simultaneously, while at the same time other groups should continue? What are the factors causing extinction? These are large and far-reaching questions, the answers to which for the most part can only be guessed at.

The extinctions that took place at the end of the Cretaceous period are particularly spectacular, since they involve in part the wiping-out of the great dinosaurs, the reptiles that had been dominant on the land for a hundred million years. These extinctions, which are deservedly famous in biologic and geologic literature, have received so much attention and have been so much speculated about that perhaps there has been some tendency to overlook important extinctions occurring at other times during geologic history. It is the purpose of this present paper to review briefly the extinctions of an age other than the Cretaceous.

One time when many tetrapod extinctions occurred was at the close of the Triassic period. Indeed, the extinctions of amphibians and reptiles that accompanied the transition from Triassic to Jurassic times were so numerous and involved so many taxonomic units that they must be regarded as of considerable significance; perhaps not the equal of the Cretaceous extinctions, yet nonetheless sufficiently prevalent to indicate a marked change in the history of life at that particular time.

The extinctions marking the close of Triassic history are only a part of a large and extended sequence of events that makes the Triassic period a time span of great significance in the evolution of the backboned animals. The Triassic was, in short, a period of transition, when various phylogenetic lines that had been successful through late Paleozoic and early Mesozoic times came to an end, and when various other phylogenetic lines made their first appearance, to continue through later Mesozoic history. It was a time of beginnings and of ends, and the ends concern us here.

In this connection a few comparisons may be useful. At the close of the Triassic period there were, according to the paleontologic record, eleven orders of tetrapods (amphibians and reptiles) on the earth. Almost certainly there were three or four other orders for which there is no fossil record. These eleven orders contained thirty families. Of these eleven orders and thirty families, four orders containing ten families became extinct during the transition from Triassic to Jurassic times, while, in addition, seventeen families distributed among the other seven orders also disappeared. This is a large degree of extinction, and it is quite evident that the continuation of tetrapod life from Triassic into Jurassic times was largely through the advent of new taxonomic groups within certain orders rather than through the continuation of families and lesser taxa from the earlier into the later period.

By way of contrast there were at the end of the Cretaceous period fourteen orders of tetrapods (certainly a few more for which there is no fossil record) containing fifty-seven families. Of these, eight orders containing twenty-four families became extinct at the end of Cretaceous times, while ten additional families of the remaining six known orders became extinct. Consequently, while the relative extinction of orders at the end of the Cretaceous period was greater than that occurring at the end of the Triassic, the relative extinction of families was less. There was a carry-over of twenty-three families of tetrapods from Cretaceous into early Cenozoic times (Fig. 1).

Perhaps the most significant aspect of these figures is that, so far as complete extinctions are concerned—extinctions of orders and all the lesser categories contained within those orders—the disappearance of life-forms at the end of Cretaceous times was about double that occurring at the end of Triassic times. It is

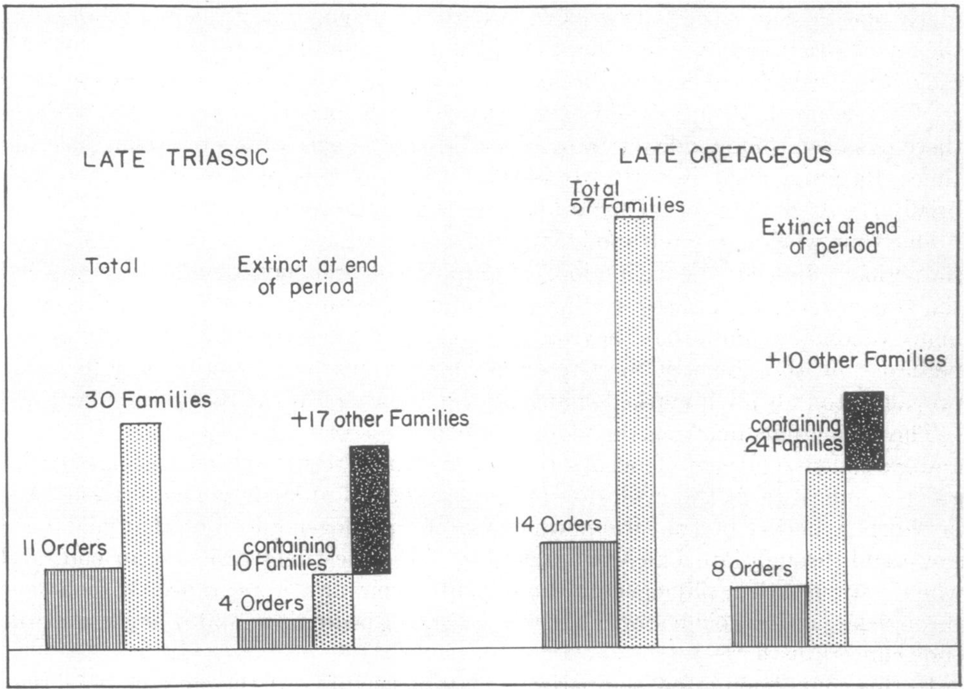


Fig. 1.—Diagram to show the total numbers of orders and families of tetrapods living in late Triassic and late Cretaceous times, and the numbers of orders and families that became extinct at the ends of those periods.

the difference between eight orders containing twenty-four families that died out with the close of the Cretaceous period and four orders containing ten families that disappeared at the end of Triassic times. When one considers what a very significant place the Cretaceous extinctions hold in paleontologic thinking, it seems valid to maintain that the Triassic extinctions, even though occurring on a scale of only half the magnitude of the Cretaceous ones, are nonetheless quite significant.

It may be that a better way to look at this problem is by a comparison of the extinction of ecologic types and their replacements in subsequent times by newly evolved forms. According to this view, the extinctions and replacements of ecologic types at the close of the Triassic period were about as shown in Table 1.

Table 1

| Extinction | Families | Environment Occupied/Diet | Replaced by |
|---|---|---|---|
| Placodonts... | 1 | Shallow marine waters/molluscivorous | Marine turtles |
| Nothosaurs | 3 | Margins of the sea/piscivorous | Plesiosaurs |
| Stereospondyls | 3 | Rivers, lakes/piscivorous | Crocodilians |
| Phytosaurs | 1 | Rivers, lakes/carnivorous | Large crocodilians |
| Rhynchosaurs | 1 | Watercourse margins/molluscivorous? | ? |
| Procolophonids | 1 | Thickets, rocks/herbivorous? | Some lizards |
| Trilophosaurs | 1 | Uplands/herbivorous | Large lizards |
| Dicynodonts | 1 | Uplands/herbivorous | Herbivorous dinosaurs |
| Ornithosuchids, etc. | 2 | Uplands/carnivorous | Small theropod dinosaurs |
| Stagonolepids, etc. | 2 | Uplands, margins of streams/carnivorous and herbivorous | Armored dinosaurs |

A comparable listing for the extinctions of ecologic types and their replacements during the transition from Cretaceous to Cenozoic times might be set down as in Table 2.

Table 2

| Extinction | Families | Environment Occupied/Diet | Replaced by |
|---|---|---|---|
| Mosasaurs... | 1 | Open oceans/piscivorous | Toothed whales |
| Ichthyosaurs | 1 | Open ocean/piscivorous | Small toothed whales |
| Plesiosaurs | 3 | Open ocean/piscivorous | Marine turtles |
| Pterosaurs | 1 | Volant over shallow seas/piscivorous | Sea birds |
| Hadrosaurs | 2 | Watercourses, margins of sea/herbivorous | Amynodont rhinoceroses |
| Titanosaurs | 1 | Swamps, rivers/herbivorous | Amynodont rhinoceroses |
| Carnosaurs | 2 | Uplands and water margins/carnivorous | Large creodonts |
| Coelurids | 1 | Thickets/carnivorous | Small creodonts |
| Ornithomimids | 1 | Open uplands/omnivorous | Large ground birds |
| Hypsilophodonts | 1 | Uplands, trees (?)/herbivorous | ? |
| Pachycephalosaurs | 1 | Uplands/herbivorous | Amblypods |
| Ankylosaurs | 2 | Uplands/herbivorous | Glyptodonts |
| Ceratopsians... | 2 | Uplands/herbivorous | Uintatheres |

When considered in this fashion, the extinctions of ecologic types and their replacements that took place at the end of Triassic and at the end of Cretaceous times were on much the same order of magnitude. But there was a qualitative difference. The replacements of ecologic types that became extinct at the end of the Triassic period were, so far as can be determined, all reptiles. The replacements of those types disappearing at the end of Cretaceous times were, for the most part, mammals and birds.

The evolutionary mechanism of replacement as outlined in these two lists was not simple. It was frequently a slow process through geologic time, so that there might be a time lapse between the animals that were dying out and those that eventually took their place. For example, while it is likely that there was an almost immediate replacement of the Triassic procolophonids by some lizards of Jurassic age (although there is no direct paleontologic evidence on this), it would seem probable from the evidence of the fossils that there was, geologically speaking, a certain time interval between the phytosaurs of late Triassic age and their ecological replacements, the Lower Jurassic crocodilians. The first crocodilians, the protosuchians, of uppermost Triassic and possibly of lowermost Jurassic relationships, were small reptiles, in no way ecologically comparable to the large, aggressive phytosaurs of the Upper Triassic. The true ecological replacements of the phytosaurs, the large crocodilians of Jurassic age, such as *Mystriosaurus* and *Pelagosaurus*, would seem to make their appearance in the Upper Lias, separated by an appreciable time interval from the date of phytosaurian extinction. Such intervals in the ecological replacement of extinct types by new and unrelated forms are even more striking in the succession of Cretaceous and Cenozoic faunas. It would seem that the earliest ecological replacements for the ceratopsian dinosaurs might have been some of the large, Eocene Dinocerata like *Uintatherium*, and these did not appear until late Eocene times, many millions of years after the disappearance of the dinosaurs. The glyptodonts—the mammals most closely comparable in adaptations to the ankylosaurs, or armored dinosaurs—did not appear until late Cenozoic times and therefore were separated by a very long time interval from their reptilian ecological precursors. Consequently, this whole problem of replacements should be viewed in broad and rather general terms.

There has been much speculation in the past, and there will continue to be speculation in the future, as to the reasons for the extensive disappearances of reptiles at the end of Cretaceous times and their replacements by the varied mammals of early Cenozoic times. Many theories have been proposed—none as yet answers satisfactorily the numerous problems raised by the extinctions of the dinosaurs and other reptiles so characteristic of Mesozoic times. The best we can do is to say that environmental conditions changed and that the dominant tetrapods of late Cretaceous times were unable to adapt themselves to the changes in the earth and its vegetation taking place around them.

If the extinctions of the dinosaurs, their cousins, and their contemporaries at the end of the Cretaceous period were brought about by some widespread changes in environments, it seems logical to suppose that the extinctions of various amphibians and reptiles at the end of the Triassic period must likewise have been brought about by changing environments. The geologic evidence points to this.

The Triassic period was seemingly a time of relatively high lands and possibly of varied climates. The world was nothing like it is today, for tropical environments must have formed broad belts on each side of the equator and subtropical conditions must have extended far to the north and the south toward the poles. This is indicated by the wide distribution of amphibians and reptiles of late Triassic times. Nevertheless, within the limits of this great tropical world there were seemingly environmental differences in space and in time that were of considerable importance. It would appear that there were areas of lush forests and swamps on the broad Triassic continents and also areas of dry and even desert environments. It is likely that there may have been some alternations of seasons, involving perhaps not so much changes in temperatures as seasonal differences in rainfall. There was much volcanic activity in many parts of the world. Such conditions, so typical of late Triassic times, probably extended back through the range of the Triassic period and on back through much of the preceding Permian. These two geologic periods were the time of "red-bed" deposition on the land masses, and the tetrapod faunas of these geologic ages, found for the most part in the red beds, are distinctive. They are faunas in which the large labyrinthodont amphibians are prominent and probably at the time were active competitors with their reptilian contemporaries. Also in these faunas are the cotylosaurs, primitive reptiles not far removed from their labyrinthodont ancestors. As descendants from the cotylosaurs are the precursors of the turtles. In addition, there are many synapsid reptiles, the pelycosaurs and the mammal-like therapsids. These groups of reptiles and some others of lesser importance continued in most cases from the Permian through the Triassic.

Beyond these similarities between Permian and Triassic faunas the Triassic assemblages are distinctive by reason of the appearance of several new and important groups of reptiles, notably the ichthyosaurs and sauropterygians (marking the first broad invasion of marine waters by the tetrapods), the ancestral lizards, the thecodonts, ancestors of all of the later archosaurians, and the first dinosaurs.

Then at the end of the Triassic period there occurred many environmental changes that were to affect the composition of vertebrate faunas in the ages to come. There were wide invasions of the continental platforms by shallow seas. The world, which had been a globe of uplifted continents and perhaps varied environmental conditions, was transformed into a world of low-lying and restricted land masses and generally uniform environments.

The changes in faunas that accompanied these changes in environments were striking. The labyrinthodont amphibians, the primitive reptiles, and the synapsids, which had characterized the Permo-Triassic scene, disappeared, and the faunas became typified in their marine facies by the prevalence of aquatic reptiles and in their continental facies by the remarkable dominance of the varied and numerous dinosaurs. Certainly the vertebrate life of the Triassic marshes and uplands, with huge labyrinthodont amphibians, dicynodonts, armored pseudosuchians, large phytosaurs, and small, primitive dinosaurs was quite differently constituted from the life of the Jurassic lowlands and marshes, with turtles, crocodilians, lizards, flying reptiles, and dinosaurs of many kinds, from small, lightly built types to great giants, from aggressive predators to inoffensive herbivores. The contrast may not be so impressive as that between the Cretaceous dinosaurs and the early Cenozoic mammals, but nonetheless it is a contrast worthy of close attention. It marks the advent of a new chapter in the history of vertebrate life. It is strong proof of the fact that the transition from Triassic to Jurassic times was a crucial stage in the evolution of various lines of tetrapod phylogeny.