

Dinosaurs' Lucky Break

Not necessarily superior competitors, dinosaurs may simply have benefited from the ill fortune of their reptilian predecessors

by Michael J. Benton

Throughout the history of life, there have been many major upheavals in which whole groups of animals were replaced by others. Perhaps the most famous was the replacement of the dinosaurs by the mammals 65 million years ago. Another major change occurred 150 million years earlier, when the dinosaurs took over the position of dominance that had been held for 80 million years by mammallike reptiles.

What triggered these great upheavals? Scientific thinking about the various factors that might have been responsible for such replacements has undergone some significant changes of its own. At times, for example, scientists have suggested that mammals caused the extinction of the dinosaurs by eating their eggs or by competing for the same food resources. Now, however, most people are convinced that the mammals played only a minor role, if any (largely because both groups had lived side by side for millions of years), and that, instead, environmental change was primarily responsible. The mammals apparently sat around for 150 million years in the Mesozoic undergrowth until, with the extinction of the dinosaurs, they had their opportunity to radiate into newly available niches.

But what about the initial radiation of the dinosaurs? The transition from mammallike reptiles to dinosaurs has been described by many authors and is frequently quoted as an example of major competitive replacement among vertebrates. (The use of the word *competition* in this context is convenient but potentially misleading. Individuals can compete, and one could even consider two species as competing, but at higher taxonomic levels, any large-scale replacements would probably be the result of numerous such events combined, together with other factors, in an essentially random way. The net result could more accurately be described as differential survival of one taxon compared with another that occupied a similar range of niches. For the purposes of this article, however, I will stick with the more familiar term of competition.)

According to nearly all published accounts, the replacement of mammallike

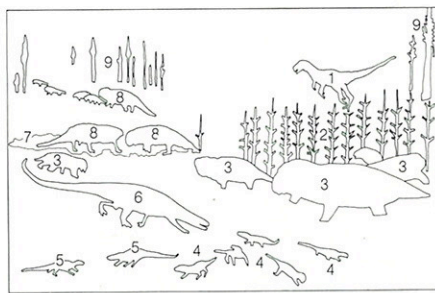
reptiles by the dinosaurs went as follows: During the Permian period and the early part of the Triassic (from 290 to 225 million years ago), the land was dominated by the mammallike reptiles, which ranged in size and shape from a rat, or smaller, to a hippopotamus. At the end of the Permian, major upheavals occurred and many lineages became extinct. In the early Triassic, faunas of herbivorous mammallike reptiles, almost certainly unbalanced by these events, were heavily dominated by huge numbers of a single genus, *Lystrosaurus*. New faunal elements also appeared at this time: the thecodontians, which included the ancestors of the dinosaurs. The carnivore niches throughout most of the Triassic were shared by advanced mammallike reptiles, such as *Traversodon*, and thecodontians, some of which, such as *Rauisuchus*, became very large. The thecodontians are supposed to have gradually outcompeted the mammallike reptiles and taken over the carnivore niches. Toward the end of the Triassic, there were still some herbivorous mammallike reptiles, such as *Dinodontosaurus*, and some herbivorous thecodontians arose. Dinosaurs, according to most of these accounts, first appeared on the scene in the middle Triassic. Eventually, the mammallike reptiles and thecodontians waned and the dinosaurs increased in importance, supposedly as a result of competition. The replacement was complete after about 40 million years.

Dinosaur superiority in this alleged competition has been variously attributed to features of their posture and locomotion or to their thermoregulation. Mammallike reptiles and thecodontians are said to have had a sprawling or semierect posture, with their legs stuck out sideways and bent downward only at the knee and elbow. In dinosaurs, the legs were tucked right under the body, giving them an erect posture, as seen in most mammals. This enabled them to take longer strides and support greater weight.

In the past decade, many authors, including myself, have devoted hundreds of pages to speculations about the thermal physiology of the dinosaurs and why it was better than that of mammallike reptiles.



This painting, based on a fossil site in Brazil, represents a community of animals that existed 220 million years ago, just 5 million years before the extinction of the rhynchosaur, mammallike reptiles, and thecodontians. At that time, dinosaurs were extremely rare, here represented by only a single individual, a *Staurikosaurus*.



1. *Staurikosaurus*, carnivorous primitive dinosaur
2. *Equisetum*, horsetail
3. *Dinodontosaurus*, herbivorous mammallike reptile
4. *Traversodon*, herbivorous mammallike reptile
5. *Belesodon*, carnivorous mammallike reptile
6. *Rauisuchus*, carnivorous thecodontian
7. *Dicroidium*, seed fern
8. *Scaphonyx*, herbivorous rhynchosaur
9. *Pleuromeia*, lycopod



without caption

A short time (geologically speaking) after the rhynchosaurs, mammallike reptiles, and thecodontians died out, dinosaurs appeared in great numbers and diversity.

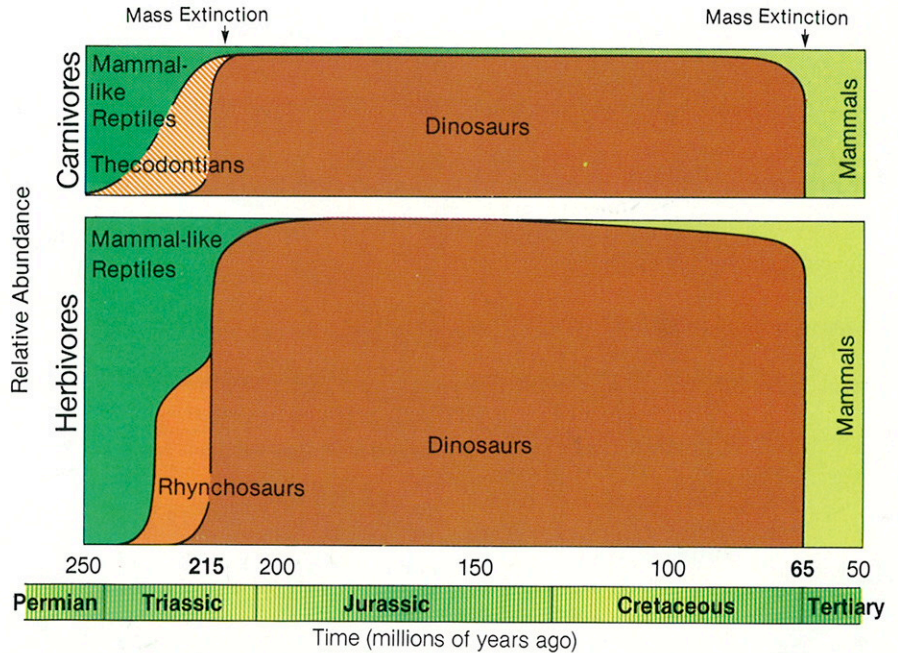
Joe LeMonnier

Impassioned arguments have been advanced for fully hot-blooded dinosaurs (with true endothermy as in mammals and birds), for coldblooded dinosaurs (with true ectothermy as in living reptiles), or lukewarm-blooded dinosaurs (something in between: ectothermic, but with relatively constant internal temperatures because of their great bulk). These speculations on the locomotion and thermoregulation of dinosaurs are exciting, but I believe that the search for particular reasons for the competitive superiority of dinosaurs is fruitless. There is simply no evidence that any large-scale competition ever took place, and even if there were, animals are too complex for us to say that one or another adaptation can by itself explain a major worldwide ecological replacement.

How *does* one set about testing what happened 200 million years ago in order to identify the kinds of ecological forces that might have been operating? As with most broadly based studies of this kind, the route by which paleontologists reach their conclusions is convoluted and guided by accident as much as by inspiration.

I carried out my doctoral thesis work on a curious animal called *Hyperodapedon*, known from fossils found near the town of Elgin in northeast Scotland. *Hyperodapedon* lived some time before the end of the Triassic and had very close relatives, such as *Scaphonyx*, living at about the same time in India, Brazil, Argentina, Texas, Nova Scotia, and possibly Tanzania. These animals are rhynchosaurs—pig-sized herbivores with hooked snouts, slicing jaws with broad batteries of teeth, wide skulls with powerful jaw muscles, and hind limbs adapted for scratch digging.

I quickly found out that rhynchosaurs were *animalia non grata* in paleontological texts—neither mammallike reptiles nor thecodontians nor dinosaurs, they did not fit the simple competitive models. But they could not be ignored, for when rhynchosaurs were present in fossil faunas, which was quite often, they were dominant. In fact, they made up approximately half of all reptile specimens found. Their relative abundance in the middle and late Triassic must have been com-



parable to that of antelope in certain African savanna faunas today. I was surprised, then, to learn that the rhynchosaurs disappeared suddenly worldwide. I set out first of all to try to explain this extinction, but my search soon broadened in scope.

I wanted to have as accurate and localized an impression as possible of changes over time in the relative composition of late Permian and Triassic terrestrial reptile faunas. This meant that I had to collect information on the numbers of specimens of each species present in each of many separate faunas worldwide. To do this, I combined the few existing published accounts with visits to many museums—to count skulls and skeletons—and correspondence with curators in many more.

One factor facilitating my search for patterns in the transition from mammallike reptiles and thecodontians to dinosaurs was the remarkable similarity worldwide among faunas at any particular time. During the Permian and Triassic, all land masses were a part of the supercontinent Pangea, and large land animals could migrate relatively freely. There was also apparently far less variation in temperature and climate from the equator to the poles than there is today.

The results of my study suggest a different sequence of events from those expected in the standard competitive model. Over the course of the Triassic, the carnivorous thecodontians did "take over" from the mammallike reptiles, and this gradual change would seem to suggest that competition might have been involved. However, the thecodontians never completely replaced the carnivorous mammallike reptiles, which were radiating and evolving throughout this time. Indeed, among the mammallike reptiles that persisted were many advanced forms (cynodonts), which gave rise to true mammals at the end of the Triassic. Both the carnivorous mammallike reptiles and the thecodontians died out toward the end of the Triassic and were replaced abruptly by dinosaurs. Thus, the fossil record of carnivores offers, at best, only weak support for an even partly competitive model.

Among the herbivores, mammallike reptiles (particularly *Lystrosaurus* and other dicynodonts) were dominant in the late Permian and early Triassic. In the middle Triassic, the dicynodonts were partially replaced by other mammallike reptiles (diademodontids) and by the rhynchosaurs. This situation continued until a few million years before the end of the

Triassic, when all rhynchosaurs and major mammallike reptile groups became extinct. A short time afterward (by geological standards), we find dinosaurs dominant worldwide. Again, the suddenness of the replacement seems to rule out competition as an important factor.

Dinosaurs, such as *Staurikosaurus*, had been present in the late Triassic rhynchosaur-diademodontid faunas, but only as rare elements (± 1 percent) and never large in size. Then, within one to two million years, the dinosaur radiation produced a range of different forms from modest bipedal carnivores (three to six feet long) to large herbivores/omnivores such as *Massospondylus* (fifteen to forty-five feet long). This changeover may be seen in Germany and the United States (Texas, New Mexico, Arizona), where successions of reptile faunas span the late Triassic and show "predinosaur" and dinosaur assemblages.

At this point, a few words about the so-called middle Triassic dinosaurs—which are discussed in most texts and which are so important in the competitive model of replacement—are in order. Most of these "dinosaurs" were described earlier this century on the basis of single teeth and other fragments. More than half have since been shown to belong to the thecodontians and various common aquatic groups of the middle Triassic. Others are literally impossible to identify as anything in particular because they are so incomplete. The remaining dinosaurs from the middle Triassic or early part of the late Triassic have apparently been wrongly dated. They are all of late Triassic age, as shown by comparison of associated fossils with those from other parts of the world. Thus, I believe that there are no dinosaurs known before the late Triassic.

A close examination of the data, then, suggests that the dinosaurs came on the scene rapidly and that their initial pattern of radiation may have had much in common with that of the mammals 150 million years later. These opportunistic replacements, in which the new forms occupy niches that are already empty, are quite different from competitive replacements, in which the replacing forms actu-

ally cause the extinction of the replaced animals. And the difference is more than just an interesting aside to any particular changeover in the history of life: in a model of competitive replacement, one is stating that the new forms are somehow better than the old ones. In a model of opportunistic replacement, this need not be the case, and we do not have to assume that dinosaurs were superior to mammallike reptiles and rhynchosaurs in any way at all.

But why *did* the mammallike reptiles, rhynchosaurs, and thecodontians all die out toward the end of the Triassic? The extinction of major groups of terrestrial vertebrates—particularly the dinosaurs—has attracted a great deal of attention. The number of explanations for the extinction of the dinosaurs is getting out of hand, and not surprisingly perhaps, there is often a close tie between the ideas suggested and the discipline of the scientist making the suggestion. Thus, astronomers and geophysicists go for asteroids or comets; atmospheric scientists go for acid rain; ophthalmologists for cataract blindness; botanists for alkaloid poisoning; and dieticians for a reduction in fiber and natural oils leading to rampant dinosaurian constipation. In comparison with these, I have a somewhat less dramatic proposal to "explain" the extinction of the mammallike reptiles, rhynchosaurs, and thecodontians: a change in the vegetation.

During the middle of the Triassic, southern parts of the world were dominated by the *Dicroidium* flora (seed ferns, horsetails, ferns, cycadophytes, ginkgos, and conifers). At the time of the reptile extinctions, this vegetation was largely replaced by conifers and bennettitaleans (large treelike cycads). The rhynchosaurs appear to have been highly specialized to the *Dicroidium* flora. Their jaws were designed for powerful and precise vertical bites, in which the lower jaw chopped into a deep groove in the upper jaw, like the blade of a penknife closing sharply into its handle. This remarkable jaw mechanism was an adaptation for cutting some of the tough vegetation found in the *Dicroidium* flora, and the loss of these food plants may have led to the animals' demise. (It is not

clear whether some of the mammallike reptiles and thecodontians were similarly specialized.) Coupled with this is a suggested climatic change: the first dinosaur-dominated faunas have been found in highly oxidized, reddish deposits, which are typical of a more arid climate and may indicate a general drying up. Perhaps the early dinosaurs were the only animals able to cope with the new vegetation and the hotter, drier climate.

If this opportunistic model for the rise of the dinosaurs proves valid, then, in combination with the later, equally opportunistic rise of the mammals, it raises an important question for paleontologists to tackle: have large-scale replacements *ever* been produced by competition? Several criteria might be looked for in the fossil record of major replacement events to determine whether they were opportunistic, competitive, or something else. Competition between one group and the group that replaced it would be suggested if, for example, the following patterns were found: as the replacing group increases in abundance over time, the other decreases; the rate of replacement is slow (for higher taxa, say, over a period of more than one million years); the two groups are found together and either can be dominant; and the replacement need not be associated with a climatic or floral change.

An opportunistic replacement, in contrast, might be suggested by the following patterns: the replacing group appears or radiates only after the extinction of the other; the rate of replacement is rapid (well below one million years); the two groups are not found together or, if they are, the new group will be unobtrusively present when the other is dominant; and the replacement is associated with environmental change.

Of course, a third kind of hypothesis to explain a replacement would be that it was neither opportunistic nor simply competitive but was caused by a mixture of different events—effectively random since we cannot define every factor involved.

Recently, a number of well-known, supposedly competitive replacements have been studied carefully, and they have turned out to be opportunistic. Stephen

Jay Gould and C. Bradford Calloway of Harvard's Museum of Comparative Zoology looked at the replacement of brachiopods by bivalves (clams, for example) in the seas from the Paleozoic to the present day. Brachiopods were abundant, diverse, and widespread throughout most of the Paleozoic but declined afterward and now occupy a limited range of sea-floor habitats. Bivalves, which were already present in the early Paleozoic seas, increased in abundance and diversity and "took over" in the Mesozoic. Considered cursorily, this replacement appears gradual and, as such, a candidate for competition. However, when Gould and Calloway put together a simple graph of the numbers of brachiopods versus clams and other bivalves over time, they showed that the switchover was rather rapid and that it occurred at the boundary of the Permian and Triassic periods. At this time—the same time that many mammallike reptiles were dying out on land—major extinctions swept through most marine groups. Whatever the cause of the wave of extinctions, the bivalves recovered from the disruption and radiated in the Triassic, while the brachiopods continued but at reduced levels of diversity ever after. Far from being a long-term competitive takeover, this was opportunism.

Another recent subject of study has been the "Great American Interchange" of mammals that occurred when the Panamanian land bridge rejoined North and South America three million years ago and allowed free mingling of previously isolated faunas. The standard view of the interchange has been that the North American mammals made a greater impression on South American faunas than vice versa. This view concedes that a few South American forms (opossums, armadillos) made it to the United States and Canada, but the traffic was supposed to be primarily one-way, from north to south. The clear implication is that North American forms were generally superior to South American ones.

Detailed studies by Larry G. Marshall of Chicago's Field Museum of Natural History and others (described by Stephen Jay Gould in the August 1982 issue of

Natural History) have shown that there was no clear, one-sided competitive replacement of South American groups by North Americans. Many South American groups were little affected by the immigration, and many South American mammals—including tree sloths, monkeys, porcupines, anteaters, and various large rodents—successfully established themselves in the warmer parts of Central and North America.

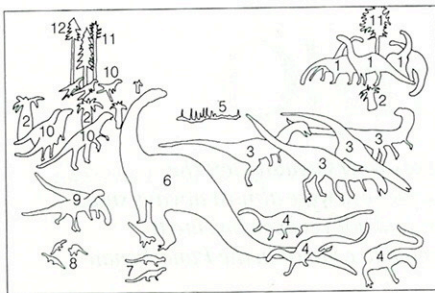
The assumption that the succession of life forms through time is a manifestation of some principle of continuous improvement is pervasive and deep-rooted. As one group becomes outmoded, it is seen as inevitably replaced by a more dynamic, up-to-date assemblage. This is one view of human history, too. A story can be made up for any "competitive" replacement that we like. I believe, however, that the 150-million-year rule of the dinosaurs was not inevitable, that it could even be seen as an interlude between the two periods of evolution of the mammallike reptiles and their descendants, the mammals. By any standard, the late Triassic mammallike reptiles were advanced and diverse. True mammals appeared at about that time too—just after the origin of the dinosaurs. If the extinctions of most mammallike reptiles (as well as rhynchosaurs and thecodontians) had not occurred 215 million years ago, there is every reason to suppose that the mammals could have radiated and come to occupy a broad range of niches during the end of the Triassic and the subsequent Jurassic period.

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In this reconstruction of a 210-million-year-old fossil site in South Africa, dinosaurs are already predominant. Mammals arose at about the same time as the dinosaurs, but they remained small and were overshadowed by them for another 150 million years.

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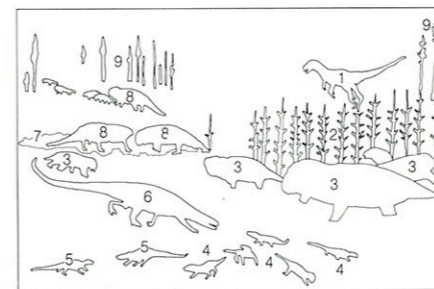
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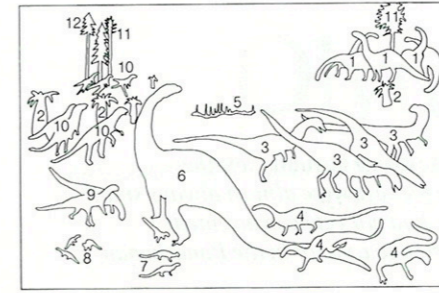
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