The age of the rhynchosaur

The dinosaurs dominated the Earth for 130 million years. But they might have remained as also-rans if the rhynchosaurs had not already been driven into extinction

Mike Benton

THE FOSSIL RECORD shows that throughout the history of life on Earth the groups of animals that were dominant in any one age were often replaced wholesale in the next age by others animal of a quite different group; and biologists have sometimes argued that such replacements occur because of direct competition between the old dominant type and the new. It has been suggested, for example, that mammals "took over" from the dinosaurs about 65 million years ago, just by competing with them. This view is essentially anthropomorphic; we are mammals after all and it is perhaps comforting to think that our own distant relatives so directly proved their supremacy over slow-witted reptiles that had nothing to fight with but their bulk.

But this simplistic account of that crucial phase of evolution has not stood the test of modern investigation. It is now clear that dinosaurs were supreme for 130 million years, and that mammals co-existed with them, albeit small and insignificant through most of that time. It is plain too, that dinosaurs in their highest forms were far from being lumbering brutes; and there is overwhelming evidence that what finally defeated them was not competition from "higher" forms of life, but changes in climate, possibly exacerbated by catastrophic events, including the impact of giant meteors. In this scenario the mammals emerge not as natural conquerors, but as opportunists, filling a gap, an "adaptive zone" with a range of ecological niches, after, and only after, the old regime had run its course.

Modern evidence suggests that this is a common pattern. Major groups do not simply obliterate other major groups by competition; rather do they radiate into the adaptive zones after the previous dominant group has become extinct. Thus the dinosaurs themselves probably gained ascendancy in precisely this fashion. In the Triassic Period, 225 to 190 million years ago, before the age of dinosaurs, the predominant groups of herbivorous land animals belonged to two quite different groups of reptiles: the synapsids, or mammal-like reptiles; and the rhynchosaurs. The most numerous were the rhynchosaurs. They are present in most of the major faunas known from the Middle and Upper Triassic, in land areas that now constitute Tanzania, Brazil, Argentina, North America, Britain and Germany; and whenever they were present they were the most abundant type of land animal. But although there has been detailed research on several rhynchosaurs, there are still important controversies surrounding their diet and their mode of life, their significance in Triassic ecosystems, and their taxonomic position (that is, their relationship to other kinds of reptiles).

A typical rhynchosaur is *Hyperodapedon gordoni*, found in what is now north-east Scotland in the late Triassic Lossiemouth Sandstone Formation of Elgin. I did my PhD thesis on this animal at Newcastle University. As shown above, *Hyperodapedon* was a squat quadruped, 1·3 m in length, with powerful limbs. The skull is specialised with a broad posterior portion to accommodate powerful muscles to close the jaw (adductor muscles). The upper dentition is borne on two maxillary tooth-plates, each of which has several rows of teeth and is bisected by a deep longitudinal groove (Figure 1). The lower jaw fits snugly into the groove when the jaws are shut, like the blade of a penknife fitting into its handle. There are two rows of teeth in the lower jaw, one row on the crest of the jaw (buccal teeth) and one row lower down on the inside (lingual teeth). There are toothless beak-like premaxillae at the front of the skull, and the lower jaws curve up on either side to a high point.

Mammal-like teeth

Detailed studies of the arrangement of teeth within the jaws, and of their cell structure (histology), have shown that rhynchosaurs did not replace their teeth in a typical reptilian way. In living lizards and crocodiles, new teeth appear in sequence below the functional teeth, which are effectively dead, and force them out periodically. By contrast, rhynchosaur teeth were more like those of modern mammals in their manner of growth. They continued to grow throughout their functional life, and new teeth appeared at the back of the jaw as the animal increased in size. The teeth were fused to specialised bones of attachment, and the hollow centre of each tooth is the root canal which was filled with blood vessels and nerves. The functional teeth were "alive" and were subject to constant internal remodelling, as is typical of most mammals.

Patterns of tooth wear, and the nature of the jaw joint, show that rhynchosaurs had a precise, straight up-and-down bite. The groove in the upper tooth-plate clearly prevented sideways movement of the lower jaw. Neither could the lower jaw slide backwards and forwards in a saw-like motion because the "hinge" between the lower jaw and skull (the joint between the quadrate bone on the skull and articular bone of the lower jaw) was tight when the jaws were shut. This is confirmed by the presence of shallow pits worn into the bone of the tooth-plate by the teeth of the lower jaw; if there was a sliding jaw action, there would be grooves instead.

What does all this tell us of the rhynchosaurs' diet? One current suggestion, that they ate molluscs, is based on the general appearance of the tooth-plate and the "tusks". But there is strong evidence against this. The teeth are not polished and hard like those of other animals that crush shells, such as the chimeras, stingrays or lungfish, which are all modern fish, or the extinct placodonts, which are marine reptiles of the Triassic. In fact, rhynchosaur teeth have only a thin layer of enamel, which apparently was readily worn away. The shape and arrangement of the rhynchosaur teeth are also different from those of living molluscivores; they were sharp and conical when unworn, rather than broad and flattened.The deep groove in the maxilla in the upper jaw, and the blade-like dentary (the principal bone of the lower jaw) are also quite different from the usual flattened, pavement-like dentition, designed to act like a pounding board, in a shell crusher. Finally, fossil animals are often found in association with the remains of their principal food, but rhynchosaurs are rarely found in association with mollusc shells.

On the other hand, there is good evidence that *Hyperodapedon* was a herbivore. The patterns of tooth wear and growth and the precision-shear bite are comparable with those seen in *Uromastix*, a thickset, stumpy-tailed modern lizard, 30 to 40 cm long, that lives in North Africa and Asia. Few modern lizards are herbivorous, but *Uromastix* is a herbivore: it efficiently crops leaves, flowers, shoots and fruit of a wide variety of plants, but does not masticate the food. The teeth of *Uromastix*, unlike those of insectivorous or carnivorous lizards, are expanded backwards and forwards to form a nearly continuous cutting edge. The jaw action is scissor-like and both tooth and jaw bone can perform the cutting function.

The body shape, too, suggests that rhynchosaurs were herbivorous. *Hyperodapedon* and other rhynchosaurs had a barrel-shaped body to accommodate a large gut for the slow digestion of plant material; they could not grind up plant food with their teeth, but may have been able to "ruminate", like a modern cow. They could gather food with the beak-like premaxillae, manipulate it with the large tongue (possession of which is suggested by the extensive hyoid bones in the throat) and crop and slice it efficiently with the powerful jaws. The hind limbs were strong and apparently adapted for scratch-digging, and *Hyperodapedon* could presumably dig up edible tubers and roots. Several rhynchosaurs have been found in association with fragments of plants (though it is not possible to say from a juxtaposition of fossils whether those fragments were ever inside the animal) and the diet probably consisted of leaves, stems, fruit and seeds of seed-ferns, conifers, ginkgos, equisitales (horsetails) and ferns (Figure 2). Final evidence that rhynchosaurs were herbivorous is that they occurred in large numbers; in general we expect the herbivores to outnumber carnivores.

Rhynchosaurs did not diversify—radiate—into so many different forms and niches as many other major groups of animals, but they are known from many parts of the world and they certainly did change and evolve with time. Small, possibly ancestral forms occurred in the early Triassic (225-215 million years ago) in South Africa; types such as *Noteosuchus*, *Howesia*, and *Mesosuchus*. The middle Triassic rhynchosaurs from Tanzania (*Stenaulorhynchus*), India (*Mesodapedon*) and England (*Rhynchosaurus*), dating from 215 to 205 million years ago, have elongate skulls, teeth on the palate, and two grooves and lingual teeth on the maxilla. The late Triassic forms from Argentina and Brazil (*Scaphonyx*), India and Scotland (*Hyperodapedon*), dating from 205 to 190 million years ago, have broad skulls, no palatal teeth, and one groove and no lingual teeth on the maxilla. Thus was the range of variation.

But where do the rhynchosaurs fit into the picture of Triassic life? At the beginning of the Triassic the dominant land animals were the mammal-like reptiles, the synapsids, although they had already been badly affected by dramatic events at the end of the Permian; catastrophic events of the kind that are now known to have turned the course of Earth's history several times. Though the synapsids survived the end of the Permian, many forms of life suffered mass extinctions. Yet at the end of the Triassic the synapsids were practically extinct and the dinosaurs, which as Figures 2 and 4 illustrate are a quite different group, were abundant and widespread. This take-over is one of the most significant events in vertebrate history. What happened in that time? And what part did the rhynchosaurs play?

To find out I looked closely at all the reptile faunas known from the Triassic; that is, I looked at each separate assemblage of reptiles that was known to live in any one place at any

Figure 2. *This scheme is based on counts of fossils. Herbivores are stippled; carnivores are hatched. Note that although there were far more carnivorous types (see chart of phylogeny, overleaf) that in terms of sheer numbers, herbivores inevitably predominate in each age. The typical flora of each age is shown in the background. Clearly, major groups of animals have succeeded other major groups. Was this because of direct competition, or because of changes in prevailing conditions, including changes in the flora?* ▶

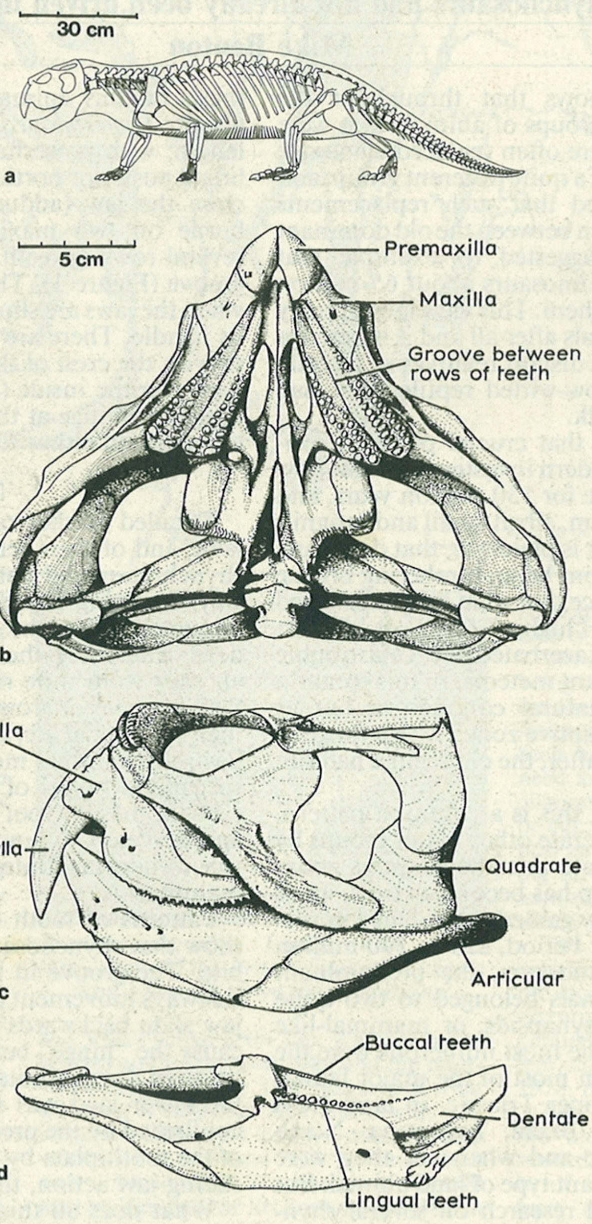
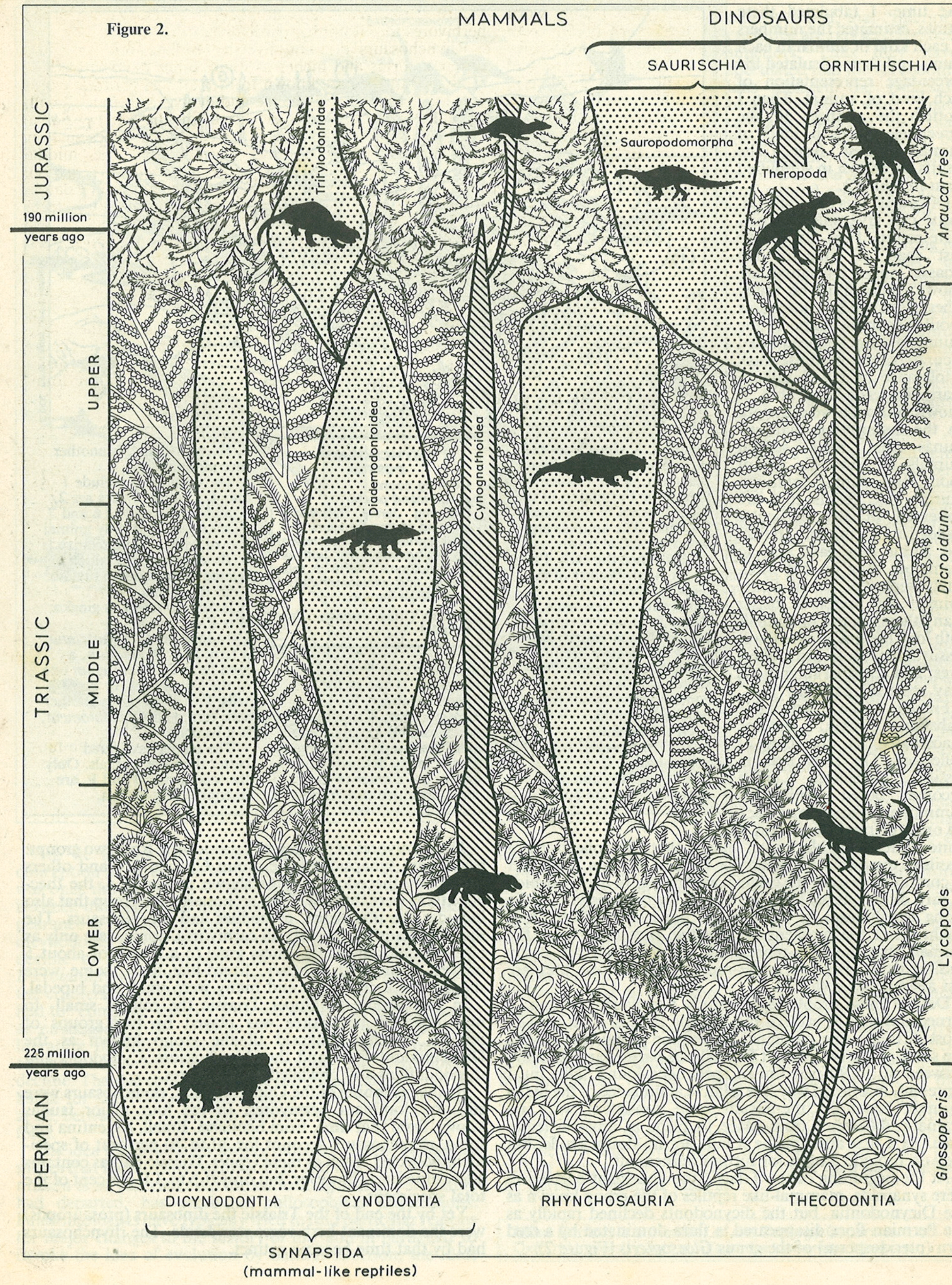


Figure 1. *Hyperodapedon, archetypal rhynchosaur from areas that are now in Scotland and India; also shown on opening page. The two rows of teeth in the lower jaw mesh neatly with the two rows on the upper, and the joint between the quadrate and articular bones of the jaws provide a simple pivot, giving the jaws a scissor-like action. Some have said rhynchosaurs ate molluscs, but they were almost certainly herbivorous.*

Figure 2.


MAMMALS
DINOSAURS
SAURISCHIA
ORNITHISCHIA
Sauropodomorpha
Theropoda
Trilylodontidae
Diademodontoidea
Cynognathoidea
JURASSIC
190 million years ago
UPPER
TRIASSIC
MIDDLE
LOWER
225 million years ago
PERMIAN
Araucarites
Dicroidium
Lycopods
Glossopteris
DICYNODONTIA
CYNODONTIA
RHYNCHOSAURIA
THECODONTIA
SYNAPSIDA
(mammal-like reptiles)

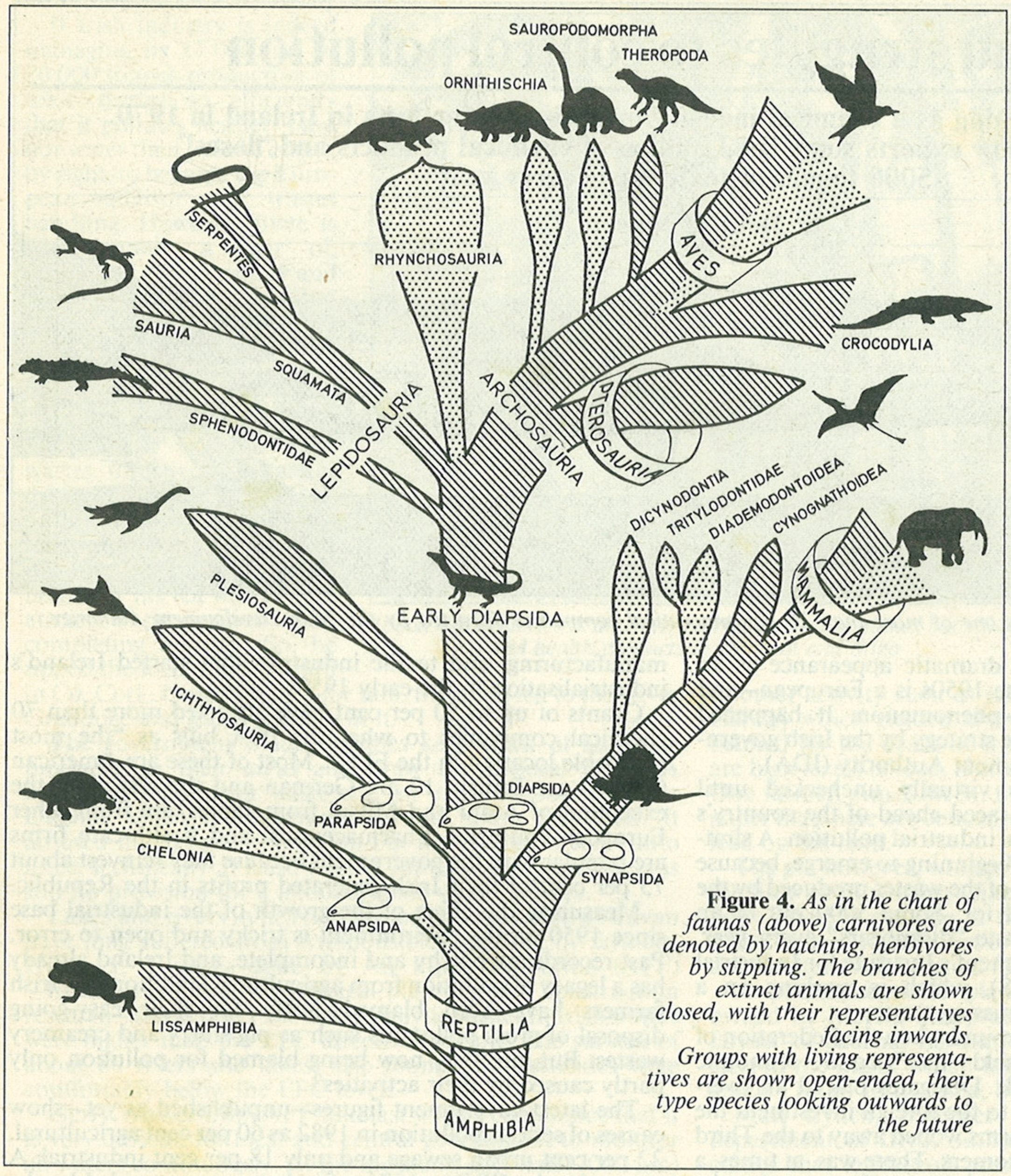


Figure 4. *As in the chart of faunas (above) carnivores are denoted by hatching, herbivores by stippling. The branches of extinct animals are shown closed, with their representatives facing inwards. Groups with living representatives are shown open-ended, their type species looking outwards to the future*

Are we talking here about direct competition, the old conception of nature red in tooth-and -claw, of the kind that was once thought to have taken place, at a much later date, between dinosaurs and mammals? Probably not. The disappearance of the rhynchosaurs, like the decline of the synapsid dicynodonts before them, seems to be associated with a decline of their food-plant; this time, of the seed fern *Dicroidium*, which was giving way to the worldwide spread of the conifers. Dinosaurs and thecodontians may never have had to "compete" directly with synapsids and rhynchosaurs, as envisaged by the authors of all technical and popular literature on this subject. They simply radiated into the adaptive zones left vacant by synapsid and rhynchosaur decline. The real competition, the old-style conception of the battle for survival, may have taken place, if it took place at all, between the plants that provided the reptiles with their food.

The idea that dinosaurs simply radiated into the ecological niches that had already been vacated, and that mammals 130 million or so years later did the same thing after the dinosaurs had departed, has profound philosophical implications. Palaeontologists have typically tried to find particular reasons for major changes in the history of life, and in particular to invoke the idea of evolution by natural selection; the idea, crudely stated, that "inferior" creatures are replaced by their superiors. Thus they have speculated that the thecodontians replaced the synapsids because they were anatomically superior, and that they were in turn replaced by the allegedly superior dinosaurs. But Darwin conceived that natural selection applied to individuals, or possibly to species, and that is how it is still understood. It is wrong to extend such concepts to explain the wholesale replacement of large groups of animals by others. It would be hard to imagine an accumulation of competitive encounters between individuals that led to the extinction of a whole group of animals distributed worldwide.

The modern evidence, of the kind I have presented here, suggests that such encounters need never have taken place. If the dinosaurs and thecodonians were superior to the types that went before them, they may never have had to demonstrate that fact. The role of natural selection in bringing about the gross changes in the evolution of animals is thus brought into question. Though competition between individuals or populations, leading to the selection of one and the demise of the other, may well fine-tune the course of evolution, the mass replacement of one dominant life-form by another may depend on environmental factors or chance events that lead to the disappearance of the first *before* the second can begin to radiate.

More particularly, reappraisal of the fossil evidence from the Triassic not only helps to undermine the old view that superior mammals ousted the cumbersome dinosaurs, but may completely reverse it. At the end of the Triassic, when the rhynchosaurs and synapsids finally disappeared, the first mammals were already in existence; they are an astonishingly ancient group. They could, theoretically, have radiated worldwide, just as they were to do 130 million years later, when the rhynchosaurs and synapsids disappeared.

But they did not. The dinosaurs took over instead; and it is tempting to suggest that the mammals failed to seize their chance precisely *because* the dinosaurs beat them to it: in the first encounter, if such it was, the dinosaurs won. If the mammals had prevailed when the opportunity first presented then the scope for speculation becomes mind-boggling. There would have been no great age of dinosaurs, but there would have been a flowering of mammals 130 million years earlier. The first men might then have walked the Earth 130 million years ago. □

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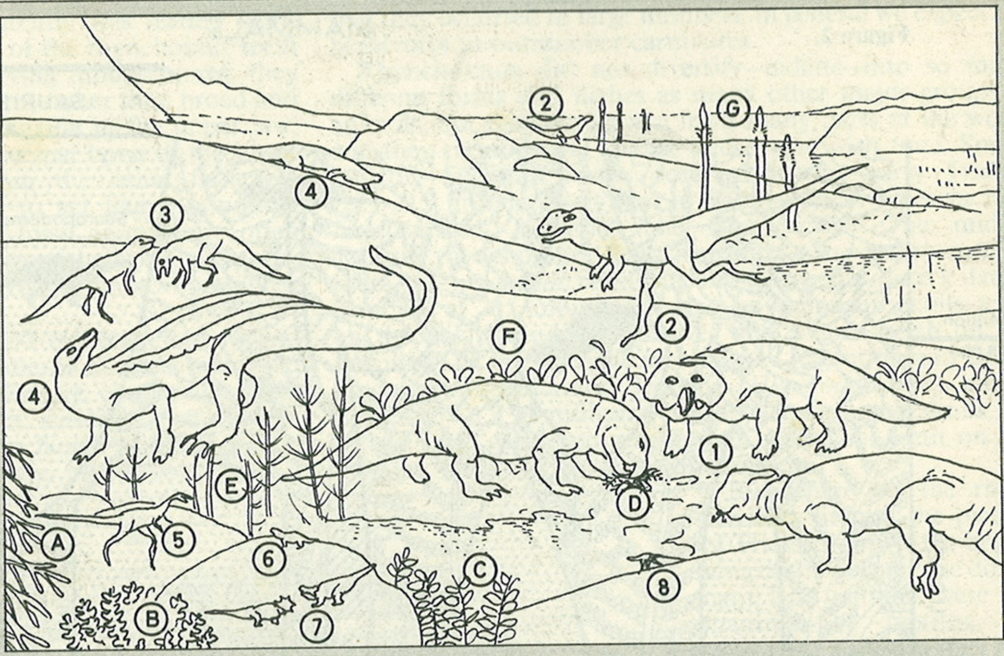
one time. I tabulated these faunas, estimated the numbers of each kind of animal in each fauna, and then calculated the percentage representation of each kind of animal. Then I plotted the changes in the percentage of each kind of animal against time. The results are shown in simplified form in figure 2.

Of course, this kind of technique can give only approximate results. First, for all the vast span of time of the Triassic, only a few faunas are known; there must be many others that we do not know about. Secondly, some of the faunas have not yet been dated accurately, and we must allow a tolerance of ±1–5 million years for each one that is known, although we can work on the assumption that two faunas that have several animals in common are of about the same antiquity. Thirdly, the fossils that are preserved in any particular geological formation reflect the fauna that gave rise to them, but they do not accurately represent them. Some animals are preserved better than others; groups of animals with long life spans leave fewer fossils than those with short lives; and seasonal migrations may upset the pattern.

Finally, the inevitable imbalance may become exacerbated by the bias of collectors. On sites rich in fossils, collectors often become bored with the commoner animals and pick up only the rarer ones. This is quite understandable, but it means that the collections of fossils in museums, which are the basis of my data, will differ in composition from the original assemblage of fossils—which in turn differs, as we have seen, from the composition of the living assemblage. In some cases, however, collector bias might offset the problems of selective preservation, as the animals that are over-represented because they are easily fossilised then become under-represented because they are less assiduously collected.



All pics, these pages Jenny Halstead

Figure 3. A scene from the early Triassic, 220 million years ago, in the Lossiemouth Sandstone Formation of the Elgin District of north-east Scotland. The animals are based on actual fossils, as studied since the early 1960s by Dr Alick Walker of the Geology Department, University of Newcastle. (Mike Benton concentrated on the rhynchosaurs). No plant fossils have been found in the formation; the flora shown here is based on contemporary fossils from other formations.

Of the animals,
1, *Hyperodapedon*, is a rhynchosaur. **2**, *Ornithosuchus*, and **3**, *Erpetosuchus*, are both thecodontians. **5**, *Brachyrhinodon*, is one of the Sphenodontidae. **7**, *Leptopleuron*, is small and specialist and loosely classed as a "stem-reptile", belonging to no closely defined major group, but similar to the most primitive early reptiles. **8**, *Scleromochlus*, is another thecodontian.

The herbivores include **1** and **4**. The carnivores are **2**, **3**, and **5**. The diet of **6** and **7** is unknown. The only animal shown with a living relative is **6**. *Brachyrhinodon*, which is related to the modern tuatara.

Of the plants,
A is *Sphenobaiera*, a gingko; **B** is *Rienitsia*, a Cycadophyte; **C** is *Kurtziana*, a fern; **D** is *Dicroidium*, a seed fern; **E** is *Equisetum* one of the Equisetales, or horsetails; **F**, *Xylopteris*, is another seed fern; and **G**, *Pleuromeia*, is a lycopod.

The plants have fared better than the animals. Only the seed-ferns, **D** and **F**, are unequivocally extinct.

Despite these problems, the study was worth making. It turned out that in each of the Triassic faunas, or at least in most of them, one particular taxonomic group (not always the same group in different faunas) was particular abundant; between 40 to 90 per cent of specimens found. This must represent, in a broad way, the relative abundance of the living animals. Secondly, the results were consistent, with no dramatic difference from place to place at any particular time. As a first attempt the results are no doubt crude, but they do provide a basis for further refinement.

At the beginning of the Triassic the dominant herbivores were synapsids, mammal-like reptiles of the group known as the Dicynodontia, but the dicynodonts declined rapidly as the Permian flora disappeared, a flora dominated by a seed fern (pteridosperm) of the genus *Glossopteris* (Figure 2).

The carnivores of the Lower Triassic were from two groups: some were synapsids of the group Cynodontia, and others were early thecodontians. As shown in Figure 4, the thecodontians were the first of the archosaurs, the group that also includes the pterosaurs, crocodiles and the dinosaurs. The thecodontians were nearly all carnivores. Some were only as big as a chicken, while others grew to a length of about 5 metres. Some had a heavy, lizard-like form, some were shaped like a crocodile, and many were small and bipedal.

In the Middle to Upper Triassic the role of small- to medium-sized herbivores was played by two groups of reptiles: another synapsid of the group known as the Diademodontoidea, and the rhynchosaurs. Cynodonts and thecodontians still prevailed as carnivores.

By the beginning of the Upper Triassic, rhynchosaurs were still the dominant herbivores. In the four major faunas known from that time, from Scotland, Brazil, Argentina and India, rhynchosaurs account for 30 to 70 per cent of specimens collected. Each of these Upper Triassic faunas contains a few dinosaurs, however; but only 0·5 to 3·0 per cent of the total specimens.

Yet by the end of the Triassic the dinosaurs (prosauropds) were the dominant herbivores worldwide. The rhynchosaurs had by that time become extinct.

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