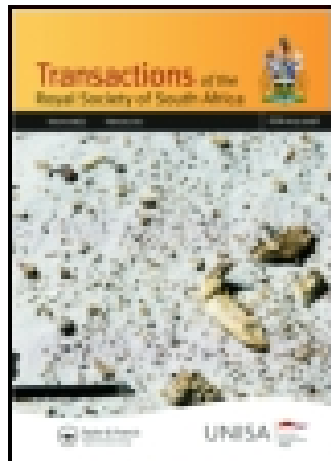


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ON THE RELATIONSHIPS OF THE SOUTH AFRICAN FOSSIL REPTILES TO THOSE OF OTHER PARTS OF THE WORLD.

By R. BROOM, M.D., D.Sc., C.M.Z.S.

When Cope first examined the American Permian reptiles he recognised many resemblances between them and the South African forms, and at different times between 1878 and his death he published a considerable number of tentative classifications of the Permian reptiles of America and Africa. In 1878 he proposed the order *Theromorpha* to include as sub-orders the *Pelycosauria* and the *Anomodontia*. Under the *Pelycosauria* he placed not only all the American Permian types but the South African Theriodonts and *Pareiasaurus*, and he believed the whole group to be allied to the *Rhynchocephalia*. As the result of fuller knowledge the types with the temporal region roofed were separated under the name *Cotylosauria*, and the older *Theromorpha*, with the name changed to *Theromora*, was held to include the South African Theriodonts and the American Pelycosaurs proper. Lydekker, Seeley, Zittel, and Gadow all published classifications on similar lines, and all agreed in placing the Pelycosaurs near the African Theriodonts.

In 1897 Baur and Case pointed out that *Dimetrodon* seemed to have a skull with two temporal arches, and that the *Pelycosauria* should for this and other reasons be separated from the Theriodonts and placed nearer to the *Rhynchocephalia*. In this most recent writers, including Smith-Woodward, Hay, Zittel, Osborn, McGregor, Boulenger, and Broom have followed the view of Baur and Case.

Notwithstanding the strong evidence that can be adduced for placing the Pelycosaurs near the *Rhynchocephalians*, there has always been a kind of lingering doubt in the minds of some of us as to whether after all the resemblances between the Pelycosaurs and the African mammal-like reptiles might not represent some genetic relationship rather than merely a parallel similarity.

During my recent visit to Europe I hoped among other things to be able to take a run over to New York to study the Pelycosaurs, but, owing to the press of other work, was on the point of giving up the American trip when I met Professor Osborn in London, and as the result of our

conversation I was persuaded rather to leave some things I was doing and to pay a flying visit to the American Museum. Through the kindness of Professor Osborn and Dr. Matthew I was enabled to examine everything I wished to see, and I had the further advantage of having Dr. Case as a fellow-worker at the Museum. Though Dr. Case was busy working at the Cotylosaurs, and had much new material on hand of both Cotylosaurs and Pelycosaurs, he most generously allowed me to study any of his specimens, and gave me every assistance in his power, including information about the specimens in Chicago. To him, to Professor Osborn, and to Dr. Matthew is largely due the fact that, though I had only a few days in New York, I was enabled to do practically all the work I had hoped to do.

Elsewhere I shall publish the detailed results of my examination of the Pelycosaur and Cotylosaur skulls, and in the present paper confine myself mainly to the conclusions and their bearing on South African problems.

As the result of the researches of Cope, Baur, and Case, and especially of Case, the anatomy of the Pelycosaurs is well known, with the exception of only a few points, and of these latter the most important is the structure of temporal region. By Baur and Case there are believed to be two fenestræ, the upper small and the lower large. According to Case's interpretation the large fenestra is bounded in front by the post-orbital and jugal, and behind by a large triangular bone which he calls the pro-squamosal. The small upper fenestra lies between bones which he believes to be post-orbital, the parietal, and the quadrato-jugal. The squamosal he believes to be a narrow bone lying behind the quadrato-jugal. In the skulls in the American Museum I cannot satisfy myself that an upper fenestra exists. The large triangular bone I believe to be the squamosal, and a small bone lying below the squamosal and on the quadrate I believe to be the quadrato-jugal. There is some evidence of a small fenestra between the squamosal and the quadrato-jugal, though in none of the specimens is this region perfectly preserved. There is not improbably a narrow distinct element behind the squamosal, and if it be really distinct it will correspond to the little bone found in the similar region in *Procolophon* and *Captorhinus* (*Pariotichus*), and which has been called epiotic or supra-temporal, but which perhaps might preferably be called post-temporal.

If my interpretation of the temporal region be correct, it follows that the structure in the Pelycosaurs is essentially similar to that in the Therocephalians, differing only in the fact that the latter have lost the quadrato-jugal and the post-temporal bones. Whether there are two fenestræ or only one, it is, I believe, pretty certain that the large opening is the homologue of the temporal fossa of the Therocephalians, and even

if a small opening exists between the parietal, the squamosal, and the post-temporal, the Pelycosaurs might nevertheless be pretty nearly related to the Therocephalians.

Taking into consideration the structure of the skull and other parts of the skeleton, the conclusion to which I come is that the Pelycosaurs and the Therocephalians are groups sprung from a common and not very remote ancestor. The Pelycosaurs retain a number of the more primitive characters, but are in many respects highly specialised. The Therocephalians are more generalised, but considerably more highly evolved. The Pelycosaurs were slow-moving crawlers with short, lizard-like limbs; the Therocephalians were active runners with mammal-like limbs. The difference in the structure of the limb girdles is in harmony with the differences in the limbs.

When we look at other American Permian types we again find curious resemblances to African forms. The order *Cotylosauria* includes a number of types which agree in having the temporal region roofed, but some of those placed in the order are manifestly not very nearly related to the others. *Diadectes*, which is the type of the order, is fortunately well known. It is a large, heavily built animal, with short, feeble limbs. The vertebræ are very like those of the South African *Pareiasaurus*, and though superficially there are striking differences in most other parts of the skeleton, fundamentally there is a surprising similarity. As the Therocephalians differ from the Pelycosaurs in having walking limbs, so *Pareiasaurus* differs from *Diadectes* in having large powerful limbs which could easily keep the body off the ground, and the girdles are modified to suit the new habit. Unfortunately the structure of the skull of *Pareiasaurus* is not well known, but the agreement is sufficient to justify us in concluding that *Pareiasaurus* is related to *Diadectes* in much the same way that the Therocephalians are to the Pelycosaurs.

Another small type that is at present placed in the *Cotylosauria* is called *Pariotichus*, or, as Dr. Case informs me, it ought to be called *Captorhinus*. This is a small lizard-like *Cotylosaur* which was of fairly active habit, and has evolved to a considerable degree along the line which gave rise to the Rhynchocephalians. It differs from *Diadectes* and *Pareiasaurus* in having a rounded instead of a flat occipital condyle, and with the exception that the temporal region is roofed and the precoracoid is still retained, there is little, if anything, to distinguish it from the primitive Rhynchocephalians. To us at present its chief interest lies in the fact that it is distinctly related to the South African forms *Saurosternon* and *Procolophon*. The African types are more specialised, but they are probably more nearly related to *Captorhinus* (*Pariotichus*) than are the Therocephalians to the Pelycosaurs.

In the American Permian beds are many Stegocephalians, of which

the best known are *Eryops*, *Trimerorachis*, and *Cricotus*; in South Africa Stegocephalians are rare in the Lower Karroo, but the only known form, *Rhinesuchus*, is probably allied to *Eryops*, and was originally referred to that genus by Lydekker.

While the Lower Karroo fauna cannot have directly sprung from the fauna of the American Permian nor the American forms from Karroo ancestors, it is manifest that the two faunas are related in such a way as to render it practically certain that they are two different modifications of the same earlier fauna. The American types are nearer the ancestral, though considerably specialised; the African, probably owing to their living in the swamps of the Karroo, have developed greater length of limb and tended to become more active. The home of the common ancestral forms was probably in a southern continent which joined Brazil and South Africa. As reptilian remains are extremely rare in beds older than those which contain *Pareiasaurus* and the Therocephalians, though the extensive Ecca beds are of exactly the same sort of shale as is found in the fossiliferous beds above, we are probably justified in concluding that in Lower Permian times reptiles for some reason were very rare in South Africa, and as the ancestral Permian fauna must have been flourishing elsewhere, we may conclude that it probably was mainly confined to the western part of the southern continent. Further, during the greater part of Dwyka times there could have been no land vertebrates in South Africa, as the land was covered with snow and ice, and similar conditions existed in Southern Brazil. Hence the probability seems to be that in Upper Carboniferous times the ancestors of the Permian reptiles flourished in the northern part of what is now South America, and that before the onset of the Permian age representatives of most of the types invaded North America, where they soon became isolated, and after undergoing considerable specialisation became extinct about the middle of the Permian period. The main body of reptiles probably passed south as the climate became more temperate. A few forms probably extended across the continent shortly after the glacial conditions disappeared, as, for example, *Mesosaurus*, and others of a more hardy sort gradually followed. But it was apparently not till near the middle of Permian times that the large body of the Permian types arrived in South Africa.

In South Africa the conditions must have been such as to promote rapid evolution, and many new types soon appeared. The most remarkable are the Anomodonts, which are evidently greatly specialised descendants of some Therocephalian-like type, but *Dicynodon* is not likely to have sprung from any known Therocephalian and may have evolved from a somewhat more primitive type more nearly allied to the Dinocephalians. From the great variety of Anomodonts found in South Africa and from

the great prevalence of certain genera, it seems probable that South Africa is the original home of the Anomodonts.

During the greater part of Permian times the Southern continent was divided from Europe by sea, but towards the end of the Permian a land connection, probably in Asia, allowed the Pareiasaurian fauna to pass into Europe, and with the fauna the advanced Southern types of vegetation. In Russia have been found Pareiasaurians scarcely distinguishable from those of South Africa, Therocephalians perhaps generically identical with African forms, Anomodonts closely allied to, if not identical with, *Dicynodon*, and Stegocephalians. Perhaps the last of the wave of South African emigration is to be seen in the lower Elgin fauna of Scotland with *Elginia*, *Geikia*, and *Gordonia*.

After Permian times there is no evidence of any European connection till we come to the Upper Triassic beds of Burghersdorp, and we find the remarkable state of affairs that while Africa received a large accession of European new types Europe apparently did not succeed in getting any of the African Cynodonts which form such a distinctive feature of the South African Upper Triassic beds. Probably the connection was an indirect one by means of a large island which became first separated off from the northern continent and later on became joined to the southern land. Whatever be the explanation, we know that in Upper Triassic times Labyrinthodonts closely allied to the European appeared in South Africa. The species of *Capitosaurus* and *Cyclotosaurus* are almost identical with those of Europe, and the species of *Trematosaurus*, though larger than the European, is closely allied.

In Lower Jurassic times the land connection with Europe must have been well established, as the Dinosaurs of the Stormberg beds are nearly identical in some instances with European forms. Further, the small mammal *Tritylodon* is very closely allied to *Triglyphus* of Europe.

There is little evidence to show how closely Africa was connected with Australia during Permian and Triassic times, but in Upper Triassic times at least there is some evidence of continuous land having been between the Cape and Australia, but whether it extended through India or the present Indian Ocean there is little evidence. The occurrence of small land reptiles in the Karroo beds of Madagascar seems to suggest that much of the Indian Ocean may in the Permian age have been land.

After Lower Jurassic times too little is known of the land faunas of South Africa to afford us evidence of the relations of Africa to the other continents. In fact, almost nothing is known of the land fauna till we arrive at Pleistocene times. A lower cretaceous Sauropodous Dinosaur is known and the frontal bone of a small cretaceous crocodile, probably a Teleosaur, has been discovered.