RELATIONSHIPS OF THE TRIASSIC MALERI FAUNA

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ABSTRACT—This embodies a critical review of the Upper Triassic Maleri fauna. The close resemblance with certain faunal assemblages found in Europe and North America is emphasised. It is also pointed out that affinities of the Maleri fauna with the Brazilian Upper Triassic fauna are less pronounced than with the European and North American, and resemble even less the South African faunas. In the light of this evidence, the author postulates land connection between peninsular India and the Northern land masses much as in present times.

INTRODUCTION

THE fossil remains of animals with backbones have long been known from the Triassic sediments of India and have been described in considerable detail by several authors. Moreover, the relationships of these fossils with comparable fossils from other parts of the world, and the significance of such relationships have been noted in various publications between 1885 and the present time. Consequently, it might seem as if there was nothing new of importance to say about Triassic vertebrates from India, considering the present state of our knowledge, and it might be argued that we should wait for additional discoveries before attempting any evaluation beyond those that already have been made. But it has been the experience of the present writer that no matter how thoroughly a subject has been covered it can always be examined anew with considerable profit to him who makes the examination, and frequently to others as well.

It is, therefore, proposed at this place to take a new look at one aspect of the Triassic life of India, namely, the Maleri fauna, and to see if new facts may be forthcoming from such a study. It is felt that even if no particularly novel ideas are derived from this review, the study may be useful in calling attention to a faunal assemblage about which information is now scattered in several sources. Perhaps this review will help to emphasise the importance of the Maleri fossils—and that may be all to the good. It does seem to this writer that the Maleri fauna has not received the attention from many paleontologists that it justly deserves.

The Maleri fauna has been collected from Triassic outcrops at two localities in the peninsular portion of India, one being in the vicinity of the village of Maleri, to the north of the Godaveri River and the other much farther north, near the village of Tihki which is south of the city of Rewah. The fossils have been described in detail by Miall, who in 1878 gave an account of some teeth of the lung fish *Ceratodus*, by Lydekker, who in 1885 described amphibians and reptiles, and by von Huene, who in 1940 presented a second study of the land-living vertebrates. The fossils described and figured by these authors are for the most part rather fragmentary, yet they are nevertheless sufficiently diagnostic so as to give us reasonably accurate knowledge concerning the known elements that constitute the Maleri fauna. They show that the fauna is composed in general terms of a typical Triassic lung fish, a large metoposaurid amphibian, a rhynchosaurian reptile, probably two pseudosuchian reptiles, a phytosaur, a small coelurosaurian dinosaur and a fairly large prosauropod dinosaur. This is without doubt a fauna of upper Triassic relationships.

THE MALERI FAUNA AND TRIASSIC CONTINENTS

Since the Maleri fauna consists for the most part of fragmentary remains, and since it is a characteristic late Triassic fauna, the components of which may be matched quite readily within Triassic faunas from other parts of the world, the question arises as to why this fauna should be particularly important. The question is especially apropos in view of the limited number of genera and species known to compose the Maleri fauna. In answering this question, it can be said that the Maleri fauna is important because of its strategic position, geologically and geographically. Maleri fossils are found in the portion of India that often is assumed to have been at one time an integral section of the ancient continent of Gondwanaland, and these fossils date from a geologic age that is supposed by many authors to have preceded the time when the present geographic relationships of peninsular India were established.

The position of peninsular India with relation to other land masses during late Triassic times has been indicated by various authors, some of whom are proponents of the theory of continental drift, others who believe in a great Gondwana land mass with extensive former land connections between the present southern continents. Among those who hold this latter view Arldt (1919, p. 367) shows a late Triassic world in which South America, most of Africa, Arabia, peninsular India and Australia are bound together as a great east to west southern continent, separated from the northern land masses by a narrow mediterranean sea. A very similar map of the Triassic world is depicted by Swinton (1934, p. 12), and generally similar concepts of Triassic continental relationships may be found in the works of other authors.

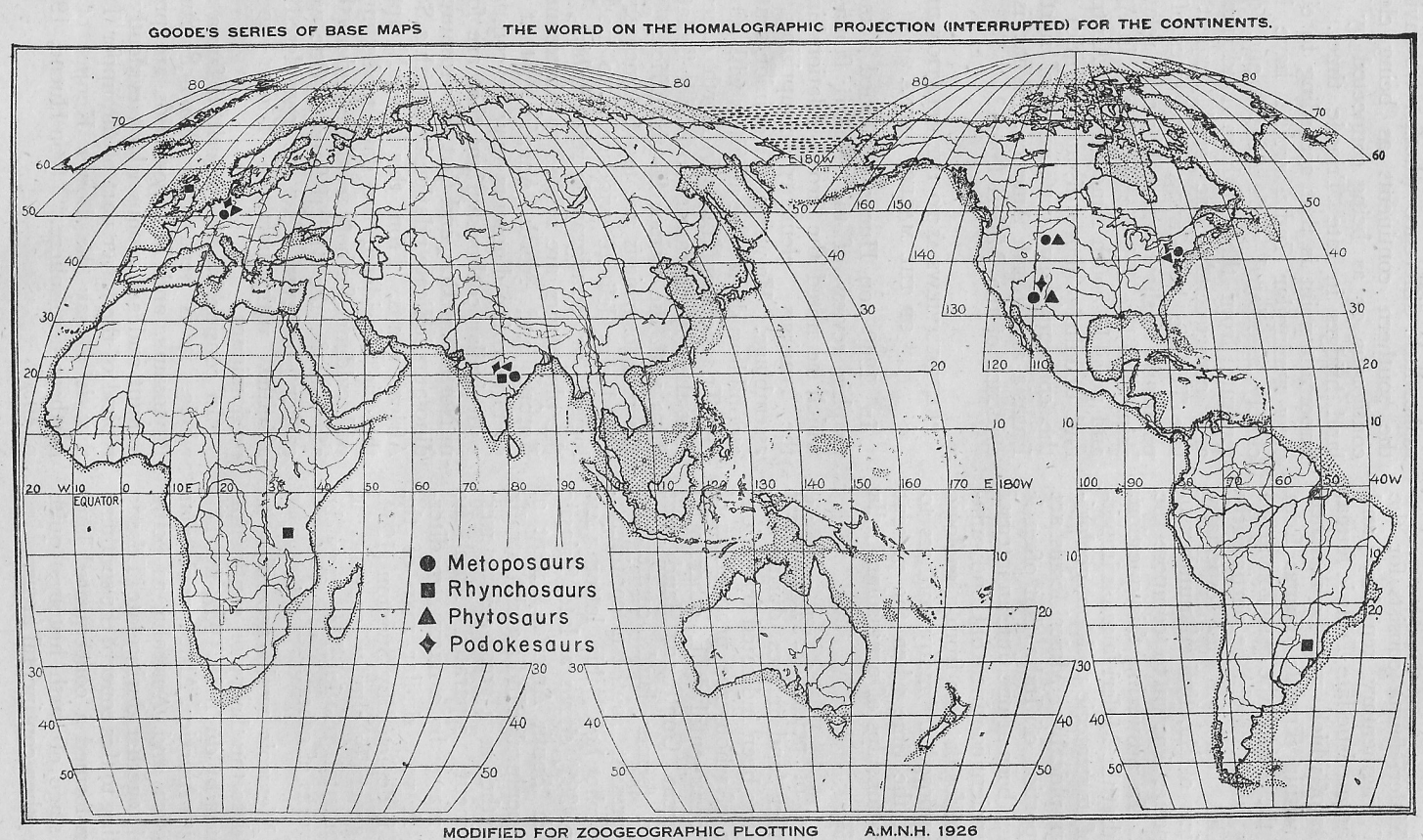
The early Mesozoic world according to those who hold to the theory of continental drift is illustrated by du Toit (1937, fig. 11), who shows South America, Africa, peninsular India, Antarctica and Australia as being closely wedged together during late Triassic times. According to this concept the southern continents thus formed a concentrated land mass at that stage of earth history, quite separate from other continental areas.

For the purposes of the present study it makes little difference whether we envisage the southern continents as being closely contiguous or as being connected by long land bridges in late Triassic times. The important point is that according to either view peninsular India would have been closely associated with Africa, and quite separate from the northern land masses, and consequently one would expect the late Triassic land-living vertebrates of the peninsula to show reasonably close relationships with late Triassic vertebrates in Africa and possibly South America and Australia, and definitely more distant affinities with the contemporary vertebrates of northern Eurasia and North America. What is the evidence of the Maleri fauna?

PREVIOUS VIEWS AS TO THE RELATIONSHIPS OF THE MALERI FAUNA

In 1940 von Huene published a monographic review of the Maleri fauna, in which he noted the broad relationships of the various elements comprising the assemblage. He was of the opinion that the amphibians show close affinities with similar late Triassic amphibians in North America, that the rhynchosaurids establish "relationships with the former South Africa," that the pseudosuchians are too fragmentary to afford any definite evidence as to morphological or stratigraphic relationships, that the phytosaurs are related to phytosaurs in Europe and North America, that the coelurosaurian dinosaurs may be compared with similar coelurosaurians that are found in North America, and that the prosauropod dinosaurs indicate relationships with a South African genus. From this it would appear that he considered the data to be mixed, with evidence for both southern and northern affinities for the Maleri fauna. One would gather, however, that he considered the affinities with northern faunas to be predominant.

"In considering the described fauna as a whole, it is seen that Rhynchosaurids, Phytosaurs, and Metoposaurids are predominant and are groups which evidently are typical of the lower part of the upper Trias, that is to say the Lower Keuper of the northern hemisphere." (von Huene, 1940a, p. 40.)



Text-Fig. 1—The distribution of certain Middle and Upper Triassic reptiles. Note that the four groups of tetrapods particularly characteristic of the Maleri fauna of India are found in other parts of the northern hemisphere. Only the rhynchosaurs occur in the southern hemisphere.

In another paper, published during the same year, in which he discussed the Karroo and Gondwana reptiles, von Huene was perhaps somewhat more definite concerning the relationships of the Maleri fauna. "Diese Fauna kann in ihrem zeitwert weniger nach Südafrika als nach Nordamerika und Europe orientiert werden." (von Huene, 1940b, p. 272.)

Finally, in 1942, von Huene published a brief paper on the upper Triassic fauna of central India in which he set forth what are apparently his most carefully considered conclusions regarding the relationships of the Maleri fauna. (von Huene, 1942, pp. 249-255.) A translation of his summation (p. 255) is attempted below.

The character of the [Maleri] fauna is indicated by the metoposaurs, the rhynchosaurs, the phytosaurs and the saurischians. The first two of the above-mentioned groups are found exclusively in the upper Triassic. Phytosaurs are mostly in the upper Triassic of the Northern Hemisphere. Saurischians appear first at the beginning of the upper Triassic. Rhynchosaurians are not known in the younger upper Triassic. Consequently, the age of the Maleri beds is determined as lowermost upper Triassic. The strong relationships of the [Maleri] labyrinthodonts and phytosaurs to [those of] North America are striking. The rhynchosaurs show connections through their ancestry to Africa, but greater similarities are with Europe (*Hyperodapedon*) and with South America. Because of numerous invasions of phytosaurs the relationships to the [faunas of] the Northern Hemisphere are accentuated, since in East—and South Africa as well as in South America phytosaurs are entirely absent, whereas in Europe and North America they are abundant. In the composition of the fauna, especially in the development of the labyrinthodonts, the rhynchosaurs and the phytosaurs, the upper Triassic assemblage of India shows unique and characteristic features. The nature of the fauna is not purely local, for it extends over a great region, since Maleri in the Godaveri Valley and Tihki in South Rewa are 600 kilometers apart in a north to south direction. The faunas in both localities are completely similar.

Haughton in 1953 accepted von Huene's conclusions with the following statement.

"The reptiles [of the Maleri fauna] present belong to the rhynchosaurs, the pseudosuchians, the phytosaurs, and the saurischians. The material known is somewhat fragmentary, but von Huene considered that the fauna was typical of the lower Keuper of the Northern Hemisphere. He pointed out that it contained no anomodonts or cynodonts and that the phytosaurs do not appear in the Triassic faunas of either South America or South Africa, although they occur in both Europe and North America." (Haughton, 1953, p. 15.)

These remarks present in general terms von Huene's conclusions as to the relationships of the Maleri fauna. It is now proposed to discuss the various elements of the fauna to see how far a close examination will support von Huene's conclusions.

A CRITICAL EVALUATION OF THE MALERI FAUNA

FISHES :

DIPNOANS

Ceratodus : The first fossil vertebrate to be described from the Maleri sediments was the lungfish *Ceratodus*. The characteristic tooth plates of this fish were the subject of a paper by Oldham, published in 1859, and they were redescribed in detail by Miall in 1878. They are the typical *Ceratodus* tooth plates so widely distributed over the world in continental sediments of late Triassic age, specifically, in addition to the Indian occurrence, at various localities in Europe, in Spitzbergen, in Arizona, Texas and New Mexico and in South Africa. Consequently, the presence of *Ceratodus* in the Maleri fauna does not give us definitive evidence as to the close affinities of the fauna either in one direction or the other. This ubiquitous fresh-water fish is a good horizon marker for Triassic continental sediments, and it can be expected to occur within almost any continental deposits of Triassic age.

AMPHIBIANS :

LABYRINTHODONTS

Metoposaurus sp. *:* Various fragmentary skull bones, portions of interclavicles and clavicles, and pieces of vertebrae of stereospondyl labyrinthodont amphibians have been collected from the Maleri sediments over the years. Some of these fossils were first described by Lydekker in 1885, in his monographic study of the Maleri tetrapods, and were designated by him as belonging to the genus *Mastodonsaurus*. There is no doubting the fact that the fossils from India represent a stereospondyl, and it is equally certain that they are not properly to be included within the genus *Mastodonsaurus*. Fragmentary as the remains may be, they show by the pattern of their sculptured surfaces that they are not of this genus.

In 1940 von Huene correctly recognized the fact that the stereospondyl remains from the Maleri beds are not referable to *Mastodonsaurus*, and he assigned them to the family Metoposauridae. He did not, however, attempt to place these fossils within any particular metoposaurid genus. Because of differences in the surface sculpturing, von Huene thought that there might be three different species or "types" of these amphibians, which he designated as "sculpture no. 1," "no. 2," and "no. 3," respectively.

An examination of Lydekker's and von Huene's figures shows quite clearly that the fragments from the Maleri sediments may be entirely assigned to the genus *Metoposaurus*. This is particularly evident from a partial interclavicle, figured by von Huene in Plate 1, figure 1 of his paper. This interclavicle shows the shape that is so characteristic of the bone in *Metoposaurus;* it is rather short in comparison with its width and the posterior border forms a rounded arc. Moreover, there is a restricted area of rounded pits in the center of the bone, from which the elongated sculpture radiates in all directions. These characters may be contrasted with the diagnostic features of the interclavicle in the North American genus, *Eupelor*, in which the bone is rather long, particularly by virtue of the forward extension of its anterior blade. Furthermore, in *Eupelor* there is generally a rather extensive area of rounded pits in the center of the bone.

Since the amphibian from the Maleri sediments, *Metoposaurus*, is generically identical with the metoposaurs of central Europe, it seems evident that there must have been a close connection between peninsular India and Europe during late Triassic times. Presumably, these areas were part of a single land mass, as they are today. Furthermore, the Eurasiatic land mass must have been connected with the North American land mass as indicated by the close similarities between *Metoposaurus* and *Eupelor*, so that generally speaking there was a reasonably easy route for the expansion of metoposaurs throughout these continental areas, whether that expansion was from east to west or in the opposite direction. There is no evidence among the amphibians to indicate a close physical relationship between peninsular India and Africa, for metoposaurs are unknown from the Triassic faunas of Africa.

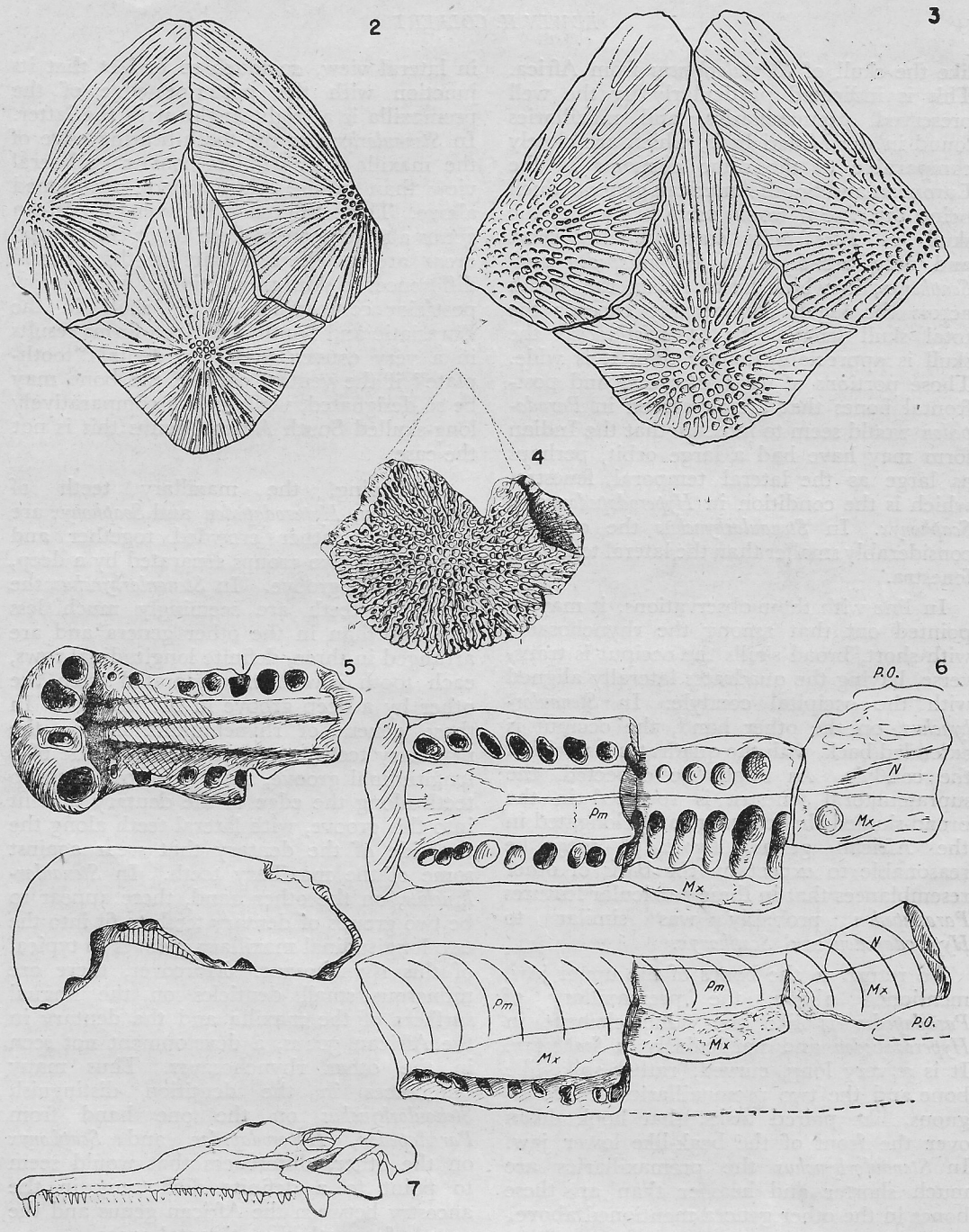
REPTILES :

RHYNCHOSAURS

Paradapedon huxleyi Lydekker : Perhaps the most abundantly represented tetrapod in the rather scanty Maleri fauna is the rhynchocephalian, *Paradapedon*. This is a rhynchosaur, known from portions of skulls and jaws, including a considerable array of tooth-bearing elements, and from certain bones of the post-cranial skeleton. It may be compared with three other rhynchosaurian genera, namely, *Hyperodapedon* from northern Europe, *Stenaulorhynchus* from East Africa and *Scaphonyx* (a name used here to include not only the original genus as defined by Woodward, but also the genus *Cephalonia*, as described by von Huene) from South America, specifically from southern Brazil.

Von Huene has made the point that *Paradapedon* is more closely comparable to the rhynchosaurs from Europe and from South America than it is to the form from Africa, a conclusion the validity of which is borne out by any critical examination of the materials.

For example, the skull of *Paradapedon* as reconstructed by von Huene from various skull bones would appear to have been much more like the skulls in *Hyperodapedon* from Scotland and *Scaphonyx* from Brazil than



Text-Fig. 2—*Metoposaurus diagnosticus*, Keuper of Germany. Interclavicle and clavicles, ventral view, $\frac{1}{6}$ natural size. From Colbert and Imbrie.

3—*Eupelor fraasi*, Dockum of Texas. Interclavicle and clavicles, ventral view, $\frac{1}{6}$ natural size. From Colbert and Imbrie.

4—*Metoposaurus* sp., Maleri of India. Interclavicle, ventral view, $\frac{1}{6}$ natural size. From von Huene.

5—*Phytosaurus maleriensis*, Maleri of India. Anterior portion of rostrum, with the palatal view above and the left lateral view below, $\frac{1}{4}$ natural size. From von Huene.

6—*Phytosaurus maleriensis*, Maleri of India. Medial portion of rostrum, with the palatal view above and the left lateral view below, $\frac{1}{4}$ natural size. From von Huene.

7—*Phytosaurus adamanensis*, Chinle of Arizona. Skull, lateral view of left side, $\frac{1}{15}$ natural size. From Camp. The bones shown in figure 5 correspond to the anterior portion of the long rostrum in this skull; those shown in figure 6 correspond to a more posterior portion of the rostrum, extending back to a position beneath the nasal opening (this latter forming the high eminence on the top of the skull, in front of the eyes.)

like the skull of *Stenaulorhyncus* from Africa. This is indicated particularly by the well preserved premaxillaries, and maxillaries found in the Maleri beds, which are closely comparable to the same elements in the European and South American genera. Such being the case it would seem likely that the skull of *Paradapedon* was probably short and very broad as in *Hyperodapedon* and *Scaphonyx*, in which latter genus the width across the jugals considerably exceeds the total skull length. In *Stenaulorhynchus* the skull is appreciably longer than it is wide. Those portions of the postorbital and postfrontal bones that are preserved in *Paradapedon* would seem to indicate that the Indian form may have had a large orbit, perhaps as large as the lateral temporal fenestra, which is the condition in *Hyperodapedon* and *Scaphonyx*. In *Stenaulorhynchus* the orbit is considerably smaller than the lateral temporal fenestra.

In line with these observations, it may be pointed out that among the rhynchosaurs with short, broad skulls the occiput is transverse, having the quadrates laterally aligned with the occipital condyle. In *Stenaulorhynchus*, on the other hand, the occiput is extended back, with the quadrates far behind the condyle. As might be expected, the supratemporal fenestra is rounded in the broad-skulled rhynchosaurs and elongated in the African genus. Again it may be reasonable to expect on the basis of other resemblances that in these particular features *Paradapedon* probably was similar to *Hyperodapedon* and *Scaphonyx*.

To return to the bones of the upper jaw, mentioned above, the premaxillary of *Paradapedon* is like the same element in *Hyperodapedon* and particularly in *Scaphonyx*. It is a very long, curved, rather spike-like bone and the two premaxillaries are contiguous, like paired tusks, that hook down over the front of the beak-like lower jaw. In *Stenaulorhynchus* the premaxillaries are much shorter and heavier than are these bones in the other genera mentioned above.

The resemblances and differences noted above are strengthened when the maxillary bones of the several genera are compared with each other. In *Paradapedon*, *Hyperodapedon* and *Scaphonyx* the tooth-bearing surface of the maxilla is strongly convex when seen in lateral view, so much so in fact that its junction with the posterior edge of the premaxilla is at right angles with the latter. In *Stenaulorhynchus* the tooth-bearing edge of the maxilla is much less convex in lateral view than in the other genera, mentioned above. These differences between the African genus and the genera from other continental areas are in effect a part of the general differences in skull proportions; the anterior-posterior compression of the skull in the Eurasiatic and South American forms results in a very convex maxillary dental "tooth-plate" if the ventral edge of the bone may be so designated, while in the comparatively long-skulled South African genus this is not the case.

Continuing, the maxillary teeth of *Paradapedon*, *Hyperodapedon* and *Scaphonyx* are numerous, rather crowded together and arranged in two groups separated by a deep, longitudinal groove. In *Stenaulorhynchus* the maxillary teeth are seemingly much less crowded than in the other genera and are arranged in three, definite longitudinal rows, each tooth row being separated from the other by a deep groove in the maxilla. In those genera of rhynchosaurs having the maxillary teeth arranged on either side of a longitudinal groove, there is a row of sharp teeth along the edge of the dentary that fit into this groove, with lateral teeth along the the side of the dentary that wear against some of the maxillary teeth. In *Stenaulorhynchus*, on the other hand, there appear to be two groups of dentary teeth to fit into the two longitudinal maxillary grooves so typical of this rhynchosaur. Moreover, there are numerous small denticles on the lingual surfaces of the maxilla and the dentary in the African genus, a development not seen in the other rhynchosaurs. Thus many differences in the dentition distinguish *Stenaulorhynchus* on the one hand from *Paradapedon*, *Hyperodapedon* and *Scaphonyx* on the other, differences that would seem to point to a definite dichotomy in the ancestry between the African genus and the genera from other continental areas.

As a final point, a comparison of the limb bones, especially of the tibiae, shows these elements in *Paradapedon* to be rather heavy, as they are in *Scaphonyx*, and in distinct contrast to the comparatively slender limb

bones in *Stenaulorhynchus* from Africa. Thus the evidence of the postcranial skeleton, in so far as it can be applied, corroborates the evidence of the skull, jaw and dentition in showing that the relationships of the rhynchosaur from India are closer to similar reptiles in South America, and presumably in Europe as well, than they are to the Triassic rhynchosaur of Africa.

From the comparisons that have been outlined above, it seems clear that the closest relationships to *Paradapedon* among the rhynchosaurs are to be found in the genera *Hyperodapedon* of Europe and *Scaphonyx* of South America. The presence of rhynchosaurs in India, South Africa and South America constitutes the type of evidence that upon superficial examination seems to give credence to the close geographical relationships of these continental areas during late Triassic times. Yet when the fossils are closely analysed, the evidence that emerges from the study of the bones is in quite another direction. From this it would seem that peninsular India was closely contiguous to the Eurasiatic land mass, and that although connections with Africa may have existed they were not intimate enough to allow for the free interchange between India and Africa of closely related rhynchosaurian genera.

THECODONTS : PSEUDOSUCHIANS AND PHYTOSAURS

Von Huene has described and figured at least two types of pseudosuchians from the Maleri sediments, quite rightly not attempting to give these fossils any formal designations. The evidence is fragmentary, and no definitive conclusions are to be drawn from it.

There is a skull fragment representing a reptile of some size—perhaps comparable in this particular to *Sphenosuchus*, a pseudosuchian from the Stormberg beds of South Africa. There are some vertebrae of about the right size for the skull fragment. Perhaps these fossils taken together indicate a *Sphenosuchus*-like pseudosuchian.

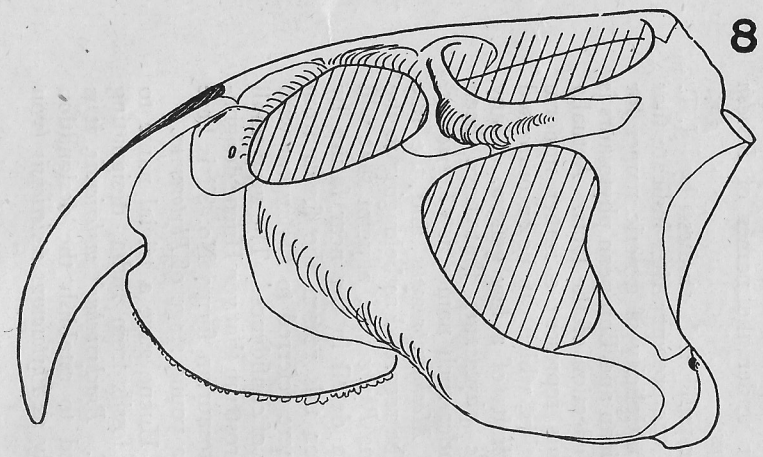
Then there are fragments of two femora that are very probably of ornithosuchid relationships. The fossils available are not unlike similar comparable portions of *Hesperosuchus*, a small, lightly built, bipedal pseudosuchian from North America. Likewise, a valid comparison may be made with *Ornithosuchus* of northern Europe, a genus closely related to *Hesperosuchus*.

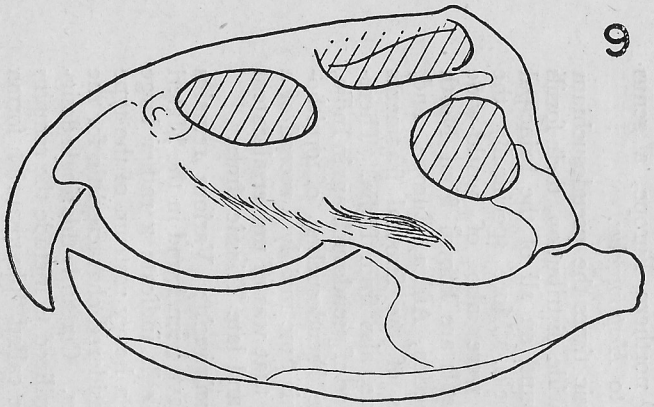
During Triassic times the pseudosuchians were of world-wide distribution, their fossils having been found on all of the principal continental blocks. More specifically the ornithosuchids were also of world-wide distribution; fossils are known from North and South America, Africa, Europe, and, upon the basis of the femoral fragments mentioned above, also from India. Therefore, the presence of pseudosuchians in India, and within the Pseudosuchia, of ornithosuchids, is at this time mainly a record of a reptilian group that was of universal extent during middle and late Triassic times.

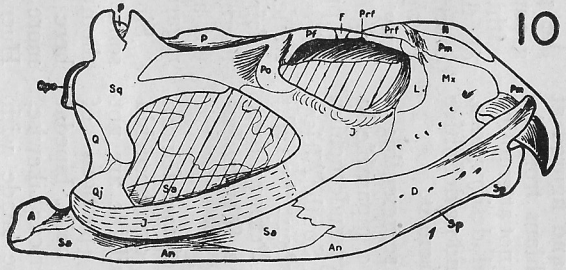
Phytosaurus maleriensis : Various remains of phytosaurs have been found in the Maleri beds. These fossils indicate a rather large phytosaur with a heavy rostrum of the type that can be considered characteristic for the genus *Phytosaurus*. Certainly this single designation can be utilized to include the remains that von Huene called "phytosaurian forma No. 1 and phytosaurian forma No. 2," as well as the fossils described many years ago by Lydekker under the names of *Belodon* and *Parasuchus*.

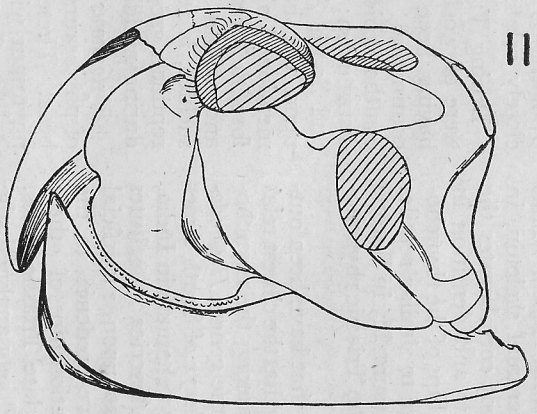
Recent unpublished studies by J. T. Gregory and the present writer indicate that the great multiplicity of generic names for North American and European phytosaurs is not a true reflection of the facts. Actually the phytosaurs represent a rather uniform group of reptiles, which can be encompassed within the limits of a few genera. Many of the large phytosaurs that have been described under such names as *Clepsysaurus*, *Brachysuchus*, *Machaeroprosopus* and the like may rightly be regarded as belonging to the original genus *Phytosaurus*, a point that will be proved in detail in the near future by Gregory. For this reason the fossils from Maleri are here referred to *Phytosaurus* with a fair degree of confidence. The very small fragmentary rostrum that von Huene designated as "phytosaurian forma No. 3" is here regarded as a young stage of *Phytosaurus*.

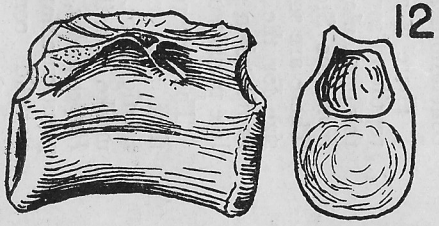
Since von Huene gave a trivial name to some of the fossils from India, designating them as "aff. *Brachysuchus*" *maleriensis*, it is here proposed to establish the designation more formally as *Phytosaurus maleriensis* (von Huene).

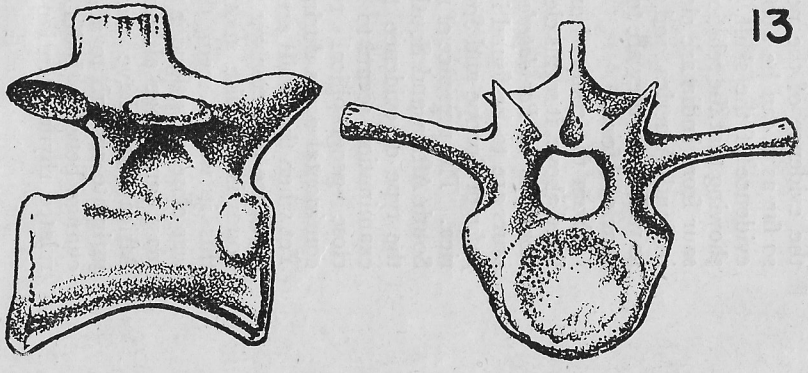












Text-Figs. 8—13

Elsewhere, except for *Mesorhinus* of Bunter age, phytosaurs are limited to the upper Triassic sediments of Europe and North America. *Phytosaurus* as represented by Maleri fossils is definitely a late Triassic form. Certainly the evidence of these fossils shows most definitely that there must have been a close connection between India, Europe and North America during late Triassic times. The absolute lack of any indications of phytosaurs in the late Triassic sediments of Africa must be significant.

SAURISCHIAN DINOSAURS

von Huene has described and figured a dorsal vertebra, the distal end of a femur and the proximal end of a tibia that indicate the presence of small coelurosaurian dinosaurs in the Maleri beds. As he rightly points out, these bones show very close resemblances to similar bones of *Coelophysis*, a lightly built, late Triassic theropod from North America. He also suggests a comparison with the Triassic genus *Thecodontosaurus*, a small prosauropod, a comparison which is much less valid than the one with *Coelophysis*.

It seems obvious that the small dinosaurian remains from the Maleri beds represent a late Triassic theropod of the family Podokesauridae. No attempt at a generic designation can be made upon the basis of the fragmentary fossils available at the present time, but the resemblances of these fragments to comparable parts of *Coelophysis* are very striking, indeed.

The vertebra figured by von Huene is in size and form much like a vertebra from about the middle portion of the presacral series in *Coelophysis*. The centrum is rather elongated and lightly built, with deepened, platycoelous articular surfaces, and the neural canal is large. These are all characters that can be closely matched in one of the mid-presacral vertebrae of *Coelophysis*. Moreover, the vertebra from the Maleri deposits shows on either side two diagonally directed buttresses beneath the parapophysis, these buttresses at angles of about 30 degrees with the horizontal line, again show a close resemblance to a mid-presacral vertebra of *Coelophysis*.

The distal end of the femur described and figured by von Huene is remarkably similar to the lower end of the femur in a small *Coelophysis*. von Huene mentions the fact that the walls of the bone are thin, and this accords with the condition in *Coelophysis* which is characterized by very pneumatic bones, the limb bones of which are essentially hollow tubes with extremely thin walls. Moreover, the femur from the Maleri beds is somewhat convex along its front border and has two prominent distal condyles, as is true for the American genus.

The proximal end of the tibia from Maleri is regarded by von Huene as representing a different type of coelurosaur from that indicated by the vertebra and the femur, by reason of its large size. It is more likely that we see here an indication of variability in size within a single species. Among the extensive materials of *Coelophysis* in the collections of the American Museum of Natural History are femora as small or smaller than the specimen from the Maleri beds, and

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Text-Figs. 8—*Paradapedon huxleyi*, Maleri of India. Skull, left lateral view, as restored by von Huene, ¼ natural size. From von Huene.

9—*Hyperodapedon gordoni*, Triassic (Elgin) of Scotland. Skull, left lateral view, ½ natural size. From von Huene.

10—*Stenaulorhynchus stockleyi*, Manda beds of east Africa. Skull, right lateral view, ¼ natural size. From von Huene.

11—*Scaphonyx fischeri*, Triassic of Rio Grande do Sul, Brazil. Skull, left lateral view, ¼ natural size. From von Huene.

12—Coelurosaurian dinosaur, Maleri of India. Dorsal vertebra, left lateral and posterior views, natural size. From von Huene.

13—*Coelophysis bauri*, Chinle of New Mexico. Twelfth presacral vertebra, right lateral and anterior views, natural size. Colbert, original figure.

tibiae as large or larger than the Maleri fragment. The American materials came from a single quarry and quite obviously represent growth stages within a single species. Therefore, it is logical to think of the known Indian fossils as representing a single species.

The presence of a member of the Podokesauridae in the Maleri sediments, as seems to be indicated by the fossils discussed above, indicates in this particular instance a close faunal affinity with Europe and North America. The striking resemblances of the scanty Indian fossils to *Coelophysis* show that closely related coelurosaurs extended across the northern portion of the earth. Of course the absence of podokesaurs from the upper Triassic beds of Africa may or may not be significant ; it may indicate negative evidence as the result of the accidents of preservation and collecting. This particular absence cannot be given the positive value that attaches to the marked absence of phytosaurs from the African region. Nevertheless, the fact at the present time is that podokesaurs seem to be present in the Maleri beds as they are in Europe and North America and as they are not in Africa.

Massospondylus ? : A complete dorsal centrum and two halves of centra were described and figured by von Huene as belonging to the prosauropod dinosaur, *Massospondylus*. He considered the specimens as having "a striking similarity in shape and size with Massospondylus of the Red Beds in South Africa." (von Huene, 1940, p. 38.) It is not quite clear to the present writer why von Huene should have stressed the resemblances of these vertebrae with comparable bones in *Massospondylus*, without making any mention of possible phytosaurian relationships. It seems to me that the possibility of these being phytosaur vertebrae is a point that should be given close consideration. It may be a bit risky to come to definite conclusions without having the original specimens for examination, but it does seem significant that the specimens figured by von Huene in Plate 10, figures 8 and 9 of his monograph, can be matched almost exactly in size, shape and general morphology by comparable elements from American phytosaurs. The size, the length of the centrum, the constriction of the centrum in its mid-portion, the shape and the concavity of the articular faces of the centrum and the symphysis on the dorsal face for articulation with the neural arch are all characters in the Maleri fossils that can be duplicated very closely in phytosaurian dorsal vertebrae.

If the vertebrae from India are those of phytosaurs, they constitute one more bit of evidence indicating a close relationship of the Maleri beds with upper Triassic sediments in Europe and North America. If they are truly the vertebrae of *Massospondylus*, as maintained by von Huene, they give evidence of a close relationship with the African region. Because of the doubt concerning the exact relationships of these fossils, their value as evidence for determining the affinities of the Maleri fauna is at the present time limited. More fossils are needed.

AN ANALYSIS OF THE MALERI FAUNA

From the foregoing critical evaluation of the Maleri fauna we see that the assemblage consists of a limited number of genera, determined by von Huene and by the present author in the manner indicated below, and that the relationships of these few genera to animals in other parts of the world are generally determinable, also as indicated below.

It is evident from the list below, which is essentially a summary of the discussions presented in the "Critical Evaluation of the Maleri Fauna," that the faunal relationships of this late Triassic assemblage of fishes, amphibians and reptiles are overwhelmingly with similar associations of late Triassic vertebrates in Europe and North America. In addition, there are some resemblances to certain elements in the known Triassic fauna of Brazil. Resemblances with Africa, such as they are, prove to be much less intimate than those that link the Maleri fauna with the faunas of the northern regions. The entire complexion of the Maleri fauna is that of a characteristic upper Triassic tetrapod fauna of the type commonly found in central Europe and in North America. In the light of this evidence there can be little doubt that during late Triassic times there must have been a land connection between peninsular India and the northern land masses.

von Huene	This paper	Relationships closest to :
FISHES		
	Ceratodus	Widely distributed in Triassic.
AMPHIBIANS		
Metoposaur, forms nos. 1, 2, 3.	*Metoposaurus*	*Metoposaurus* in Europe; *Eupelor*, a closely related genus in North America.
REPTILES		
Paradapedon huxleyi and *P.* (?) *maleriensis*	*Paradapedon huxleyi*	*Hyperodapedon* of Europe and *Scaphonyx of* S. America. Less closely related to *Stenaulorhynchus* of Africa.
Pseudosuchian form No.1	*Sphenosuchus*-like?	Too fragmentary for any definite conclusions to be made.
Pseudosuchian form No.2	Ornithosuchid	*Ornithosuchus* of Europe or *Hesperosuchus* of N. America.
Brachysuchus (?) *maleriensis*	*Phytosaurus maleriensis*	*Phytosaurus* of Europe and North America.
Coelurosaur form No. 1 and No. 2.	*Podokesaurid*	*Coelophysis* of North America
Massospondylus (?) sp.	*Massospondylus?* or phytosaur?	Material too limited for definite conclusions to be made.

Let us look at the Maleri fauna briefly in terms of ecological relationships. The fauna as it is known would appear to have been composed of riparian and lacustrine forms, of small terrestrial animals living perhaps under the protection of low vegetation, and of large terrestrial types that may have wandered freely across the land.

The riparian and lacustrine animals included within the Maleri fauna are the lungfish, *Ceratodus*, the large labyrinthodont amphibians, *Metoposaurus* and the large crocodile-like thecodont reptile, *Phytosaurus*. It might be imagined that these water-loving types could have negotiated a seaway between peninsular India and the lands to the north, where congeneric forms were living at the same time, but this postulate has no weight whatsoever. The lungfishes have been, and still are freshwater vertebrates, and their dispersal has taken place by means of connecting river systems. The fact that *Ceratodus* was so widely distributed in late Triassic times is merely evidence of land connections between all of the major continents at that period of geologic history. The amphibians are notoriously intolerant of salt water, so the presence of *Metoposaurus* in Europe and in India indicates movement back and forth across well-watered land areas. Only the phytosaurs might conceivably have crossed seaways, as do the modern salt water crocodiles, yet even in this instance the chances are strongly in favour of their spread accross the northern land masses, including India, Europe, and North America by way of land connections in which rivers and lakes were abundant.

The small terrestrial vertebrates in the Maleri fauna are the rhynchosaurs, the small ornithosuchid pseudosuchians and the small coelurosaurian dinosaurs. These are all such obvious land-dwellers that the only possible means of accounting for their presence in India, Europe and North America is the supposition of firm land connections between these regions. The evidence against a direct connection between peninsular India and Africa is not quite so overwhelming in the case of these reptiles as it is in the case of the metoposaurs and the phytosaurs. Thus rhynchosaurs and ornithosuchids are present in the African Triassic. Furthermore, the accidents of collecting cannot be ruled out entirely in evaluating the absence of coelurosaurs from Africa. The fossil remains of

these animals are small and very fragile, which makes them rare, and possibly for this reason they are not in the the African record.

The distribution of the ornithosuchids does indicate some relationship between peninsular India and Africa, but as pointed out above, these reptiles were widely distributed in late Triassic times. Their presence in India and Africa may not be so much an indication of any direct connection between the two areas as that of general connections between all of the continental land masses. Ornithosuchids, and rhynchosaurs as well, may have crossed from the European region into Africa by way of a land connection in the present Mediterranean region, and this may have taken place before the advent of late Triassic history. Such a sequence of events might then account for the considerable differences between the African and Indian rhynchosaurs. The same may be true of the ornithosuchids as well, but as yet the materials are too fragmentary for close evaluation.

The presence of rhynchosaurs in Africa and their absence in North America requires careful evaluation. It has already been shown that the rhynchosaurs of Africa are more distantly related to those of India than are the rhynchosaurs of Europe and South America; therefore, it seems reasonable to suppose that the presence of these reptiles in the African region antedates late Triassic times. Certainly there was no direct movement of rhynchosaurs back and forth between Africa and India in late Triassic times, as there was a movement of metoposaurs, phytosaurs, ornithosuchids and coelurosaurs between India and Europe. The absence of rhynchosaurs from the Triassic sediments of North America is very possibly the record of a real absence of these reptiles in this region.

The large terrestrial vertebrates in the Maleri fauna are the large pseudosuchian, known from a skull fragment, and the few bones attributed by von Huene to *Massospondylus*. In view of the uncertain nature of these fossils no valid deductions can be made as to possible migration routes between peninsular India and other continental areas.

The evidence as presented in the foregoing cirtical evaluation and analysis of the Maleri fauna points quite clearly to the fact that this is essentially a northern assemblage of vertebrates that extended to the peninsular region of India from the Eurasiatic land mass at the beginning of late Triassic times. There is no valid evidence that this fauna had ready access to the African land mass. Such considerations argue for continental relationships during late Triassic times that were generally similar to the continental relationships at the present time. The theories of continental drift and of a broad southern Gondwanaland separated by a seaway from the northern land masses seem to be postulated without regard to the evidence of land-living vertebrates such as those that make up the Maleri fauna. This is evidence that cannot be ignored.

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