Systematic and Biological Remarks on the Permian Genus *Lysorophus*[*]

By: F. Broili, Munich.

On his last collections tour to the Permian deposits of Texas, which he made during the summer of 1906 for the American Museum in New York, the indefatigable collector and highly meritorious investigator E. C. Case succeeded in finding five skulls of the species *Lysorophus tricarinatus*. They were in a very remarkably good state of preservation and enabled the fortunate finder to make a series of new observations, especially on the hitherto unknown underside of the skull of *Lysorophus*, which he recently published in the *Bulletin of the American Museum of Natural History*, Vol. 24, Art. 26, p. 531-533 (with figures).

Based upon this find, Case in his article arrives at conclusions that differs materially from the interpretations previously given by me. For instance, Case had before him the completely preserved underside of the skull and occiput of an individual, the structure of which led him to regard *Lysorophus* as an amphibian and not as a reptile – as I had done – although he expressly declares certain qualities of *Lysorophus* to be reptilian characteristics.

The writer of these lines cannot, however, agree with Case's opinion, and he will endeavor to prove in the following statement that according to the new illustrations and opinions given by Case, the very characters that the latter regards as amphibian tend to show that *Lysorophus* is a reptile.

---

[*] Original citation: Broili, F. 1908. Systematische und biologische Bemerkungen zu der permischen Gattung *Lysorophus*. *Anatomischer Anzeiger* 33(11-12):290-298. Unknown translator. Transferred to electronic copy and edited by Mark Uhen and Michell Kwon, Smithsonian Institution, 2008.

Now, the two principle points which Case brought out in support of his view regarding the amphibious nature of *Lysorophus* are the possession of a parasphenoid and the presence of two condyles on the occiput.

With regard to the first point, the possession of two condyles, in view of the illustrations given by Case, which are here reproduced, I would like to call attention to an obvious error in the drawing, apparently unimportant but which, examined more closely, might be of great importance. If, for example, one compares Fig. B, the back view, with Fig. D, the view of the skull from below, while the measurements are otherwise almost equal, the width of the two condyles amounts to nearly a whole centimeter in the former figure, whereas in the latter, which shows the underside of the skull, the width is only one half, namely ½ cm. This error of ½ cm, however, in an object which is small in itself, is rather considerable, and decisive for the entire picture of the skull and the characteristics to be inferred from it. For example, it makes "the two condyles" in Fig. B appear to be separated from one another by a proportionately wide space, so that one could really take them for the two articular facets of a *Stegocephalus* occiput, although the latter elsewhere when it comes to an ossification of the occiput, are usually really developed as plainly projecting condyles, and not as smooth surfaces converging toward one another, as is the case here.

In my earlier works on *Lysorophus* (I, p. 96 and II, p. 506) I had expressed the opinion, based on imperfect material, that *Lysorophus* does not possess a basioccipital, and that this element of the skull had either been lost or had only been gristle. According to Case's new finds, which represent the entire underside of the skull, this opinion can no longer be upheld; but I am of the opinion that the hind part (designated by Case bs? =

basisphenoid) of the palatal surface, separated by a suture, represents the basioccipital, whereas the fore part is the basisphenoid (named by Case Ps = parasphenoid).

[Fig. 2 here]

The dorsal, rounded surface of the basioccipital forms, with the two similarly formed end surfaces of the lateral exoccipitals closely adjacent to it, the articulation for the atlas, as may be plainly seen in three uncrushed specimens in the State Paleontological Collection at Munich (Fig. 2). We have here a typical tripartite condyle, which is by no means a rare occurrence among reptiles. Thus basioccipital and lateral exoccipitals are usually divided at the union of the occipital condyle in most of the tortoises, so that it frequently appears to be tripartite. Tripartite occipital condyles occur also in fossil forms, as in *Dicynodon*, of which genus Seeley says: "It includes a rounded occipital condyle, which is formed by the basioccipital and the two exoccipitals, which are usually developed backward somewhat further," and of which he earlier gives an illustration in comparison with the "exoccipital articulation" of labyrinthodonts.

Whether this tripartite condyle in our *Lysorophus* was still possibly connected with a kind of cartilaginous epiphysis, as it is found somewhat analogous on the condyle of living reptiles, must of course remain undecided.

Generally the number of occipital condyles in reptiles is variable. As a rule the single condyle, formed from the basioccipital only, predominates. Moreover we have, as we have just seen, the tripartite condyle composed of basioccipital and lateral exoccipitals. And finally we also find, though certainly not as abundant as the tripartite, a distinct double condyle; thus in a number of Cynodontia, especially in the genus *Cynognathus* and the Gomphodontia (*Gomphognathus*), which have it imprinted upon

them, sometimes in an unusually characteristic manner. Also the occipital condyle is frequently double in recent reptiles. Thus in the Munich Zoological Collection I was able to establish the existence of a distinct double condyle, isolated in *Varanus*. In this connection, Mr. Lorenz Müller, artist, rendered most friendly aid, and was also good enough to make drawings. Such a one, however, is constant in *Amphisbaena* (*alba*). Nevertheless here, as in all other lizards, it arises from three elements: one piece of the basioccipital and two of the lateral exoccipitals.

This last-named genus *Amphisbaena*, which is restricted to tropical America and Africa, presents yet other characters very strikingly like our genus *Lysorophus*.

The entire structure of the skull is very much alike in both genera, in which resemblance is brought about especially by the similar position of the relatively large nasal apertures, by the ample orbit and temporal fenestra, which lacks an osseous border below (the eyes themselves were presumably rather small in *Lysorophus* and were situated in the front corner of the orbit, as in *Amphisbaena*), and particularly by the characteristic position of the quadrate, directed forward, of which the latter peculiarity, moreover, constitutes for the Amphisbaenidae especially a character distinguishing them from other lizards.

Examination of the underside of the skull of the two forms produces still more surprising results. Thus *Lysorophus* shares with *Amphisbaena* the remarkably broad and flat basioccipital, with just as broad a basisphenoid attached to it and gradually diminishing toward the front in the form of a triangle. These elements of the skull in their outlines coincide almost exactly in the two genera.

[Fig. 3 here]

Also in the front parts of the under side of the skull tolerably analogous relations in the structure exist. A greater difference is noticeable only in the circumstances that *Lysorophus*, in contradistinction to *Amphisbaena*, can show a second row of teeth on the vomer parallel to the premaxilla and the maxilla.

In his earlier works on the Permian vertebrates the author was able, on the strength of his material, to establish the fact that *Lysorophus* possessed either very insignificant limbs, perhaps only developed as cartilage, or no limbs at all with their girdle. Of amphisbaenians we know that they also lack the limbs (with the single exception of *Chirotes*).

With regard to vertebrae, there likewise exists great similarity between *Lysorophus* and *Amphisbaena* in general structure, although the former has amphicoelous, the latter procoelous vertebral centra. This similarity is particularly noticeable in the flat neural arch, shaped like the top of a roof, sinking downward toward the front. The ribs also show many points of agreement in their saber-like curved form; in their position and moderate inclination backward; and dimensions.

From these points of comparison we may therefore draw the conclusion that *Lysorophus* is not an amphibian, but, as we have said before, a reptile; that, like *Amphisbaena*, it was a worm-shaped animal, tolerably abundant in the Permian beds of Texas, without limbs, and that accordingly led a subterranean, digging life. Its movements were at all events wormlike. Moreover these animals possessed in high degree the ability to roll themselves up laterally; for all the skeletons found in the Munich Museum, except the remains found isolated, show this peculiarity. The average length

must have been about 10–15 cm; but a few unusually large vertebrae permit us to infer that some individuals were considerably larger, perhaps 25–30 cm in length.

In the earlier works treating this subject, *Lysorophus* was assigned with reservation to the Rhynchocephalia as representative of a separate family, the Paterosauridae, expressly calling attention, however, to the similarity of the skull to that of the lepidosaurians: I, p. 95, "the skull of *Lysorophus tricarinatus* has an elongated triangular outline, which, viewed from above and from the sides, has quite the character of a Lacertilia"; and II. p. 586, "the elongated, narrow little skull of *Lysorophus* possesses in general the characters of a Lepidosaurian"; and p. 587, "from these diagnostic remarks it follows with absolute certainty that we must regard *Lysorophus* at all events as the representative of a group of reptiles still in a very low stage of development, whose nearest, but already much more highly organized relatives, we have to seek among the Proterosauridae or Mesosauridae."

According to the new discoveries of Case, it would therefore no longer be possible to retain *Lysorophus* among the Rhynchocephalia, which in doing so one would have to regard the characteristic formation of the underside of the skull as merely a phenomenon of convergence.

For the Rhynchocephalia possess upper and lower temporal arches, together with distinct intercentra, to at least between the cervical and caudal vertebrae. These decisive characters, however, are entirely missing in our *Lysorophus*. The latter, although it lacks a distinct parietal foramen (compare *Amphisbaena* and *Chamaeleopsis*), presents much more the typical characters of a lepidosaurian, especially of a lacertilian, which is noticeable in its entire habitus, in the lack of the osseous lower border of the temporal

arch, and in the forward inclined position of the quadrate, and especially in the lamelliform structure of the basioccipital and basisphenoid.

It therefore seems more correct, according to the principles recognized as valid in taxonomy, to place *Lysorophus* among the lacertilians.

It is true that great objection might be made to such a step, based mainly on considerations of time, since the oldest remains of Lacertilia (if we except the genus *Macellodon*, of uncertain placement, from the Purbeck), the Dolichosauridae and Aigialosauridae, which may be considered in this connection, come from the Cretaceous. The latter are lepidosaurians with a Pythonomorpha-like head, 7 cervical and 21 dorsal vertebrae. The former are snake-like, elongated reptiles with a small head, built partly according to Varanidae patterns, with a cylindrical body; and of the presacral vertebrae not less than 13 fall in the long neck and 26-27 in the body region. The limbs are well developed.

With *Dolichosaurus* the closely related genus *Acteosaurus* H. v. M. especially may be considered here. H. v. Meyer has already referred to the similarity of this genus to the Ptychapleurae among the Brevilinguia; *Pseudopus*, *Bipes*, *Ophiosaurus* (p. 231).

From that we see that the points to be compared between *Lysorophus* from the Permian and the Dolichosauridae and Aigialosauridae from the Cretaceous, – of which the former lead over to the Pythonomorpha, and the latter, according to the latest investigations of Nopcsa, to the Ophidians, – are very few. It accordingly seems hardly admissible to draw further conclusions based on this faulty paleontological material, as the first remains that are ascribed to *Amphisbaena* come from the Oligocene of the White River beds (*Aciprion*, *Cremastosaurus*, *Diacium*, ?*Hyporhina*, *Platyrhachis*, *Rhineura*),

genera that for the most part are based only on a few vertebrae and incomplete remains of skulls. The conditions are not so favorable here as in *Palaeohatteria* and *Hatteria*, where connecting links are to be found in the different formations.

All that we can infer is that the Lacertilia, which in their organization and in their manner of living are remarkably like the Amphisbaenia, appear as early as Permian times. It seems probable, indeed, that they are related to one another; but a sure inference in this respect could be drawn only after the discovery of additional irreproachable connecting links.

From all these considerations it appears that the Permian Paterosauridae with *Lysorophus* are no longer to be left with the Rhynchocephalia, but are to be regarded as the oldest lacertilians.

In conclusion let the following generic diagnosis of *Lysorophus* be established, based on the new discoveries:

Skull elongated, narrow, in general with the characteristic peculiarities of a lepidosaurian. Quadrate directed forward.

Occipital condyle tripartite, formed of the ossified basioccipital and the lateral exoccipitals. Nasal apertures large. Lateral temporal fenestra and orbital opening not separated by an osseous span. The former not bordered by bony structure below. Basioccipital and basisphenoid developed as broad plates, as in *Amphisbaena*.

Lower jaw very short, amounting to about half the length of the skull. Teeth pointed, small, of equal size. Beside the maxillary-premaxillary row of teeth, still a second row parallel to these on the vomer. Between the lower jaws ossifications of membrane, analogous to the jugular plates of the fishes.

Vertebra spongy, deeply amphicoelous, with persisting chorda. Neural arches separated by suture from the vertebral centrum; dorsally the two halves of the arches not yet grown together. No intercentra between the vertebrae. Ribs one-headed and ?two-headed, powerful. Without limbs.

For the distinguishing trait of the Permian deposit in Texas, the faunal element *Lysorophus* as such is of great interest; for the entire Permian fauna shows a decided advance in development as compared with the Stegocephalia, which occur in the Carboniferous beds of Ohio. Instead of the Lepospondyli, which predominate in Ohio, mostly rather small forms meet us in Texas, such as temnospondyl batrachians, cotylosaurians, and pelycosaurians. With the single exception of *Diplocaulus*, the Lepospondyli have entirely disappeared. In their stead, however, a Lacertilia confronts us in *Lysorophus*, which plainly owes its origin to the same living conditions as certain footless batrachians (*Molgophis*, *Phlegethontia*) of Ohio, and had analogous modes of living, but in its organization (ossification of the vertebrae, for example) had not yet attained the same relatively high position.

Footnote – Hugo Schwarz, On the vertebral column and the ribs of holospondyle Stegocephalae (Lepospondyli Zitt.). *Contributions to the Geology and Paleontology of Austria-Hungary and the East*, Vol. 21, Heft 1 and 2. In *Molgophis*, *Phlegethontia*, *Thyrsidium* the neural arches have almost coalesced with the centrum of the vertebrae, are merged into one another dorsally, and endowed with spinous process.

EXPLANATION OF THE ILLUSTRATIONS.

Fig. 1. *Lysorophus tricarinatus* Cope. Enlarged to twice natural size. A. Side view of the skull. B. Back view. C. Upper view. D. Lower view. Copy after Case. L. Lacrimal bone. N. Nasal plate. F. Frontal bone. P. Parietal bone. So. Supraoccipital. Sq. Squamosal. Ps. Parasphenoid. Bs. Basisphenoid. (In the author's opinion Ps = bs and bs = Basioccipital)

Fig. 2. *Lysorophus tricarinatus* Cope. Double size. (Original in the State Paleontological Collection, Munich.). Back view. Exo. Lateral exoccipital. So. Supraoccipital. Sq. Squamosal. Bo. Basioccipital.

Fig. 3. *Amphisbaena alba*. Skull with lower jaw. Double size. (Original in the State Zoological Collection, Munich.) A. Ventral view. B. Side view. Bo. Basioccipital. Bs. Basisphenoid.