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THE AFFINITIES OF *PROTEROCHAMPSA BARRIONEUVOI* REIG

by

A. R. I. Cruickshank

ABSTRACT

Proterochampsa barrioneuvoi Reig is re-examined and is confirmed as a proterosuchian thecodont. None of the features previously thought to ally it to the Crocodilia are solely characteristic of that group. On the other hand it is not a phytosaur nor phytosaur ancestor, only showing one real trend towards these animals in the rearward migration of the internal and external nares. *Proterochampsa* and its relatives *Chanaresuchus*, *Gualosuchus* and *Cerritosaurus* are too late in time to be phytosaur ancestors. They are grouped together in the Proterochampsidae, a family within the Proterosuchia.

INTRODUCTION

Recently while visiting the Museum of Comparative Zoology in Harvard I had the opportunity to examine skull material ascribed to this taxon and which had been dealt with in some detail by Sill (1967). In addition there were available casts of the type and one other skull (Reig, 1959). In view of the comments made by Walker (1968) and Romer (1972) concerning the affinities of this species it seemed advisable to re-examine it and the observations made form the body of the following notes, which have been made possible largely as a result of my recent work on the Proterosuchia.

MATERIAL

MCZ 3323; Cast of the type PVC 2063 (Instituto Lillo, Tucuman) (Figured Reig, 1959, Figures 1 and 2).

MCZ 3408; a well preserved but crushed skull with few of the sutures clearly seen. Associated with this skull are a series of cervical and anterior dorsal vertebrae and ribs. (Figured Sill, 1967, Figures 1, 2, 3, 4b, 5 (in part), 6b, 7b, 8a and 9b; plates I—V, VIII and IX.)

MCZ 3409; cast of skull MACN 18165. (Museo Argentino de Ciencas Naturales.) The original lacks the greater part of the left maxilla, all the bones of the left side behind the antorbital fenestra, the entire occiput, the braincase and parts of the right squamosal and quadratojugal. It is dorso-ventrally crushed. (Figured Sill, 1967, plates VI and VII.)

Of the three, the type is apparently the best preserved but is damaged in the snout region so that the external nares were reconstructed as being lateral and terminal by Reig in contradiction to the real state of affairs where they are dorsally situated against the midline of the skull, a situation which was ascertained only after more material was found subsequent to Reig's description.

All the specimens came from the Ischigualasto Formation. Romer and Jensen (1966, p. 16) are in doubt as to whether it is Ladinian or Carnian but feel that it ". . . is essentially Middle Triassic". On the other hand others (summarised in Anderson and Anderson, 1970) place the age of these beds as high as the Norian. The weight of evidence would seem to prefer an Upper Triassic age, though not as late as the Norian.

THE AFFINITIES OF PROTEROCHAMPSA

Reig in his original description stressed the crocodilian affinities of *Proterochampsa* and his view was followed by Sill who believed that it should be included formally in the Crocodilia as representative of the family Proterochampsidae of the new suborder Archaeosuchia. Included in this new suborder was a second family, the Notochampsidae comprising *Notochampsa* and *Erythrochampsa* (Reig, 1959; Sill, 1967).

Walker (1968) took strong exception to this classification and raised fourteen points (op. cit., pp. 6—11) to deny its crocodilian affinities and concluded (p.11) that "there seems ample evidence then for regarding *Proterochampsa* as a very primitive phytosaur and not a crocodile".

Romer (1972, p. 5) concludes his discussion on the family Proterochampsidae (in which he places the additional genera *Chanaresuchus, Gualosuchus* and *Cerritosaurus*) with the statement that "the proterochampsids are long-snouted amphibious forms which have advanced little beyond the proterosuchian grade of organisation and may well be placed in the Proterosuchia".

It is quite clear therefore that there are three views on the matter. Is *Proterochampsa* a crocodile, a phytosaur or a proterosuchian?

Crocodilian features of Proterochampsa (Sill, 1967)

1. Flat broad skull with long snout.

2. Highly sculptured surface to bones of skull.
3. Large dorsally placed orbits.
4. Small supra-temporal fenestrae.
5. External nares near midline of snout.
6. Similarities to crocodilian conditions in the otic notch and external auditory meatus.

There are in addition other features of doubtful validity but quoted by Sill as being diagnostic of the Crocodilia, e.g. the relationship of the exoccipital to supraoccipital.

Considering the points listed above, the flattening of the skull is a result of dorso-ventral crushing as much as a natural shape. This feature also exaggerates the orientation of the orbits. The sculptured surface of the skull is paralleled in the undoubted proterosuchians *Chanaresuchus* and *Gualosuchus* and is therefore not exclusive to the Crocodilia. Likewise the position of the nares — both internal and external — are similar in all three genera, as are the small supra-temporal fenestrae. These latter are also much the same as in *Proterosuchus*.

However, the point which was emphasised by Sill was the presumed similarity of the crocodilian external ear region to that of *Proterochampsa*. It is now believed that incorrect information on this region in the Proterosuchia led Sill to misinterpret these structures in *Proterochampsa*.

In MCZ 3408 considerable dorso-ventral crushing has occurred so that the exoccipitals (with the opisthotics attached) have been moved laterally and have thus allowed the basisphenoid to ride up against the interior of the braincase. As a result of this, the two prominent openings ". . . assumed to be the carotid foramina" (Sill, op. cit., p. 423) have been misidentified. They are in fact the ventral portions of the large vagus foramina. The two "flange-like processes" are the basal tubera (somewhat weathered) and the median cleft between them runs antero-dorsally into an area of crushed bone and is clearly part of the median backwardly facing excavation similar to that seen on the basisphenoid of *Proterosuchus* and figured as such by Reig (1959, p. 262, Figure 2). It has nothing to do with the eustachian system.

The groove that Sill figures (op. cit., Figure 5) purporting to be the homologue of the crocodilian external auditory meatus is in fact the stapedial groove running on the anterior face of the paroccipital process of the opisthotic and exactly similar to that in *Proterosuchus*. From what can be seen of the rest of the braincase in MCZ 3408 it is clear, moreover, that it is essentially the same as in *Proterosuchus* (Cruickshank, 1972). The inward slope of the head of the quadrates has been exaggerated by the dorso-ventral crushing and their relationship to the palatal bones is strictly as in *Proterosuchus*. In addition, there seems no evidence for the quadrate head being in primary contact with the prootic as might be expected in a crocodile (Walker, 1972). The reconstruction of the occiput figured by Sill (op. cit., Figure 3) does not seem to have taken into account this very obvious dorso-ventral crushing and thus the quadrates have been splayed too far laterally in his figure; so much so that the lower jaw, if in natural articulation with the quadrates, would be far removed from the steadying influence of the pterygoid flanges. This is borne out by a close examination of specimen MCZ 3408 itself. For greater realism, the quadrate should therefore be orientated more vertically, which would deepen the line of the skull posteriorly in lateral view, narrow it slightly in dorsal view and bring the lower jaw nearer the pterygoid flange, and in all make it less superfically crocodile-like. There is present a small triangular interparietal and it would also seem that the parietals at least are not fused on their midline for their entire length. *Proterochampsa* has no post-temporal fenestrae, another character in common with *Proterosuchus*. Therefore it would seem that there are no real grounds for allying this form with the Crocodilia as Walker has already pointed out.

Phytosaurian features of Proterochampsa

Walker (1968) enumerated fourteen points in his claim for phytosaurian affinities of *Proterochampsa*. It is not necessary to repeat them here except to comment on his conclusions and to note that, with the exception of the relationship of the internal nares, the majority of them are primitive for the Phytosauria or are similar to the conditions seen in the Proterosuchia.

The most important of Walker's points (No. X) is that dealing with the position of the internal nares, which in *Proterochampsa* agree proportionately more with the Phytosauria than with the Crocodilia. However, Romer (1971) described subsequently to Sill's paper two genera of closely related proterosuchian thecodonts (*Chanaresuchus* and *Gualosuchus*) with, in the former, a palate closely comparable to *Proterochampsa* and additionally a braincase and ankle of the proterosuchian pattern, showing that the palatal characters of *Proterochampsa* cannot be taken to indicate relationships higher than the Proterosuchia. The ratio of posterior margin of the "primitive" internal nares to a line joining the posterior ends of maxillae/length of maxillae in the midline is in *Chanaresuchus* 15,5%, a slightly lower value than in *Proterochampsa* (Walker, 1968).

Proterosuchian features of Proterochampsa

Proterochampsa has many features characteristic of primitive thecodonts which were recognised by both Walker and Sill. It is in fact these characters which are the more important in assessing the affinities of *Proterochampsa*.

The palate, apart from the backwardly placed internal nares, is basically primitive and very similar to that of *Proterosuchus*. There are teeth on the pterygoids and the basal articulation seems to have been free. Associated with this feature is an almost

certain lack of an ossified laterosphenoid element. Although the rearward movement of the internal nares is cited by Walker as being the most important feature of this genus linking it to the phytosaurs, they are hardly a significant distance farther back than in *Chanaresuchus* (see above) which is clearly a proterosuchian. The outline of the lower temporal opening is very much more like that of *Chanaresuchus* and *Gualosuchus* than is indicated in Sill's figures, having among other characters a small postero-ventral extension as in the two aforementioned genera. The position of the external nares is almost identical in all three of these and the occiput of *Proterochampsa* has no post-temporal fenestra, in common with most other Proterosuchia.

CONCLUSIONS

It must therefore be clear that, as Romer pointed out, and after a re-examination of skull material, *Proterochampsa* has strong affinities with the Proterosuchia in general and *Chanaresuchus* and *Gualosuchus* in particular. All three, plus *Cerritosaurus*, can conveniently be placed together in the same family (the Proterochampsidae) within the Proterosuchia. They probably represent a lineage of primitive thecodonts, evolving in parallel with the phytosaurs, but they themselves, particularly *Proterochampsa*, because of the time relationships involved, are too late to be phytosaur ancestors, and were probably the last representatives of the Proterosuchia. This family shows advances over the earlier proterosuchians in the rearward migration of both the external and internal nares, the tendency to acquire ornamentation on the skull roof, the loss of post-frontals and the development of a fenestra in the lower jaw.

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