[A translation of R. Hoffstetter, 1943, “Varanidae et Necrosauridae fossiles,” *Bulletin du Muséum national d’Histoire naturelle* 15(3): 134-141. The numbered footnote is Hoffstetter’s. In cases of uncertainty, the original text, in quotes, is given in square brackets after the text; other text in square brackets is for clarification. Translation ©2007 by Krister T. Smith]

FOSSIL VARANIDÆ *AND* NECROSAURIDÆ

By Robert HOFFSTETTER.

The superfamily *Varanoidea* CAMP 1923 contains, beside the marine or littoral forms of the Cretaceous (*Aigialosauridæ* and *Dolichosauridæ*), also continental representatives, generally grouped in a single family, the *Varanidæ*. These have been studied at length by Ch. W. GILMORE (1928) for the American fossils, and by G. J. DE FEJÉRVÁRY (1918 and 1935) for the forms of the Old World. The latter author separates from them the *Megalanidæ* as a new family. But the characters on which he relies do not permit the acceptance of this invention. At the very most one can accept the existence of a subfamily, the *Megalaninæ*; still, its individuality is far from proven.

On the other hand, the study of the fossil European material obliges me to separate from the *Varanidæ* a new family, the *Necrosauridæ*, which will be the subject here. This invention, as will be seen, profoundly changes ideas accepted following the works of G.-J. DE FEJÉRVÁRY on the history of the terrestrial *Varanoidea.*

I. – NECROSAURIDÆ Fam. nov.

H. FILHOL reported then described and figured a form from the Phosphorites du Quercy under the successively following names: *Palœosaurus* [*sic*] (non *Palæosaurus* Williams 1838) *Cayluxi* (1873: p. 89), *Necrosaurus Cayluxi* (1876: p. 27), *Palæovaranus Cayluxi* (1877: p. 268; pl. 26, fig. 434, 445, 446)*. If the abandonment of the first generic appellation, already used for a dinosaur, is justified, that is not so [“il n’en va pas de même”] for the second, which must be retained. *Palæovaranus* thus falls into synonymy.

In his first study, made of too poor material, G. J. DE FEJÉRVÁRY (1918) refers the species of H. FILHOL to the genus *Varanus* MERREM 1820 and included it in a series of monitor lizards which had inhabited Europe throughout the Tertiary. In 1935, new material obliged him to resurrect the genus of H. FILHOL, under the name *Palæovaranus.* The author essentially relies on the characters of the maxilla, which he describes at length. Briefly, this bone, fairly tall in the anterior part, shows a strong internal crest which supported the normally developed nasal bones. One could not overemphasize the importance of this arrangement, unique in *Platynota.* In effect, the nasals are reduced to the point of no longer touching the maxillae, not only in the *Varanidæ* but likewise in the *Aigialosauridæ* and *Dolichosauridæ*, just as in the *Mosasauridæ*, as far as one can determine from the figured skulls.

I have been able to observe other cranial characters of *Necrosaurus* which separate it from the *Varanidæ.* The premaxilla has an arched and rather short nasal process, indicating a realtively tall and moderately elongate snout. The frontals, solidly united [fused] with one another, show descending processes that do not meet below on the midline. The parietal, although of the

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* Actually, only fig. 434.

varanian style, also shows some unique features.

As regards the vertebral column, it is curious to note that G. J. DE FEJÉRVÁRY did not come across, in the material from Quercy, any vertebrae likely to pertain to this otherwise abundant form. At least the author did not recognize in the material any "varanian" vertebrae, and this remark appears to me significant. I have studied in the Laboratoire de Paléontologie of the Muséum abundant material from Quercy. I have thus been able to attribute numerous vertebrae to the genus *Necrosaurus* and to find the characters of practically the whole column. It results from the observations that one could consider as pertaining to *Necrosaurus* the vertebrae already figured by R. LYDEKKER 1888, p. 279, fig. 62 (dorsal vertebra of "*Placosaurus margariticeps*"), K. A. VON ZITTEL 1889, p. 603, fig. 534 (axis and anterior caudal vertebra of *Palæovaranus Cayluxi*), G. DE STEFANO 1903, pl. X, fig. 3, 9, 10 (sacral and dorsolumbar vertebrae of *Palæovaranus Filholi*) and pl. X, fig. 4, 5, 17 (caudal vertebrae of "*Iguana europæa*"). The vertebrae, which would call for better illustration, indeed do not present the physiognomy so characteristic of those of monitor lizards. They have a more elongate centrum, in which the inferior face is much less regularly convex; their condyle as well is far from being enlarged transversely and is not preceded by a strong constriction of the centrum. However, the cervical vertebrae with their epiphyseal hypapophyses ["hypapophyses épiphysées"], and the caudal vertebrae with their articulated chevron bones clearly remain in the varanian style.

Finally, a character of importance is to be emphasized: the presence of osteoderms very particular to this animal. I had already considered referring to the genus *Necrosaurus* osteoderms from the Thanetian of Cernay-les-Reims. A recent work by O. KUHN (1940) will confirm this hypothesis. The author describes and figures *Melanosauroides giganteus*, new genus and species, from the middle Eocene of Geiseltal, which he refers to the *Anguidæ*. Examination of the photograph which he gives (pl. IV) clearly shows that it is a *Varanoidea* very similar to *Necrosaurus*, which I propose to name *Necrosaurus giganteus* (KUHN 1940). And yet, the specimen shows, associated with the skeleton, oval osteoderms, ornamented, with a median keel, almost identical to those which I have noted in the Cernay material, in both cases very different from those of the *Anguidæ*. It must be a loose armor, reproducing exactly the horny squamation, and not adhering to the bones of the head. It is to be emphasized that the presence of osteoderms is very rare in the *Platynota*. Only *Varanus komodoensis* OUWEN[1] [sic] has a complete armor, likewise separated from the skeleton; moreover, some other varanians show smooth osteoderms in the region of the nape.

These various characters would appear to me to demand the erection of the family *Necrosauridæ*. Indeed, the presence of "normal" nasals applied to ["appuyés sur"] the maxillae disallows the inclusion of the studied form in any of the known families of the *Platynota*, whose every representative, since the Cretaceous, has possessed reduced nasals. *Necrosaurus* must derive directly from an unknown common stock, probably Jurassic, of a less evolved nature. In addition, the form of the vertebrae and the presence of osteoderms especially confirm the unique position of the *Necrosauridæ*.

This family appears specifically European. It existed from the Thanetian until the upper Eocene and possibly the Oligocene; remains are encountered indeed in Cernay, Cuis, Egerkingen, Geiseltal and Quercy.

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[1] I cannot accept, for this species, the genus *Placovaranus* proposed by G. J. DE FEJÉRVÁRY. The osteology of *V. komodoensis*, which I have studied in the Laboratoire d'Herpétologie in the Muséum, is absolutely similar to that of the other representatives of the genus *Varanus*. As for the existence of osteoderms, it does not suffice to characterize a new genus, as there exist intermediate forms endowed with osteoderms in the region of the nape.

II. – VARANIDÆ COPE 1864.

1. **Saniwinæ** CAMP 1923.

While the family *Varanidæ* presently inhabits the Old World, it is curious to find the first representatives in North America.

First there is *Palæosaniwa* GILMORE 1923, a monotypic genus from the Upper Cretaceous (Belly River). The only species is founded on a dorsolumbar vertebra. But a comparison of the figure with the vertebrae of *Placosaurus* from Quercy leads me to suppose that it is instead from a placosaurine anguid.

Two species from the Upper Cretaceous (Lance) constitute the genus *Parasaniwa* GILMORE 1928. They are founded on dentary fragments which clearly appear ["paraissent bien"] to pertain to the *Varanidæ*, but of course do not allow any exact discussion.

The genus *Saniwa* LEIDY 1870 is very well known. Five species are reported in America from the lower Eocene (Wasatch) to the Oligocene (*Oreodon* beds). Of these, the genotype *Saniwa ensidens* LEIDY is excellently described by Ch. W. GILMORE (1922 and 1928). It is incontestibly a varanid. But in its cephalic bones, in its pectoral girdle ["ceinture scapulaire"], and in its vertebrae, provided with a rudimentary zygosphene, the animal shows unique characters which plainly justify the erection of a subfamily.

L. DOLLO (1923) has reported *Saniwa orsmaelensis* DOLLO in the upper Landenian of Orsmael and of Erquelines (Brabant). The species if based on a maxilla, some dorsal vertebrae and a femur. Unfortunately the cursory diagnosis is not accompanied by any figure, and I have not yet been able to examine the original specimens to form a personal opinion. According to L. DOLLO, the vertebrae have all the characters of the *Varanidæ* but show a rudimentary zygosphene. One can therefore accept the systematic position given to the species by the Belgian scientist.

I will additionally report the presence, in the *Agéen* (upper Ypresian) of Cuis and of Monthelon (Marne), of clearly varanoid but worn vertebrae, which do not permit one to determine the presence or absence of a zygosphene. These are then doubtlessly descendents of the species of L. DOLLO.

The *Saniwinæ* thus constitute one subfamily of the *Varanidæ*, characterized notably by the presence of a rudimentary zygosphene. They appeared in North America, perhaps as early as the Upper Cretaceous (*Parasaniwa, Palæosaniwa* ?), surely from the lower Eocene (*Saniwa*) and survived there until the Oligocene. The presence of related forms in western Europe indicates an incursion of short duration, as one only finds remains from the Sparnacian to the upper Ypresian.

2. **Varaninæ** CAMP 1923 (in part).

The appearance of true monitor lizards ["Varans"] is much later than G. J. DE FEJÉRVÁRY believe it to be.

It is necessary first of all to eliminate *Varanus? Lemoinei* NOPCSA 1908 (*cf.* G. J. DE FEJÉRVÁRY 1918: p. 418-19, fig. 18), first reported and figured by P. GERVAIS (1877). It is a distal portion of a reptile humerus, which I was able to re-discover in the Muséum in Paris, and which comes from the *Agéen* of Ay (Marne). The unusual form of the articular faces of the bone, principally that of the radial condyle, the peculiar position of the ectepicondylar canal, and finally the morphology of the entepicondyle, which is truncated here, are so many characters which allow one to assert that it cannot be a varanid, not even a saurian. It is doubtlessly among the turtles ["Tortues"] that one must look for related ["parentes"] forms.

During the Eocene, the Oligocene, and the lower Miocene, one does not find any varanine remains. The subfamily is still not represented in the horizon of Sansan (Gers). One must come to the middle Vindobonian of Grive-Saint-Alban (Isère) to see the group appear. Remains of *Varanus* have already been reported by O. JOURDAN (1865), CH. DEPÉRET (1887, p. 289) and have wrongly been compared to *Necrosaurus Cayluxi* by G. J. DE FEJÉRVÁRY (1918 and 1935). In fact, I know at present of numerous vertebrae, a quadrate, dentary fragments and a femur of the animal from Grive. It is very much the genus *Varanus*, already clearly characterized, and perhaps represented by two species of different size.

It is doubtlessly to the upper Vindobonian that one should assign *Varanus Hofmanni* ROGER 1898, from the "Dinotheriensande" of Stätzling. Once again, it is very much a monitor lizard ["Varan"], possibly identical to the large species of Grive.

Appearing next, in the *Pontien* of Pikermi, is *Varanus marathonensis* WEITHOFER 1888 (= *Varanus sp.* GAUDRY 1862 = *V. atticus* NOPCSA 1908).

Finally, in the Quaternary, as yet poorly known remains, figured by St.-J. BOLKAY (1913) and N. MORELLI (1891), indicate that the genus persisted in Europe until a recent time.

The other continents are much poorer as far as remains of *Varaninæ* are concerned. Asia has only delivered to us fossils from the Pliocene and the Quaternary, close to modern forms (*cf.* G. J. DE FEJÉRVÁRY 1918). Australia and Java have likewise provided recent remains. As for Africa, more disappointing still, it has furnished us with nothing even up to today.

If one tries to reconstruct the history of the *Varaninæ*, one sees that it is impossible to derive them from the *Necrosauridæ*. Moreover, the two groups are separated in time by a significant lacuna, extending from the Oligocene to the Vindobonian. In contrast, the idea of descent from the *Saniwinæ* is quite acceptable. It would then be necessary to accept a migration ["migration"] of these forms which, while their representatives died out in America, were to spread to Asia and reach western Europe in the middle V[i]ndobonian.

The subfamily has prospered in the Old World, where it spread widely throughout every warm region. It has not, however, been able to reach Madagascar, doubtlessly completely separated at the time of the late arrival of *Varanus* in Africa.

3. **Megalaninæ** CAMP 1923 (= *Megalanidæ* FEJÉRVÁRY 1918.)

The gigantic *Varanidæ* of the Australian upper Pliocene was first reported and studied by R. OWEN (1859 to 1886), then they were made the object of study of A. S. WOODWARD (1888), C. W. DE VIS (1885 and 1889), and G. J. DE FEJÉRVÁRY (1918 and 1935). The only certain species, *Megalania prisca* OWEN 1859, is now known from its vertebrae, the proximal part of a rib, the humerus, the ulna, the occipital part of the cranium, the maxilla, lacking its teeth, and some isolated teeth.

The vertebrae, according to the author of the genus, are particularly distinguished by their large size, the smallness of the neural canal, the presence of rudiments of a zygosphene, and the precondylar constriction of the centrum.

Above all the third character has attracted attention, and it has always been accepted by the authors who have occupied themselves with the genus. G. J. DE FEJÉRVÁRY (1918) uses it in characterizing a special family, the *Megalanidæ*. Ch. L. CAMP (1923) relying on the same character, considers the group as a subfamily, the *Megalaninæ*. Ch. W. GILMORE (1928), based still on this character, moves *Megalania* closer to *Saniwa* and groups the two genera in the subfamily *Saniwinæ*.

However, H. A. LONGMAN, in a letter addressed to G. J. DE FEJÉRVÁRY (*in* G. J. DE FEJÉRVÁRY 1935, p. 2 and 18), quite rightly points out that one cannot distinguish a well-developed zygosphene or zygantrum in *Megalania*. In order to hold his first position, G. J. DE FEJÉRVÁRY responds at length but unconvincingly ["répond par de longs développements peu convaincants"]. He admits that the zygosphene of *Megalania* represents an "orimental structure,"[†] arrested in its phylogenetic development. The zygosphene was in a state of "paracmic epistasy," modified as a result of the hyperostosis of the vertebra.

There is no need to emphasize the very hypothetical nature of these considerations. Neither the figures of R. OWEN or G. J. DE FEJÉRVÁRY nor the long and meticulous descriptions of G. J. DE FEJÉRVÁRY (1935) show the existence in *Megalania* of a true zygosphene, that is to say, an anterior projection of the neural arch provided with articular facets. Nor, as in *Lacerta*, for example, of a rudimentary zygosphene, formed by articular facets not supported by a wedge-shaped ["cunéiforme"] projection. The same observations apply to the zygantrum.

In fact, *Megalania* presents a pars tectiformis arcus vertebrae, with tubercles probably owing to the presence of especially strong intervertebral ligaments. And this character is encountered in other saurians, apart from any hyperostosis.

It follows from this discussion that *Megalania*, deprived of a zygosphene, cannot be classified in the *Saniwinæ*.

Moreover, the "family" of the *Megalanidæ* remains quite vaguely defined. For G. J. DE FEJÉRVÁRY, *Megalania* represents an extinct Pleistocene branch of the platynotan line, characterized by a "pathologic" tendency in its skeletal evolution, from which a beginning of pachyostosis results. I fully accept this opinion. But the characters invoked allow for the consideration of this aberrant branch as at most a subfamily unique to Australia. That is at least a provisional conclusion, susceptible of revision when one knows more completely the characters of the cranium of *Megalania*.

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As one can see, the history of the terrestrial *Varanoidea*, less simple than G. J. DE FEJÉRVÁRY believed it to be, shows quite well analogies with that of the horses ["Hippiens"]. The principal branch, *Saniwinæ-Varaninæ*, is of an American origin, like that of *Hyracotheridæ-Equidæ*; but it persists for a shorter time than the latter in its cradle. The population of the Old World is likewise achieved by migrations ["migrations"], taking successively the route of the west (*Saniwinæ*) and that of the east (*Varaninæ*). But the premature extinction of the group of the *Saniwinæ* in America prevented the migrations from repeating themselves, as for the horses, during the Neogene. Finally, it is also in the Old World ["Ancien Continent"] that the branch attained its maximum development.

In parallel to the *Palæotheridæ*, the *Necrosauridæ* represent another branch, cryptogenic ["cryptogène"], which is encountered only in Europe, and only during the Eocene.

[†] Hoffstetter (p. 139) appears to render Fejérváry's (1935: 21) term "orimental" as "orimentaire" in French. Fejérváry possibly meant "ornamental" in reference to the small size of the structure in question and its consequently limited potential function. See Fejérváry (1935: 20) for the following phrase, "paracmic epistasy."