ON THE *VARANUS*-LIKE LIZARDS OF ISTRIA

by

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Über die Varanusartigen Lacerten Istriens
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Among the palaeontologically most important reptiles, and perhaps phylogenetically the most interesting finds of any kind in the last decade, belong without doubt those lizards which were found in recent times in Istria.

No less than three very thorough descriptions have been presented by Dr Kornhuber, of just as many lizards: *Pontosaurus*, *Carsosaurus* and *Opetiosaurus* ; one other lizard-like animal has been described by each of Herman von Meyer (*Acteosaurus*), Seeley (*Adriosaurus*) and Gorjanovic-Kramberger (*Aigialosaurus*), and a similar form (*Dolichosaurus*) has been made known by Owen from the Cretaceous formation of England.

Their systematic position has been discussed by Owen, Boulenger, Baur, Kornhuber and Gorjanovic-Kramberger, and all these authors agree that in some of them, more pythonomorph characters can be found than on any other recent or fossil lizards.

Their last classification was given by Gorjanovic-Kramberger (1892) in the following schema:

Group (Suborder:) **Dolichosauria**[*]

Family **Aigialosauridae**	Family **Dolichosauridae**
A. *Acteosaurus*	*Dolichosaurus*
Adriosaurus	
Pontosaurus	
B. *Aigialosaurus*	

[*: G-K actually proposed a new name Ophiosauria, preoccupied. JS]

I believe on the basis of renewed investigations, especially on *Opetiosaurus*, that this classification must be fundamentally transformed. In order to be able to carry this out, the individual genera should first be discussed, and only after this can we pass on their systematic position as well as their phylogenetic significance.

Pontosaurus

The great similarity between *Pontosaurus* and *Dolichosaurus* was first mentioned by Boulenger; G. Kramberger also apparently accepts this in 1901, but peculiarly, does not see himself forced to modify his classification of 1892 in any way.

Boulenger (1891) said the following on *Pontosaurus* : [in English] "There can be no shadow of doubt that the Cretaceous *Hydrosaurus lesinensis* belongs to the Dolichosauridae, possibly to the genus *Dolichosaurus* proper." I myself can only determine from the illustrations that the skull of both does not stand in the same proportion to the presacral vertebral column, which in *Dolichosaurus* consists of 35 + x, in *Pontosaurus* 39 vertebrae, and in the first shows ten times the skull length, in the latter six times. Kornhuber counts just 9 cervical vertebrae in *Pontosaurus*, Boulenger 15, while Baur (1892) is satisfied to accept fewer than 15 cervical vertebrae: "One thing however seems certain, that the number of cervicals [in *Pontosaurus*] was not 15-17 but considerably less."

I myself believe I can accept 13 cervical vertebrae, and I might also bring this number into use for *Dolichosaurus*, in which Owen counts 17, and Boulenger 15 cervical vertebrae. In this way in *Dolichosaurus* and *Pontosaurus* there are 26 dorsal vertebrae left over.

Further differences between the two forms could possibly also be found, in that the ribs of *Dolichosaurus* are somewhat shorter than in *Pontosaurus*, while in *Pontosaurus* a stronger reduction of the forelimbs is noticeable. But nevertheless there exists an extremely intimate relationship between the two forms, which lets their inclusion in the same family seem in no way [JS: lapsus, or sarcasm?] justified.

Acteosaurus

H. v. Meyer's *Acteosaurus* is also very similarly built. Here too Boulenger accepts 15 cervical and 24 dorsal vertebrae, and here too I believe I can count 13 cervical and 26 dorsal vertebrae; moreover, here too the ratio of the humerus to the femur (1:2) is the same as in *Pontosaurus*, the ribs are in both cases uniformly long, and the only difference is that the forelimb in *Acteosaurus* is 5 times, that of *Pontosaurus* 5.5 times, the hindlimbs respectively 3.5 and 3 times shorter than the presacral vertebral column; and the forelimbs are in the following proportions to the hindlimbs:

in *Acteosaurus* as 11 : 18,
in *Pontosaurus* as 11 : 22 (1 : 2).

Despite these differences put forward here, there is also a very close relationship noticeable between these two lineages, as already stressed by G. Kramberger.

Adriosaurus

According to Seeley's description, *Adriosaurus* seems to be somewhat differently shaped. Seeley says the following about it: [in English]

"Caudals show no trace whatever of a neural spine, though the chevron bones are well developed. The neural arches of the caudal vertebrae were low, without any indication of neural spines, the neural arch being concave superiorly from front to back and articulating with the arches of adjacent vertebrae by zygapophyses, which were elevated high above the surface... the hindermost vertebrae appear to develop a slight neural spine. There is no trace of a transverse process such as may be presumed to have existed. The centrum of the dorsals instead of having the concave lateral outlines of *Hydrosaurus* has its sides rather convex in outline. There thus appear in the tail differences from *Hydrosaurus lesinensis* in the relatively small development of the neural spine which never extends upward as a broad plate in this form, and when it does exist is a slender backwardly directed process. It is of course with this type (*Hydrosaurus*) that the present specimen must be chiefly compared, and form and proportion of the dorsal vertebrae, the mode of articulation of the ribs and the character of the caudal vertebrae, especially the neural spine and transverse processes, indicate a distinct type."

It can be seen that Seeley in his deductions lays the greatest weight on a negative character, namely on the lack of spinous processes of the tail vertebrae, but this particular character can not be confirmed by recent far-reaching preparation. **Through careful personal preparation of the 'type specimen' of *Adriosaurus* I was able to discover long, well-developed spinous processes on several tail vertebrae**, which are not insignificantly reminiscent of those of *Acteosaurus*, and as the remaining differentiating characters of Seeley can be explained in part by unfavourable preservation, though in part have at most the value of specific characters, I am in a position to propose a great similarity of *Adriosaurus* with *Acteosaurus, Pontosaurus* and *Dolichosaurus*.

The development of the limbs, which is strongly reminiscent of *Acteosaurus*, is to be stressed as a minor, though perhaps generic difference from *Pontosaurus*.

As only twelve dorsal vertebrae are preserved, the number of presacral vertebrae can not be even approximately determined; though I believe on account of the similarity of our animal in other respects with the other Dalmatian lizards hitherto discussed, that here too one could accept 13 cervical and 26 dorsal vertebrae.

Dolichosaurus

The similarity of *Dolichosaurus* with *Pontosaurus*, that of *Acteosaurus* with these and the close relationship of the last two with *Adriosaurus* have already been emphasised; and a further comparison of this last-named, anteriorly incompletely known form with *Dolichosaurus*, only known anteriorly, would be difficult to carry out and also, as it seems to me, easy to do without. It will hence be proposed here for the first time that *Dolichosaurus, Acteosaurus, Adriosaurus* and *Pontosaurus* belong together.

Omphalosaurus

In *Opetiosaurus* we meet a totally different type. But as the comparison of *Opetiosaurus* and its kind with the *Dolichosaurus*-like forms will be carried out in a section of its own, our next task is only to compare *Opetiosaurus* with the remaining Neocomian lizards of Dalmatia.

Carsosaurus

The first thing to note is a great similarity between *Opetiosaurus* and *Carsosaurus*. In *Opetiosaurus* 28, in *Carsosaurus* 24 + x (28?) presacral vertebrae can be observed, and indeed according to Kornhuber in *Carsosaurus*, where the thoracic ribs are preserved in situ, 21 dorsal and 3 cervical vertebrae can be distinguished. The first dorsal vertebra is here regarded as the one on which the first large rib is observable. If the same criterion is applied to *Opetiosaurus*, in which the order of the ribs is less distinctly observable, one obtains on the trunk section of this saurian, likewise, 21 dorsal and 4 cervical vertebrae. On the skull section of *Opetiosaurus* I now believe, like Kornhuber, that I can count three cervical vertebrae and in this way I obtain the same number of vertebrae as in *Carsosaurus* and also *Aigialosaurus.*

The ribs in *Carsosaurus* are about 4, in *Opetiosaurus* about 5.5 times shorter than the whole presacral vertebral column; the forelimb in the former is somewhat more than 3 times, in the latter exactly 3 times, the hindlimb in both 2.5 times shorter than the same body length.

The ratio of the upper and lower arm to upper and lower leg is in both likewise approximately the same, and the forelimb is in the following ratio to the hind:

in *Carsosaurus* as 11 : 11 (1 : 1),
in *Opetiosaurus* as 11 : 13.

Apart from these ratios of measurements, the following similarities and differences can be noted:

	Carsosaurus	***Opetiosaurus***
Cervical vertebrae:	Spherical hypapophyses.	Spherical hypapophyses showing a projecting keel anteriorly.
	Both lack that median furrow on the centrum which is noticeable on the dorsal vertebrae.	
Dorsal vertebrae:	The centra of the anterior thoracic vertebrae resemble the cervicals, and the centra of the posterior vertebrae show a furrow on their base bordered by lateral ridges, which are absent from the anterior thoracic and all cervical vertebrae in both forms. The largest dorsal vertebrae are noticeable in the middle of the back.	
	Length of dorsum 63 cm.	Length of dorsum 38 cm.

Sacral vertebrae:	The two sacral vertebrae in both forms are shorter than the presacral vertebrae, the transverse processes are strongly developed in both animals.	
	They are built on the type of the tail vertebrae, their centra are broad and stocky.	They are more reminiscent of the presacral vertebrae and provided with a longitudinal furrow on the base.
Caudal vertebrae	and haemapophyses are similarly developed in both forms.	
Ribs,	sternal and intermediate pieces are present in both reptiles, the following 'false ribs' show a quite significant length.	
	The seven last ribs are noticeable for rapid decrease in size.	The rapid decrease in size is only visible on the last five ribs.

As is clear from this summary, there are indeed differences between *Carsosaurus* and *Opetiosaurus*, whose specific value stands beyond doubt, but whose value in a generic separation could only be accorded slight worth, so that in time (if the skull of *Carsosaurus* becomes known) perhaps a unification of the two genera will come to seem necessary. In any case these two forms stand so close to one another that one is justified in reconstructing one based on the other.

Aigialosaurus

With this type (*Carsosaurus-Opetiosaurus*) we have now to compare *Aigialosaurus.* Its skull is indeed much more slender than in *Opetiosaurus* [footnote: It is to be remarked that our skull reconstruction differs somewhat from the indication of the skull impression given by Kornhuber (pl. II)] (compare Pl. I, Figs 2, 3), though the peculiar quadrate is built almost identically in both forms, and these skulls also show the same type in the arrangement of individual elements. The length of the skull in *Aigialosaurus* comes to 7/21, in *Opetiosaurus* 6/21 of the presacral portion of the vertebral column. Cervical vertebrae in *Aigialosaurus* are counted by G. Kramberger as 7, dorsal vertebrae 20. Boulenger made the following remarks on this in his frequently cited work: "I would therefore say that *Aigialosaurus* had nine cervical vertebrae or even ten in the event of the atlas having been overlooked."

In agreement with this author I regard it as certain that in *Aigialosaurus* the atlas is not preserved, and this principally because of the first illustrated cervical vertebra, which I could convince myself is certainly an axis. Moreover it can also be determined that the larger ribs, as in *Opetiosaurus* and *Carsosaurus*, begin with the seventh known vertebra (which would thus correspond to the eighth vertebra), and the cervical and thoracic region of *Aigialosaurus*, as in the other two reptiles mentioned, is made up of 28 presacral vertebrae, which probably

In contrast to *Carsosaurus* however, the ribs in *Aigialosaurus* are perhaps somewhat shorter [footnote: The complete length of the ribs is at this time unknown, but in any case they have a quite considerable length], and also the ratios of the limbs to each other and to the presacral vertebral column are not the same; the first comes to

in *Aigialosaurus* 11 : 14,
in *Opetiosaurus* 11 : 13,
in *Carsosaurus* 11 : 11 (1 : 1)

and hence *Aigialosaurus* is in this point somewhat reminiscent of *Opetiosaurus*.

Moreover, some errors occur in G. Kramberger's description of *Aigialosaurus* : the so-called hypapophyses of the cervical vertebrae are present in **pairs**, and **in any case not hypapophyses but cervical ribs**. Only on the original third cervical vertebra is the small hypapophyses correctly known. G. Kramberger's two illustrations represent the region from the 4th to the 7th cervical vertebrae quite unreliably. The ribs are in reality shaped quite differently than is apparent from the drawing. Where Kramberger writes 'sc.' (scapula) on plate II, a coracoid is distinctly visible. The metacarpals of the right foot likewise lie quite differently than they are shown in G. Kramberger's sketch. The most important thing is the fact that *Aigialosaurus*, by its only known hypapophysis, does not differ essentially from *Opetiosaurus* (cf. Kornhuber 1901: 20, where the hypapophyses of *Aigialosaurus* have already been indicated as cervical ribs by this prominent researcher).

Mesoleptos

The specimen is unfortunately badly preserved, but in any case 22 ribs and numerous trunk vertebrae can be recognised; from the great reduction in rib size anteriorly it even seems that the first [thoracic] rib is preserved, and this allows us to conclude there were 27 dorsal vertebrae. [footnote: It is not uninteresting to note at this point the difference between *Clidastes* with 42 and *Tylosaurus* with 30 precaudal vertebrae.] There is no skull, neck, pelvis, shoulder girdle or forelimb, the poorly preserved hindlimb seems relatively small. The long ribs as well as the shape of the vertebral centra (cf. in G. Kramberger's work on *Aigialosaurus*) resemble *Opetiosaurus*.

Gorjanovic-Kramberger emphasises the varanid nature of this fossil and separates it from the Dolichosauria, and it is precisely the varanid nature of *Opetiosaurus* that was recently so excellently stressed by Kornhuber. In this way I see, apart from the number of vertebrae, no compelling grounds to place *Mesoleptos*, despite being somewhat differently built, in a different family from *Opetiosaurus*, *Carsosaurus* or *Aigialosaurus*.

So we see how all the Dalmatian Neocomian lizards arrange themselves in **two sharply separate groups**: **one group comprises the long-necked genera *Dolichosaurus*, *Pontosaurus*, *Acteosaurus* and *Adriosaurus*, the other the short-necked and large-headed genera *Aigialosaurus*, *Carsosaurus*, *Opetiosaurus* and (?) *Mesoleptos***

The similarities and differences of these two groups can best be expressed by the following summary.

	A. *Pontosaurus* Type	**B. *Opetiosaurus* Type**
Skull	6-10 times shorter than the presacral vertebral column, small and lightly built. Quadrate probably slender*.	3-4 times shorter than the presacral vertebral column, robustly built. Quadrate pythonomorph.
Vertebral column	39 presacral vertebrae, of which 13 are allotted to the neck, 26 to the trunk. The cervical vertebrae decrease in size quite significantly anteriorly. The trunk vertebrae are just as wide as long.	29 presacral vertebrae, among which 7 cervical and 21 thoracic vertebrae can be counted. A significant decrease in size of the anterior cervical vertebrae is not noticeable. The trunk vertebrae are longer than wide.
Ribs	The ribs are proportionally very short and the body is hence pronouncedly cylindrical in shape. Ventral ribs (sternal and intermediate pieces) are not present.	The ribs are proportionally long, which produces a stockier body shape. Ventral ribs are very strongly developed.
Limbs	The forelimb is very strongly reduced, its length is contained in the presacral vertebral column 5 times, and its proportion to the hindlimb is approximately 1 : 2. The hind foot shows a primitive type according to Boulenger.	The forelimb is only insignificantly reduced, it is only 3 times shorter than the presacral vertebral column and its proportion to the hindlimb is about 1 : 1. On the hind foot the varanid modification of the fifth metatarsal is pronouncedly noticeable (cf. Pl. II, Figs 8, 9)

*It is a mistake to ascribe to *Pontosaurus*, built totally unlike *Aigialosaurus*, an aigialosaur-like quadrate (cf. G. Kramberger 1901).

It is necessary to note just at this point that Boulenger found primitive features in the foot structure of *Pontosaurus* and wished to derive the foot of the varanids and pythonomorphs from it, while Baur flatly denied the primitive foot structure in *Pontosaurus* (cf. Pl. II, Figs 5, 8, 10).

Incidentally, Kornhuber already recognised the most basic difference noticeable between *Acteosaurus* (a representative of the Dolichosauridae) and *Carsosaurus*, and in the description of *Carsosaurus* he said the following: "**There can thus be no talk of our fossil belonging together with *Acteosaurus*. Indeed they differ so much in the cited characters that the animal described here does not fit at all in the family Dolichosauridae, but rather is closer to the Varanidae.**"

Thus we now see how a whole series of quite constant important differences sharply separate the two groups of Dalmatian lizards, dolichosaurs and aigialosaurs, and I regard it as necessary, in order not to [over-]expand the palaeontological nomenclature, to name these groups (families) Dolichosauridae and Aigialosauridae.

The Dolichosauridae, which do not fully correspond to Gorjanovic-Kramberger's Dolichosauridae, are **characterised by a small head, numerous presacral vertebrae, a cylindrical body cavity not closed below by ventral ribs, and strongly reduced forelimbs**, while the Aigialosauridae, likewise not identical to Gorjanovic-Kramberger's family of the same name, **are distinguished by a large head, relatively few presacral vertebrae, a more stocky body and less reduced forelimbs**.

Our scheme differs from the classification of Gorjanovic-Kramberger in that he included in his Aigialosauridae all the dolichosaurs of the new grouping, with the exception of *Dolichosaurus*, and created the family Dolichosauridae for the latter alone. It is strange that Gorjanovic-Kramberger, in his last work on these matters - where he refers to Boulenger - does not mention that Boulenger already spoke out against this classification.

Passing on to the third section of our examinations, we have to discuss the phylogenetic relationships of the Dolichosauridae and Aigialosauridae to the varanids, pythonomorphs and, for the sake of completeness, also with *Pleurosaurus* :

Relationships to *Pleurosaurus*

Neither in the dolichosaurids nor the aigialosaurids can a greater similarity with *Pleurosaurus* be found. Yet *Pleurosaurus*, according to Boulenger likewise a lacertilian, according to Dames certainly a rhynchocephalian (cf. Pl. I, Fig. 6), recalls the Dolichosauridae to some extent by its large number of presacral vertebrae (42) as well as the strong reduction of the forelimbs, though it is distinguished fundamentally by numerous points from this family as well as from the Aigialosauridae.

The size of the skull and the number of cervical vertebrae (7) [footnote: Lortet gives five cervical vertebrae, Boulenger counts nine of them, I myself believe I can determine seven cervical vertebrae based on the illustration] are the only features which *Pleurosaurus* and *Opetiosaurus* have in common, the structure of the skull (Pl. I, Fig. 6), the biconcave dorsal vertebrae, the rod-shaped neurapophyses, the haemapophyses closed at their proximal end, and the limbs themselves are completely different in structure from those of our reptile, apart

from which *Carsosaurus* and *Pleurosaurus* can be very well distinguished by their integument (cf. Pl. II, Figs 12 and 14). Also there can be no talk of *Pleurosaurus* somehow occupying an intermediate stage between the aigialosaurids and dolichosaurids, for it shows pronounced specialisation in the structure of its very short neck and the reduction of the forelimbs. *Pleurosaurus* must therefore be designated as a reptile that, apart from convergence phenomena called forth by an aquatic way of life, shows no further similarity to the dolichosaurids and aigialosaurids.

Relationships to Varanids

Significantly greater are the similarities which our reptiles, especially the aigialosaurids, show with the varanids.

a) Dolichosauridae

These are distinguished from the Varanidae by the smallness of the head, the great number of cervical and thoracic vertebrae, further in that the first ones decrease significantly in size towards the head, by the strong reduction of the forelimbs and the shape of the tarsus and metatarsus; while otherwise, as Kornhuber proposes, they are strongly reminiscent of the varanids (*Hydrosaurus*). From Kornhuber's work only the following parts should be lifted: "Among the saurian families only the lacertilians or true lizards have similar properties of the foot to those our fossil shows, namely five toes provided with curved, laterally compressed claws, of which the fourth toe, provided with five phalanges, exceeds the others in length. Hereby the Lacertines differ, as is well known, from the Ascalabota with their short almost equal-toed feet, as well as from the Chamaeleontids with slender toes split into two opposable groups. Our fossil can not be brought together with the family of Iguanoids on account of the significantly high number of its vertebrae in the trunk and tail - a differentiating character which also applies for the previously mentioned families - which ... only the monitors meet... The head of the fossil shows at first a surprising similarity with that of a recent *Varanus* from Sydney... But as much as there is agreement of the head with related creatures of today, the proportions of the other parts of the skeleton differ as widely... Thus the Sydney *Varanus* has only twenty dorsal vertebrae..."

It seems in this way that the dolichosaurs, among all recent lizards, on the one hand stand closest to the varanids, while on the other hand Boulenger and Hermann v. Meyer stress their similarity with the Anguidae.

The differences which exist between Baur's and Boulenger's interpretation of the *Pontosaurus* foot have already been stressed, and thus I believe, putting it all together, that one can accept Baur's interpretation, as a result of which at this stage only a relationship of the dolichosaurs with Varanidae or Anguidae can be determined. [In English] "**From all that we know it seems to me that the Dolichosauridae are related to Anguinidae or Varanidae.**"

b) Aigialosauridae

The similarities of the Aigialosauridae with the Varanidae can be followed even further than was the case for those of the dolichosaurs, indeed they are so great at first sight that Kornhuber was almost satisfied to place *Opetiosaurus* in the genus *Varanus*. "From the structure of the skeleton one would almost have tried to place it immediately in this speciose lineage (*Varanus*), were it not that the properties of its... teeth... exclude it from the genus *Varanus* and from all other lacertilians." Indeed I now believe that the similarity is not quite as great as Kornhuber stressed, as some important factors are present which separate *Opetiosaurus* from the varanids, but in any case the structure of the skull roof (Pl. I, Figs 1, 2, 3), the number of presacral vertebrae, the modification of the fifth metatarsal, the presence of ventral ribs (sternal and intermediate pieces), the ratio of tibia to femur (1 : 1) and the shape of the vertebral centra, can be determined as important common points. The Aigialosauridae can be distinguished from the varanids by: the shortening of the limbs called forth as a result of an aquatic lifestyle; the more complete structure of the jugal bone; the **articulation of the angular and splenial** which apparently took place (which can be followed from the thickening of the opposing ends of the same [footnote: In *Aigialosaurus* these two elements are separated from each other by 1 mm], see Kornhuber 1901, pl. I), **the structure of the teeth**, **the shape of the quadrate**, the size of the skull, **the number of cervical vertebrae** (7), as well as the **shape and arrangement** of the rhomboidal **scales**. Incidentally the arrangement of the scales was also already stressed by Kornhuber as a differentiating character. "A further, not insignificant difference is finally to be seen in the shaping of the integument." As a last difference, Kornhuber puts forward the manner in which the sternal ribs relate to the sternum:

"... Such are the generically significant differences in the structure of the rib-cage. Specifically, in the monitor only three pairs of ribs take part... But our fossil from Komen clearly has five true rib pairs, which are all attached to the posterior margin of the sternal cartilage" (cf. Pl. I, Figs 7, 8). As those two small bones which project caudally beside each other from the midline of the sternum (Kornhuber's 'xiphosternum'), can perhaps also be interpreted as sternal ribs, I believe that in *Carsosaurus*, and correspondingly perhaps also in *Opetiosaurus*, six pairs of true ribs can be accepted (cf. Pl. I, Figs 7, 8). However this may be, in any case along with some differences a very significant similarity can be noted between the aigialosaurids and the varanids.

Relationships to Pythonomorpha

a) Dolichosauria

Only few characters in the dolichosaurs recall the Pythonomorpha, namely the reduction of the limbs in general, and besides the high number of presacral vertebrae - though the dolichosaurs have this in common only with a few pythonomorphs, specifically *Clidastes*, in which 42 presacral vertebrae have been noted, while this number is only 30 in the other pythonomorphs. Differences between the dolichosaurids and pythonomorphs are to be found in the skull structure, the number of cervical vertebrae, the size of the ribs and lack of ventral pieces, the reduction of the forelimbs, the stronger pelvis and shoulder girdle in the former, and finally yet from the previously mentioned *Clidastes*, that in this the haemapophyses co-ossify with the vertebral centra, while they constantly appear free in the dolichosaurs. The foot of *Pontosaurus* can only with difficulty be compared with that of *Platecarpus* (Pl. II, Fig. 10). Also Osborn speaks out against a relationship of Dolichosauridae and pythonomorphs: [in English] "There are positively 7 cervicals [in *Tylosaurus*] and this point is of considerable importance, as bearing against the supposed Dolichosaurian affinities with the Mosasaurs."

b) Aigialosauridae

The most essential differences between the Aigialosauridae and Pythonomorpha are located in the shape of the individual vertebrae, the strong development of the sacrum, pelvis and shoulder girdle, the presence of clawed feet in the first, and in that the skull of *Opetiosaurus* and *Aigialosaurus* is relatively smaller than those of *Tylosaurus* or any other pythonomorph. Against these differences can be given as common characters **the dentition** of *Opetiosaurus*, **the shape of its quadrate** [footnote: cf. also G. Kramberger's drawing of the quadrate of *Aigialosaurus* ; 1892: pl. III, fig. 2], **the articulation of the splenial and angular**, **the equal number of cervical vertebrae**, **the number of dorsal vertebrae**, which differs only insignificantly from most pythonomorphs, and **the shape of the scales** (cf. Pl. II, Figs 11, 12). Additionally, somewhat reminiscent of the pythonomorphs is the **attachment of the ventral ribs to the sternum** (cf. Pl. I, Figs 8, 9) as well as the broad foot of *Opetiosaurus*, which takes up a kind of intermediate position between the walking foot of *Varanus* and the paddle of the pythonomorphs (Pl. II, Figs 8, 9, 10).

These similarities and differences having been determined, we can pass on to the last part of our examinations and investigate whether any of the new forms spread some light over the phylogeny of the pythonomorphs. Before this happens, though, it would be good to give a short recapitulation of the different recent views over the pythonomorphs in general.

Boulenger says the following on the descent of the pythonomorphs: [in English] "Gorjanovic-Kramberger describes a new form *Aigialosaurus* which shows points of affinity

group named Ophiosauria to comprise the Aigialosauridae and Dolichosauridae... Kramberger is therefore fully justified in regarding this type [meaning *Aigialosaurus* in particular] as one of the original stock from which the Varanoids and Mosasaurs are derived." In the course of the further work the foot structure of *Pontosaurus* was touched on, this was designated as primitive and its allegedly intermediate position between the varanid and the pythonomorph foot stressed. For the descent of the mosasaurids the following schema was given:

Dolichosauria (G.-Kramb.)
Pythonomorpha _
Varanidae _ [unresolved trichotomy]
Ophidia _

For all the Squamata the following classification was given:

Ordo Squamata.

A. Pectoral arch or its rudiment present, caudal hypapophyses forming chevrons.

Dolichosauria: 15-17 cervical vertebrae, extremities archaic.

Pythonomorpha: 9-10 cervical vertebrae, extremities paddle-shaped. - Hyperphalangy.

Lacertilia: 8-9 cervical vertebrae. Fibula reduced proximally. Vth metatarsal reduced in length and strongly modified.

Rhiptoglossa: 5 cervical vertebrae, extremities pincer-shaped, all metatarsals reduced in length and strongly modified.

B. No trace of pectoral arch, caudal vertebrae [JS: haemapophyses] disconnected distally.

Ophidia.

This classification of Boulenger is opposed by the North American herpetologist **Baur**: [in English] "It is evident that the Mosasauridae are closely related to the Varanidae, they simply represent highly specialized aquatic forms. There cannot be any doubt whatever that the hind foot of *Hydrosaurus lesinensis* has no trace of any archaic structure, not approaching in any way whatever the Batrachian type."

Speaking of the cervical vertebrae, he says further: "All the generalized Squamata originally showed this number [i.e. 8]. -- That the Dolichosauridae are not ancestral to any of the larger groups of Squamata is absolutely evident. I do not see any difficulty in assuming that the Mosasaurs developed from unguiculate Lacertilia which were very close to the Varanidae."

Merriam puts forward the following as characteristic for the skull structure of the pythonomorphs: "The quadrate is distinguished by its shape from the quadrate bone of all other reptiles. The lower jaw agrees in general with that of the lizards, but differs in that a well developed joint is formed between splenial and angular. On the caudal vertebrae of *Tylosaurus* and *Platecarpus* the chevron bones [English!], which in *Clidastes* grow together with the vertebral centra, are flexibly attached. As differences in cranial osteology of *Varanus*

and *Platecarpus* only the following would be mentioned: the quadrate is longer, narrower and the supracollumellar process at the proximal end very small. The processes of the exoccipitals, which extend over the dorsal side of the hypapophysis [sic] of the basioccipital, are very broad and vertically flattened, the superior occipital is very broad dorsally, the wing-bones [pterygoids] are edentulous."

Williston (1898) says the following on the pythonomorphs: [in English] "The more important cranial differences from *Varanus* are as follows: The premaxillary of *Varanus* is flattened and the conjoined nasals are united by a distinct suture. There are 8 premaxillary teeth. The nares are much larger, the prefrontals smaller, the palatine smaller and its anterior process longer, the lacrymal bone is larger. There is a superciliare present, wholly wanting in all Mosasaurs. The frontal bones are united by suture, the jugal is incomplete, the transverse bone unites with the maxillary and jugal, the pterygoids are without teeth, the basipterygoid processes are longer and the pterygoids hence much more widely separated. The basioccipital processes are much smaller, the exoccipital elements larger, the quadrate is more slender and has no suprastapedial process, the splenial and presplenial [=angular and splenial] interdigitate and do not unite by distinct articulation, the presplenial extending much further proximally and articulating with the coronoid, the sides of the parietal are not decurved to form the sides of the braincase, anteriorly there is a frontal subrhinencephalic bridge... The vertebrae of *Clidastes* may readily be distinguished... by the presence of a more or less complete zygosphene... While in *Clidastes* there are as many as 42 precaudal vertebrae, in *Tylosaurus* and *Platecarpus* there are not more than 30... In paddles and skull *Tylosaurus* is more specialised than any other genus, however. Although *Clidastes* may retain some of its primitive characters, it certainly shows in many other respects a high degree of specialization." Additionally, the formation of a fin at the end of the tail, which comes about by local greater development of the neurapophyses and haemapophyses, is especially stressed.

Osborn has given the latest reports on mosasaurs: [in English] "The exposure of the left pterygoid is interesting because it displays a large fossa for the epipterygoid. This element itself is probably represented by a large rod-like bone lying beneath the basisphenoid... Below the jaw is a small element which can only be identified as a portion of the supraciliare. The facts derived from this skeleton do not strengthen Baur's extreme opinion as to the intimate connection of this type with the Varanidae. There are certain fundamental differences in the basioccipitals and ribs, in fact in all parts of the skeleton. These differences fully balance or overweigh the likenesses and do not even justify the assertion that the Varanidae and Mosasaurs sprang from a common stem. The only conclusion we are absolutely warranted in drawing is the following: The Mosasaurs are a very ancient marine offshoot of the Lacertilia presenting a few resemblances in the skull to the Varanoids... Basioccipitals with prominent basipterygoid processes which are lacking in *Varanus*... The sternocoracoid plate thus corresponds closely with the lacertilian type and

bears a general resemblance to those of *Trachydosaurus*, *Varanus* and *Cyclodus.* Axis and atlas more complex and primitive than in any recent lizard or in *Sphenodon.* Manus and pes with abbreviated Vth metapodials."

If we now put all that has been said here together, we see how the different authors who have been concerned with the mosasaurids arrive at seemingly diametrically opposed conclusions, and how except for the development of the paddle organs, the teeth and the lower jaw, it is impossible to find one feature characteristic exclusively for the pythonomorphs.

Under this illumination, the possibility of the descent of the pythonomorphs from the aigialosaurids should now be discussed. For the time being let it be emphasised that the aigialosaurids are such that they perfectly correspond to Baur's and Boulenger's postulates.

Baur wants pronounced varanid characters from the ancestors of the pythonomorphs, and Boulenger himself admits that *Aigialosaurus* could quite probably be a precursor of the Pythonomorpha. If Baur polemicises against Boulenger's assumption, especially where the foot of *Pontosaurus* is concerned, this is in any case fully consistent with the aigialosaurid-mosasaurid relationship, for *Pontosaurus* is totally unrelated to the aigialosaurids. Even the objection that Osborn makes against the descent of the mosasaurs from dolichosaurs becomes invalid if one separates the latter sharply from the aigialosaurids.

The only characters which can be offered as differentiating the aigialosaurids from the varanids are those points in which the Aigialosauridae approach the pythonomorphs, while on the other hand it is typical varanid characters which separate the aigialosaurids from the pythonomorphs.

As we now recognise in the aigialosaurids a mixture *par excellence* between varanids and pythonomorphs, it is easy to go a step further and take account of the differences which, becoming ever more prominent, eventually separate the mosasaurs so distinctly from the varanids.

1. The slender **skull** of *Clidastes* (Pl. I, Fig. 4) resembles that of *Aigialosaurus* (Pl. I, Fig. 3) much more than that of *Platecarpus* (Pl. I, Fig. 5) or the similar skull of *Tylosaurus*. Thus an enlargement of the most anterior part of the body is noticeable, as we can observe in some swimming animals.

2. **Vertebrae**. As *Tylosaurus* and *Platecarpus* with their 30 presacral vertebrae stand closer to the aigialosaurids than *Clidastes*, the assumption that an increase in the number of vertebrae took place in *Clidastes* is not without all basis; incidentally the specialisation in the structure of the chevrons also shows a stronger deviation from the aigialosaurid type than is the case in *Tylosaurus* or *Platecarpus*, which in any case is again compensated by the fact that *Tylosaurus* and *Clidastes* developed a tail fin, which is lacking in *Platecarpus* and the aigialosaurids. One can also see an analogous structure in the tail fin of *Geosaurus* (cf. Pl. II, Figs 1-4). The primitive structure of the cervical vertebrae can be interpreted as a reduction in consequence of the aquatic lifestyle.

3. **Sternal structures**. A third point in which our Aigialosauridae take up a pronouncedly middle position between the recent varanids and the pythonomorphs is the sternum. In *Varanus* only three ventral ribs articulate with it, in *Carsosaurus* already six, in *Tylosaurus* finally not less than ten. An episternum seems not to be present in *Tylosaurus*, but probably it is handed down to us by *Platecarpus* (Pl. I., Figs 7, 8, 9).

4. **Pelvis**. In the pelvis *Carsosaurus* agrees perfectly with the varanids, and the reduced pelvis of the pythonomorphs can easily be explained as its pelagic modification.

5. **Extremities**. The broad feet of *Opetiosaurus* stand between the walking foot of the varanids and the pythonomorph paddles. No weight at all can be placed on hyperphalangy, and the paddles of the mosasaurids (Pl. II, Fig. 10) are thus related to the clawed foot of *Opetiosaurus* (Pl. II, Fig. 9) in an analogous way to that in which the paddle of *Geosaurus* (Pl. II, Fig. 7) is related to that of its likewise clawed ground-form, which may perhaps have been not unlike the foot of *Alligator* (Pl. II, Fig. 6).

From the figures given (Pl. II, Figs 5, 9), at the same time the difference of the *Pontosaurus* and *Opetiosaurus* feet can easily be seen.

What we can surely determine from the total of our examinations is thus the following:

1. The Pythonomorpha are descended from the Aigialosauridae.

2. The Aigialosauridae already show phenomena of adaptation to aquatic life (structure of the foot).

3. Aigialosauridae and Varanidae have common (Jurassic) ancestors, which as terrestrial reptiles must have been very similar in structure to the varanids.

If we now regard the Pythonomorpha as a distinct suborder on account of their prominent pelagic specialisation, it is self-evident that the Aigialosauridae must be included as an independent family of Lacertilia in the vicinity of the Varanidae.

The Dolichosauridae represent just a distinct family of the same suborder [Lacertilia], as yet unclear with regard to descent.

Diagnosis of the new families.

Order Squamata.

Suborder **Lepidosauria**.

Family: **Dolichosauridae** G. Kramb. emend.

Varanid-like, head small. Long neck of 13 vertebrae decreasing in size anteriorly, 26 trunk, 2 sacral and numerous caudal vertebrae. Body cylindrical and elongate. The short ribs all approximately equal in length, ventral ribs not present. The extremities strongly reduced; the forelimbs only half as long as the hindlimbs. Hand and foot somewhat simplified due to reduction. Pelvis and shoulder girdle moderately developed (Neocomian).

Genera: *Dolichosaurus* Owen.

Acteosaurus Meyer.

Pontosaurus G.-Kramberger

Adriosaurus Seeley.

Family: **Aigialosauridae** G. Kramb. emend.

Varanid-like lepidosaurs with large pythonomorph-like skull, short neck consisting of 7 vertebrae, 21 trunk, 2 sacral and numerous caudal vertebrae. Trunk stocky, ribs long and strongly curved. Six ventral ribs meet in articulation with the sternum. Fore- and hindlimbs approximately equally long and only slightly reduced. Hand and foot broadened. Vth metatarsus modified as in the varanids. Shoulder and pelvic girdle well developed (Neocomian).

Genera: *Aigialosaurus* G.-Kramberger.
Carsosaurus Kornhuber.
Opetiosaurus Kornhuber.
?*Mesoleptos* Corna[g]lia.