Eidolosaurus and *Pachyophis*

Two new Neocomian reptiles

by

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Eidolosaurus und *Pachyophis* : Zwei neue Neocom-Reptilien
Palaeontographica **65**: 96-154, Plates VII-VIII (**1923**)

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INTRODUCTION

When I published my overview of the fossil lizards in 1908, the genera *Opetiosaurus* (Kornhuber 1901), *Aigialosaurus* (Gorjanovic-Kramberger 1892), *Pontosaurus* (Kornhuber 1871) and *Adriosaurus* (Nopcsa 1908) were well known, *Acteosaurus* (von Meyer 1860) and *Carsosaurus* (Kornhuber 1893) less well, while only fragments of *Mesoleptos* (Nopcsa 1903) were available. Through the acquisition of new slabs, of which one is held in the Geologische Staatsanstalt, two in the Naturhistorisches Museum in Vienna, our knowledge of the diversity of Neocomian squamates has recently been expanded.

The slab found in the Geologische Staatsanstalt shows the impression of a quadrupedal animal which I name *Eidolosaurus*, on those of the Naturhistorisches Museum the remains of three snakelike forms are visible, for which I choose the name *Pachyophis*.

Some of the photographs of these remains presented in Plate 1 [Pl. VII] are those of Frl. Lotte Adametz in the Geology Department of the Naturhistorisches Museum in Vienna, the others were taken in the Vienna main library.

I thank the management of the Geologische Staatsanstalt in Vienna, and also that of the Geology Department of the Naturhistorisches Museum, for allowing me to prepare and describe both of these valuable specimens.

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1ST PART: *EIDOLOSAURUS*

1. General

When I set eyes on the *Eidolosaurus* slab, which had been first discovered on the occasion of the demolition of a house, there was almost nothing left of the original mass of bones, and in place of the bones one saw in most places just their quite well-preserved impression. In places even the finest details were visible, only the end of the tail was indistinct. In order to conveniently make a clear photographic reproduction of the piece, the last remains of the bones were first removed from the original slab, then a plaster cast was made and this was examined with low-angle lighting from varying directions. In this way even the gentlest relief was made visible. An illustration of the cast with such low-angle lighting is given in Plate VII.

As the cast shows, the anterior part of the animal lies in general on its back, thus presenting the ventral surface to the observer, while the unusually large tail, detached from the anterior part, lies on its side.

Behind some skull fragments follow the cervical and trunk vertebrae in undisturbed sequence. In the shoulder region they have suffered a barely visible interruption, as will be shown later. The ribs are preserved on the left in their natural position, on the right all the anterior ones have their ventral ends reversed, that is directed cranially. The posterior ribs on the right also retain their natural position.

The only major disturbance in the skeletal remains of our beast appears just before the sacrum. Here the natural articulation of the vertebral column is interrupted. The sacrum and the tail are rotated through approximately 160˚; the posterior end of the tail lies over the forelimb and is directed almost cranially. The hindlimbs are both still in tight association with the girdle, and lie directed diagonally backwards, regularly on both sides of the sacrum.

The disturbance in the pelvic region demands a few words, for it is also noticeable in almost all other lizards known from Istria. In *Acteosaurus* there is a dislocation of the vertebral column visible anterior to the sacrum and also one behind; in the London specimen of *Adriosaurus* there is a weak dislocation before the sacrum and a strong one just behind the presumed region of the anus; in the Vienna specimen the only, rather strong dislocation lies just behind the sacrum. In *Pontosaurus* one can observe weak disturbances of the vertebral column lying before the sacrum and in the anal region.

Similar dislocations, obviously facilitated by the gases of putrefaction of the digestive tract as in the dolichosaurs, are also noticeable in the aigialosaurs, though to a weaker extent; but what the aigialosaurs always lack is the deflection or folding-over of the tail which is common in the dolichosaurs. One could take this folding-over to be a disturbance to the corpse caused by a carnivore, but there are factors which speak against this.

In most of the dolichosaurs, almost all the other bones of the skeleton lie in undisturbed positions, but our new fossil shows in addition a displacement, in the same direction as that of the tail, of several of the ribs of the right side, which have been moved away from the body. This rotation of the ribs indicates that the force responsible for the displacement of the tail also affected the whole body in the course of putrefaction, whereby the concave side of the body naturally offered a better surface of attack than the convex one. Instead of a local attack by carnivores, one must think of an influence working overall. As the long haemapophyses of our new fossil indicate, the animal had a long and broad, oarlike tail, which naturally presented a large surface of attack for any water current, and for this reason a displacement of the posterior part of the body could follow immediately with the inception of putrefaction. Especially in our fossil this displacement of the tail must have occurred by a movement of water directed diagonally craniad and against the ribs. As the displacement of the tail referred to here is constantly absent in the aigialosaurs, we can conclude that they lacked a broad oar-like tail.

2. Description of the remains

1. The Skull. Unfortunately only a small piece of the skull of our reptile is visible. It shows a generally triangular shape, pointed anteriorly. Posteriorly its outline shows two dents with a caudally directed prominence between them; one could almost take this to be the occipital condyle, but the possibility is not excluded that it is the medial, basal part of the atlas. On the sharply tapering posterior skull roof on the left side, one supposes the suspensorium of the quadrate bone can be seen, in this case short and rod-like. Directly opposite the putative occipital condyle lies an awl-like process; I take this to be the parasphenoid. Between the condyle and this process lie the basioccipital tubera, 3 mm apart. From these, two ridges run towards the parasphenoid rostrum. The pterygoid processes of the basisphenoid are not preserved; but what is preserved is reminiscent of the proportions of some agamids (*Gonyocephalus*). The presence of strongly developed basioccipital tubera is of some significance. In *Varanus* these knobs seem mostly to be missing, but they are present in other lepidosaurs including *Megalania* and the mosasaurs.

In general the skull base of our animal indicates a quite lightly built skull ca. 6 cm long.

To the left of the remains of the skull a small, curved ?projections ['*Erhabenheit* = 'grandeur', but *erhaben über etw.* = to be above or beyond something] is visible, separated from the skull. From the shape, size and position this corresponds to a rod-like quadrate, but unfortunately the weathering of the negative slab prevents a conclusive decision. While there is thus only very little known of the skull, its remains are nevertheless important on account of it, because they determine the length of the cervical vertebral column.

2. The vertebrae and ribs. The vertebral column of our animal remains anteriorly in articulation with the skull. In total 34 presacral, 2 sacral and, in present condition, 48 postsacral vertebrae are present.

Of the atlas the two flat lateral parts are distinctly visible. Behind the pieces of the atlas and partly also between them lies the epistropheus [axis]; the posterior end of the epistropheus is perhaps somewhat hidden by the third cervical vertebra. The length and position of the next cervical can not easily be determined precisely, but in general the length of the following vertebra seems to marginally exceed its width. Behind the epistropheus follow at least three rib-free vertebrae; in contrast remains of a rib possibly belong to the following already, thus the sixth cervical. This is a small bone fragment, which one can find on the left side of the seventh vertebral centrum. That the seventh vertebra itself, in any case, was already provided with cervical ribs, can be shown by the presence of small awl-shaped ribs on either side. The isolated hypapophyses of the second to seventh cervicals were quite strongly developed; in the cast one sees them as small, compressed and longitudinally directed lumps, which lie on the posterior part of these vertebrae. The 4th and 5th hypapophyses are the strongest. The epistropheus apparently bore two hypapophyses, as in *Varanus*; the posterior one lay relatively far forward. The eighth, ninth and tenth vertebrae differ somewhat from the preceding ones by their breadth. Instead of rectangular outlines they show a more square shape. Also these three vertebrae are provided with needle-shaped cervical ribs. The length of the cervical ribs increases quite markedly from anterior to posterior; the seventh rib has a length of only 5 mm, the ninth already measures 11 mm, the tenth can be followed for a distance of 16 mm.

Unfortunately the proportions are somewhat unclear where one expects to see the eleventh and twelfth vertebrae, for adjacent to the centra of these two vertebrae one sees on one side another elongate bone, which probably corresponds to a humerus, and on the other side lies part of a shoulder girdle; but despite this piling up of bones, inconvenient for a cast, one can still distinguish the centra of both vertebrae. Under these centra, in any case partly hidden by these bones, lie two distinct ribs; these are different from each other. The first of these ribs, which belongs to the eleventh vertebra, is still thin like the preceding ones, but the rib of the twelfth vertebra is quite markedly thickened at its proximal end. This thickening is a property which further characterises all the following trunk ribs, and its appearance at the twelfth indicates fairly well that we have to count this one already as a trunk rib. Thus we can recognise eleven cervical vertebrae in *Eidolosaurus*.

For the centrum of the thirteenth vertebrae (following the twelfth rib), the length of 5 mm is still, as with the tenth, the same as the width; in the fourteenth and following vertebrae, on the other hand, one notices an increase in width. In the 27th vertebra, which is still only 5 mm long, the width has increased to 7 mm.

All centra of the trunk vertebrae have, as in *Adriosaurus*, a drum-like shape and are different from the posteriorly tapering vertebrae of *Pontosaurus* and also those of *Mesoleptos*. This drum shape is, as will be shown later, a consequence of pachyostosis. The sculpture on the base of the drum-shaped vertebra is different according to the body region. The centra of the anterior cervical vertebrae are somewhat laterally compressed at the base, on the posterior cervical vertebrae the centrum apparently becomes round, from the thirteenth to 26th vertebrae one can notice on the underside of the centrum a broad shallow median longitudinal groove. On the 26th vertebra this longitudinal groove appears to double, and on the 27th, 28th, and 29th vertebrae a duplication is indisputable. Whether the 30th and the following vertebrae possessed a double longitudinal groove, can unfortunately not be determined.

From the thirteenth to the 30th vertebrae the trunk rubs of the left side all lie beside the corresponding vertebrae in magnificent preservation. From anteriorly up to the 26th vertebra they increase in size steadily; from there on a slight size decrease is noticeable. All trunk ribs are uniformly and strongly curved for their whole length and all show a strong pachyostosis particularly at the upper end. With a length not more than 40 mm, the thickness of one of the ribs reaches a full 4 mm, i.e. it is almost as thick as the corresponding vertebra is long.

It might be thought that, on the impression of our animal, the conspicuous thickness of the impression of the trunk ribs could be taken for the result of weathering; but seeing that even the impressions of the most distal and delicate phalanges of the right hind foot show on the impression of the 23rd rib, the supposition of strong weathering out of the rib-negative is on that ground rejected.

Behind the 32nd vertebra the articulation of the skeleton of our animal is unfortunately disturbed; as the 33rd vertebra I identify a bone found to the right of the 31st, and as the 34th the one connected to the sacrum, characterised by the large sacral ribs. The ribs of the 34th vertebra lie somewhat before and below the pelvis, those of the 33rd vertebra are not recognisable.

Whether our new reptile possessed ventral ribs is unfortunately not clearly recognisable, but this is in any case possible, for some fine, curved rods lying behind the 32nd vertebra give this impression. While the presence of ventral ribs characterises aigialosaurs and their absence the dolichosaurs, this point would indeed be important, but it must remain undecided.

Of the sacrum of our animal one sees only the two sacral ribs of the left side lying close together; the first is only partly preserved, the second is complete. The latter reaches a length of 6 and thickness of 2 mm. A forking of its distal end is not noticeable.

The caudal vertebrae lie undisturbed and articulated all on one side. There are 48 of them, though the end of the tail is not preserved. If one wished to reconstruct the tail after the type of *Adriosaurus*, there would still be a third missing; whereas in a reconstruction after the other Neocomian type *Opetiosaurus*, only a fifth is missing. From the reconstruction of the outline of the part that is present, the gap comes to a quarter. The length of the caudal vertebrae decreases only insignificantly posteriorly. The second caudal vertebra has a length of 6, the 25th still 5 mm. By the 40th vertebra the centra are definitely shorter, but in any case here the impressions of the vertebrae on the original slab are blurred. Based on the impressions of the knob-like prezygapophyses, the length of the vertebral centra here comes to 3 mm.

Of the transverse processes there is only very little recognisable on the caudal vertebrae of our animal. On the first caudal vertebra the transverse process is broken away and lost, on the following vertebrae it appears generally as a lump. Whether an ascending part of this lump has also broken off, I can unfortunately not decide. From the sixth caudal vertebra onwards, this would seem improbable. Beyond the fourteenth caudal vertebra lateral processes were absent, the tail was thus laterally compressed.

The neural spines of the caudal vertebrae are reminiscent of those of *Adriosaurus*. In each, their direction and size very according to the part of the tail. The anterior neural spines, as in *Adriosaurus*, are inclined only slightly backwards; but the further posteriorly one examines, the greater inclination one sees. On the 24th vertebra, the end of the neural spine lies above the prezygapophyses of the 26th, and on the 40th the position of the neural spine is still approximately the same with respect to the 42nd. The length and breadth of the neural spines are likewise subject to variation. The breadth, which in the anterior neural spines measures approximately 3 mm, reduces to 2.5 mm in the middle of the tail and 2 mm at the end; the length climbs from 6 mm on the anterior vertebrae to 7 mm in the middle. Beyond the middle of the tail a reduction in length is again noticeable.

The haemapophyses [chevrons] are all strongly developed. Since they have been entirely removed, they are exceptionally visible. It is peculiar that the haemapophyses begin already at the first caudal vertebra; in varanids they constantly begin further back, while in some iguanids such as *Amblyrhynchus* and *Conolophus* (Steindachner 1876) haemapophyses are noticeable already on the second caudal vertebra.

The four most anterior haemapophyses in our fossil lie on both branches of their forks, and they show that these are separated by approximately 4 mm at the upper end. While possibly somewhat enlarged after death by the pressure of overlying sediment, this measurement is important for the assessment of the caudals which are now crushed together. The length of these haemapophyses remains constantly under 16 mm. We think that this measurement is the maximum length development of these [anterior] haemapophyses. Around the middle of the tail, at about the 28th vertebra, the haemapophyses increase. At the 33rd to 36th vertebrae the length generally amounts to 18 mm. As these haemapophyses and the neural spines show, our animal possessed a high and long, strap-like oar tail.

3. Shoulder Girdle and Pelvis. Little is known about both girdles in our fossil. The shoulder girdle lies between the tenth and fourteenth vertebrae, and it is extremely badly preserved - it is no longer possible to recognise what is scapula, what coracoid; in place of recognisable elements lies a quite large surface strewn with bony debris. The only thing that can be recognised is that the bony shoulder girdle was thin and large.

The pelvic elements of the left side are better preserved than the shoulder bones, [while] those of the right side are mingled with the last trunk vertebrae. The 8 mm long, rodlike caudally directed part of the ilium shows clearly; anteriorly it thickens to a knob cut off by a break. The position of the ilium with respect to the sacral ribs is only insignificantly displaced. This is important for the interpretation of the remaining pelvic elements. From the position of the ilium one can recognise where the ischium would have to lie; this facilitates the identification of this bone. This bone of our animal is an elongate, flat, well-developed piece, its median end lies on the 34th dorsal vertebra. The anterior edge of the ischium is weakly concave, the posterior edge convex, in the vicinity of the acetabulum the outline bends sharply against the anterior edge of the ilium. The bone is broadest at the acetabulum, beyond the middle it narrows rapidly, in the middle of the body it is relatively narrow. It shows at the posterior edge a strongly projecting tuber, which I also find on the rear edge of the ischium of *Varanus varius*.

The pieces of bone lying cranial of the ilium and ischium are to be interpreted as remains of the pubis. Recognisable is just the tuber pubis, lying exactly opposite the ilium. This tuber forms a well-developed point. Unfortunately all these observations are not sufficient for a reconstruction of the pelvis, but the pelvis is built as in most squamates.

4. Extremities. As already mentioned, both extremities are preserved in our animal. The right fore-foot, lying by the eleventh cervical vertebra, is poorly preserved, the left hind-foot very well preserved. The left fore-foot and right hind-foot are recognisable [only] in their basic features.

The upper arm is a strong bone 13 mm long. The crista radialis is weakly developed as a blunt knob. On the distal end of the humerus a well developed thickening is visible. A strong constriction of the middle of the humerus shaft is not present. The shaft is about 3 mm thick in the middle, the distal end of the humerus is 4 mm wide. The articular surfaces are perfectly developed at both ends of the humerus, in any case they are not especially well rounded. Without going further, a similarity to the humerus of *Adriosaurus* is recognisable.

Ulna and radius are two thin bones, strongly diverging towards the carpus. These bones seem to reach a length of 8 mm, the separation of their outer edges at the distal end would have to come to more than 6 mm, the lower arm was thus broad.

The carpus and metacarpals on the left side of our fossil are unfortunately hidden by the caudal vertebrae, [but] pieces of the delicate small phalanges are visible between the seventeenth and eighteenth haemapophyses. It seems that the hand possessed five fingers. Its total length including the carpus can be estimated at 16 mm.

The elements of the hind foot can be seen quite well in our fossil, their underside is turned toward the observer. The length of one femur comes to 21 mm, its shaft thickness at the thinnest point some 3.5 mm. The femur is apparently a flattened bone. Proximally, but especially distally, it is strongly broadened. The transverse measurement at the proximal end seems to come to a full 5 mm, compared to 8 mm at the distal end. Especially on the right femur the good ossification of the epiphysis on the distal end is visible.

Tibia and fibula both attain a length of 13 mm. The outer edges of both are nearly straight, while their inner margins are concave. In this way the inner margins of the bones extend very far apart in the middle of the lower leg. The total width of the lower limb skeleton comes to 13 mm. At the distal and proximal ends both bones, on account of the concavity appearing in the middle of their shafts, are quite strongly broadened; in the tibia this broadening is significantly stronger proximally, in the fibula distally. The tarsus of the left foot is sadly well [lapsus for 'badly'!] preserved; it seems one can recognise on the slab an upper row of bones made up of larger elements, and a lower one of smaller elements.

The ossification of the tarsus was quite considerable, but the individual elements lie very close together. This makes their analysis difficult. Considering their delicacy, the toe-elements are also quite well preserved; but unfortunately their number can not be determined exactly. Some transverse breaks can no longer be distinguished with the necessary sharpness from the joint surfaces. In general the number of phalanges seems to correspond with those of *Varanus*, but the overall length of the thumb is striking. Together with the carpus the total length of the foot came to a good 22 mm.

3. Comparisons

After the description of the piece, its comparison with the other lepidosaurs already known from Istria and Dalmatia becomes necessary.

First let us consider the dolichosaurs. In respect of size, our fossil with a trunk length of 21 cm stands between *Acteosaurus* with 16 cm and *Pontosaurus* with a length of 35 cm. *Adriosaurus* with its 14 cm long trunk stays somewhat below *Acteosaurus.*

A comparison of skull with trunk length is only possible in the roughest terms for most dolichosaurs. [Such] a large difference in the proportions present between *Adriosaurus* and *Pontosaurus* seems not probable. Apparently the skull (naturally only as far as hypothetically reconstructible) to presacral body length is in the proportion

Dolichosaurus	4:42 (?)

Pontosaurus	7:42
Adriosaurus	7:42
our animal	8:42 (?).

In relation to the other dolichosaurs our form possibly has a somewhat larger head. The number of all presacral vertebrae, which comes to 34 in our animal, reaches a constant 39 in the dolichosaurs. 13 of these vertebrae are cervicals in the dolichosaurs, here 11. In contrast to the 23 trunk vertebrae stand the 26 of the dolichosaurs. The form of the trunk vertebrae of our animal is reminiscent of that of *Adriosaurus*; in *Pontosaurus* a narrowing of the posterior part of the vertebra of each dorsal vertebra is noticeable.

Differences are noticeable in the neural spines in so far as the broadest neural spines are found in *Pontosaurus*.

The number of cervical ribs is apparently subject to variation in the dolichosaurs, but some of it can be explained by the differing states of preservation.

In *Pontosaurus* there seem to be three, in *Acteosaurus* four, in our animal five pairs of transitional ribs. In *Eidolosaurus*, as in *Adriosaurus* there are 29 pairs of ribs present, in *Acteosaurus* 30, in *Dolichosaurus* 37.

The needle-shaped trunk ribs of *Dolichosaurus* stand in contrast to the strong ribs of *Pontosaurus*, then the still more thickened ribs of *Adriosaurus* and the pachyostotic ribs of our animal. Differences are also noticeable in the length development of ribs. In consequence of the uniformity of their ribs the dolichosaurs have a roller-shaped [i.e. cylindrical] body, [whereas] in our fossil the trunk shows a spindle-like shape as a result of the increase in size of the ribs.

The pelvis and shoulder girdle are much too badly preserved to allow comparisons; it is interesting, however, to compare the extremities which stand in correlation with the spindle shape of the trunk. First let the proportion of the two pairs of extremities be briefly discussed.

The forelimbs are in the following proportions to the hindlimbs:

Pontosaurus	11:22
Acteosaurus	11:18
Adriosaurus	11:16
Eidolosaurus	11:13.

If one takes into consideration that the carpal bones of our animal are possibly somewhat dislocated through the superposition of the caudal vertebrae, so one obtains for our form a proportion of perhaps 11:14, in which case here the forelimb is proportionally large.

Differences are also visible between the development of the trunk and the limbs. The forelimb in *Dolichosaurus* is possibly included in the trunk length ten times, in *Pontosaurus* eight times, in *Adriosaurus* six and a half, in our animal five and a half. The hindlimb, which in all dolichosaurs is four times shorter than the trunk, is in our form three and a half times shorter. All these figures indicate that the forelimbs are more strongly reduced in all previously known dolichosaurs than in the new form, and the comparison between humerus and femur leads to the same conclusion. The proportion of the humerus to the femur is as follows:

Pontosaurus	1:2.4
Dolichosaurus	1:2.3
Acteosaurus	1:2.0
Adriosaurus	1:2.0
Eidolosaurus	1:1.5.

Comparison of other portions of the limbs lead to similar but not identical results. So for example the proportion of upper to lower arm:

Pontosaurus	1.2:1
Adriosaurus	1.4:1
Acteosaurus	1.5:1
Eidolosaurus	1.6:1.

In all these comparisons our animal, despite its size, is at the beginning of a series leading from *Adriosaurus* and *Acteosaurus* to *Pontosaurus*, thus it represents the starting-out point of a group which culminates in *Pontosaurus*.

A comparison of our animal with the short-necked aigialosaurs illuminates its position from another side.

The aigialosaurs all possess a disproportionately large skull. In *Aigialosaurus* the skull length comes to 6/21, in *Opetiosaurus* 7/21, in our animal conjecturally 4/21 of the presacral part of the vertebral column.

In respect of the presacral vertebrae themselves the aigialosaurs, in which there are constantly 29, are surpassed by our animal with 34 vertebrae, and indeed of its excess vertebrae three are allotted to the neck region and two to the trunk. The appearance of haemapophyses on the second caudal vertebra places *Eidolosaurus* quite strikingly in the neighbourhood of *Carsosaurus*. Also the significant increase in rib length around the middle of the body in *Eidolosaurus* is an *Aigialosaurus*-like character.

The proportion of humerus to femur in *Aigialosaurus* is 1:1.1, in our form 1:1.5 and in *Carsosaurus* 1:1.6. The proportions of the upper to lower arm are as follows: *Aigialosaurus* 1.4:1, *Carsosaurus* 1.6:1 and in our animal 1.6:1. The proportion of the whole forelimb to the whole hindlimb in *Carsosaurus* is 11:11, in *Aigialosaurus* 11:14 and in our animal 11:13 or 11:14.

While there obviously exists a correlation between elongation of the trunk and reduction of the extremities, it ensues that the proportion of these parts also shows a certain regularity in the short-necked lepidosaurs of Istria. In *Carsosaurus* and *Opetiosaurus* the forelimbs are approximately three times shorter than the trunk, in *Aigialosaurus* about three and a half times, and in our new form five and a half times shorter. As for the hindlimbs, their proportion to the trunk can be expressed in *Carsosaurus* by the numbers 1:2.5, in *Aigialosaurus* 1:3, and in our new animal 1:3.5.

The results of comparison with the short-necked Neocomian lepidosaurs of Istria are that in *Eidolosaurus* the trunk is narrower, and that both pairs of extremities, but especially the anterior, are more strongly reduced. In comparison with the long-necked forms, it is shown that our form had better developed extremities than these.

Intentionally, one Istrian fossil lizard already known since 1851, namely *Mesoleptos*, has been completely left out of the comparisons up to this point. While insufficiently described and only partly known, precisely this animal is considerably reminiscent of our form. In the torso of *Mesoleptos* 23 vertebral arches are to be seen before the sacrum, and to the narrow vertebrae articulate long, unthickened ribs. Before the 23rd vertebra anterior of the sacrum, another three shorter, transitional ribs are visible on the left side and these seem to indicate that this form had 23 trunk vertebrae and at least nine cervical vertebrae. So the number of trunk vertebrae and probably also of cervicals in *Mesoleptos* and *Eidolosaurus* is approximately the same. Since the femur length in *Mesoleptos*, as in our animal, corresponds to the length of three middle dorsal vertebrae, and the number of presacral vertebrae is a quite constant quantity in the different Neocomian lizards of Istria, I believe that *Mesoleptos*, although it lacks any trace of pachyostosis and although the form of its posteriorly tapering dorsal vertebrae is different from that observed in *Eidolosaurus*, is nevertheless closely related to *Eidolosaurus*. As *Eidolosaurus* must be specifically and even generically separated from *Mesoleptos* on account of the differences mentioned, it is entitled to a new name, and since for the present we know only its shadowlike imprint, I held the Greek word τ□ο ειδολον (the shadow) to be an appropriate one from which to construct a generic name. As I was made aware of this new fossil by Dr Trauth, I name the only presently known species: *Eidolosaurus trauthi* Nopcsa[1].

The genus *Eidolosaurus* is characterised by the number of vertebrae, the spindle-shaped body, the proportions of the extremities and the pachyostosis.

4. Systematic Position

Among the Neocomian lizards of Istria, as explained above, two extremes and one intermediate type can be differentiated. One extreme type includes the genera *Aigialosaurus*, *Carsosaurus* and *Opetiosaurus*, the other the genera *Acteosaurus*, *Adriosaurus* and *Pontosaurus*. The intermediate type represents the genera *Eidolosaurus* and *Mesoleptos*.

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[1] An undescribed fossil discovered by Professor Jaekel, which came to my attention while this work was in press, shows 18 posteriorly tapering vertebral centra, which bear long, little curved, proximally club-shaped ribs. The length of the piece comes to 28 cm. The vertebral centra show a shallow but well developed median longitudinal groove. The anterior centra are almost triangular and wider than long. The general habitus is *Mesoleptos*-like, but the ribs are somewhat pachyostotic. Probably this form is related to *Eidolosaurus*.

That *Carsosaurus* and *Opetiosaurus* on the one hand, and *Adriosaurus* and *Acteosaurus* on the other are perhaps only specifically distinct was already emphasised in 1908; and hence all the forms mentioned can be ordered approximately in the following series: *Opetiosaurus* (*Carsosaurus*), *Aigialosaurus*, *Mesoleptos*, *Eidolosaurus*, *Adriosaurus* (*Acteosaurus*), *Pontosaurus*. In the middle of the series one finds relatively small forms (with the exception of *Mesoleptos*), at both ends relatively large ones.

Analogous differences to those between particular forms in this series are found today between the two iguanas living on the Galapagos Islands, *Conolophus* and *Amblyrhynchus*; and since the differences between the now-living forms may illuminate some features of the Neocomian forms, it seems useful first to speak of the differences that exist between them. Only then will we know how to estimate the value of the differences present among the fossil forms.

Their custodian Siebenrock allowed me to examine Steindachner's types of *Conolophus* and *Amblyrhynchus*. The most conspicuous differences of these two genera, with similar head- and trunk ornamentation, are those which can be identified as adaptations to aquatic life. They consist, in the aquatic form, in a reduction in the size of the head, its shortening and anterior rounding conditioned by feeding on algae, in the chest becoming flatter and broader, and the development of a rather cylindrical body. The latter change is obtained by a strong shortening of the cartilaginous portions of the ribs, a marginal shortening of the bony ribs, and elongation of the sternum. Apart from these differences one can also notice in the aquatic form a reduction of fenestration of the shoulder apparatus, shortening of the phalanges, reduction of the claws, and lastly the development of a laterally compressed oar-tail. The less steep orientation of the pelvis in the aquatic form hangs well together with the slighter depth of the chest.

As all these differences are also found, in an analogous manner, in the mosasaurs, it seems on the Galapagos Islands as if the aquatic form *Amblyrhynchus* had only just originated from a terrestrial *Conolophus*-like form. Intermediary forms between *Amblyrhynchus* and *Conolophus* are today totally lacking; but in the Neocomian of Dalmatia, as we see, intermediates are present for a quite analogous process. Of the two extreme groups, it is the aigialosaurids which make a non-too-distant approach to the mosasaurs; the dolichosaurs are considerably reminiscent, as has already been said once, of the snakes. Between the aigialosaurs and dolichosaurs the *Eidolosaurus-Mesoleptos* type pushes in as a connecting member. However, as *Amblyrhynchus* shows, one may not put too much weight on the differences between these groups.

This new grouping of the Neocomian lizards of Istria influences their systematics. **The view proposed by myself in 1908, that the aigialosaurs and dolichosaurs were only distantly related, is to be rejected as incorrect**. The representatives of the two groups must, as Gorjanovic-Kramberger already concluded in 1892, be bound together in one systematic unit, but in any case the group so composed only has the rank of a family. For this family, unfortunately several names come into consideration. It was regarded as a suborder by Gorjanovic-Kramberger (1892), and he proposed the name Ophiosauria for it, since he regarded the name 'dolichosaurs' as misleading. He named two families of this suborder Aigialosauridae and Dolichosauridae. *Mesoleptos* was referred by him to the varanids.

As the name Ophiosauria was already preoccupied for another group of animals in 1892, Boulenger (1893-96) and Dollo (1903) decided to name the suborder Dolichosauria. If we allow the suborder Dolichosauria the rank of a family, the name must become Dolichosauridae; but the name Dolichosauridae is already used in a different sense. The Dolichosauridae of G. Kramberger, as it contains only the genus *Dolichosaurus*, does not correspond to Dolichosauridae of Nopcsa (1903), and Dolichosauria of Dollo, as a suborder, was also something else again.

Professor Dollo, to whom I turned on account of this nomenclatural question, now proposed to retain for the new family comprising the Dolichosauridae of Nopcsa and Aigialosauridae of Nopcsa, despite the objections above, the name Dolichosauridae Dollo; and I believe I must concur on account of the unification of the nomenclature.

Within Dollo's Dolichosauridae, the aigialosaurs and dolichosaurs have the value of two subfamilies to be named Dolichosaurinae Nopcsa and Aigialosauridae Nopcsa, and to these two subfamilies is added, as a third unit of equal rank, the Mesoleptinae Nopcsa.

In the system of lepidosaurs the Dolichosauridae Dollo lie on the one hand between the Varanidae, with which they have in common the structure of the scales, the skull roof, the lower jaw and the cervical vertebrae, and the iguanids, teiids and true lacertids, among which in contrast to the Varanidae but like part of the Dolichosauridae, we find basioccipital tubera on the skull and zygosphenal articulations on the vertebrae. The lack of dermal ossifications separates the Dolichosauridae from the Helodermatidae, Anguidae and the Scincidae.

A very similar mixture of varanid and non-varanid characters as in the Dolichosauridae is also found again in *Megalania*, as G.J. v. Fejérváry (1918) recently explained, and for this reason Fejérváry separates *Megalania* from all Platynota. The Platynota, according to Boulenger, is a unit of lepidosaurs comprising the Helodermatidae and Varanidae and, as also recognised independently by Schmidt on the basis of studies of the skin, is closely related to the anguids. Now *Megalania* and the Dolichosauridae are related to the Platynota such that the non-aquatically-specialised ancestors of the Dolichosauridae together with the megalanids could count as ancestors of the varanids, anguids and eventually also the helodermatids, and hence one can separate these forms [dolichosaurids] and *Megalania* together from the Platynota as Proplatynota. Their primitive and central position conforms well with the appearance of *Megalania* in the usually archaic fauna of Australia: it simply turns out to be a relict. The few iguanid characters of the Mosasauridae have been emphasised by Owen.

In the just-mentioned work of Fejérváry, which is certainly exemplary as far as the varanids are concerned, apart from these observations there are also further remarks to be found concerning the relationship of the large-headed Aigialosauridae and the mosasaurs. Fejérváry denies, in opposition to Abel, any relationship between these two groups: Abel on the other hand, in his book "Die Stämme der Wirbeltier" (Leipzig 1919), placed the aigialosaurs within the mosasaurs. To these two mutually contradictory views I could, as I had taken up an intermediary standpoint, draw back the not ungrounded remark "duobus litigantibus tertius gaudet" [when two are litigating, a third rejoices]. But as has been explained in detail in the whole foregoing work, as a result of new discoveries I must give up my own earlier standpoint; and since I can also not adopt Abel's view, so it seems a good idea to briefly go into Fejérváry's view in what follows.

As a foundation for his view Fejérváry brings up the following seven arguments:

1. As the aigialosaurs lived in the Lower, while the mosasaurs lived in the Upper Cretaceous, the lapse of time is too short for such great differences to appear as actually exist between these two groups (p.435).

2. The similarity, in any case remarkable, in skull structure in these two groups of forms is, while no special significance should be attached to the stronger or weaker development of the jugal arch, a purely superficial one ("merely a suggestion" [in English]) (p.436).

3. The mosasaurs possess a sclerotic ring, which is constantly absent in the Platynota. This point seems very important to Fejérváry (p.437).

4. There are great differences noticeable in the structure of the vertebrae. Unfortunately Fejérváry gives no suggestion at all of what these differences consist. But since of all the illustrations of mosasaur vertebrae at his disposal he figures just one cervical vertebra with a large hypapophysis, presumably this is what he means (p.437).

5. One notices great differences between both types in the shoulder girdle. Also here Fejérváry does not cite which, but obviously he means the lack of a fenestration and the great number of sternal ribs (p.437).

6. The differences in structure of the extremities reach the maximum (p.437).

7. It has so far not been demonstrated that such great differences as mentioned under 2-6 could appear in an explosive manner, and therefore the mosasaurs are not to be regarded as descendants of the animals related to the varanids, provided with claws, but rather as a very old branch of lepidosaurs, whose similarities with the varanids are based on convergence phenomena (p.437, 438).

To these seven points of Fejérváry, the following remarks can be given:

To 1. Firstly, the time difference between the formation of the fish-slates of Comen and the upper Cretaceous is not so small as Fejérváry assumes, for Schubert (Handbuch der Regionalen Geologie, Vol. V, 1914), which Fejérváry admittedly does not know how to find, at least not without protest, shows the fish-slate even in the Tithonian, but then the duration between the upper and the lower Cretaceous itself is not at all so short as Fejérváry assumes, for it is possibly equal to at least a good part of the Tertiary formation. Secondly, during the time taken by Fejérváry to be short, even greater differences take place in the reptiles on dry land than in the aquatic forms (*Triceratops, Pteranodon*). Thirdly, changes take place very quickly in explosive speciation; and fourthly, to which we shall yet return, precisely in the lepidosaurs of the Istrian fish-slates a clear case of explosive speciation lies before us.

To 2. **In consequence of the different ways of life** of these animals, the structural similarities of the snout, the parietal region and the lower jaw, and even of the perforated quadrate, which one meets between the aigialosaurids and the mosasaurs and which also, if only to a slighter extent, occur again in the varanids, could not be convergence phenomena; they must therefore be primary. On these grounds the skull of the aigialosaurs also takes an intermediate position between the other two types. I have already emphasised since 1903 that on my consideration the varanids, as terrestrial reptiles, have retained more primitive features than the aigialosaurs.

To 3. The sclerotic ring of the mosasaurs, on which Fejérváry lays so much weight, is trivial to such an extent that even to mention it was superfluous, and of course so much the more the remark that it had never been paid sufficient attention. In several species of animals it is simply a result of adaptation to aquatic life and is thus found again in closely related forms; thus it is found for example in *Geosaurus*, while it is absent in other crocodilians, and then it occurs also in the marine thalattosaurs, but is absent already in their close relatives the varanosaurs. The sclerotic ring seems still to be absent in *Iguanodon*, whereas it is found in the more strongly aquatically adapted trachodontids, and similarly a sclerotic ring appears in *Chelone*, as already emphasised, incidentally, by Dollo. The facts that in marine mammals the sclera is very hard and thick (Hilzheimer, Biologie der Wirbeltiere. Stuttgart, 1913), and that the ichthyosaurs have a conspicuously large sclerotic ring (which incidentally is not the case in their distant relatives the mosasaurs), should have made Fejérváry investigate this question in detail before, in a somewhat over-hasty manner, laying such great weight on it. [JS: SOME *VARANUS* HAVE OSSIFIED SCLEROTIC RINGS, E.G. *V. ACANTHURUS* PERS. OBS.].

To 4. It is not to be denied that there are differences between the vertebrae of the swimming mosasaurs and those of the mainly terrestrial varanids. But nobody has supposed that the mosasaurs descended directly from the varanids. Then it is to be remarked that some of the peculiarities of the cervical vertebrae of mosasaurs possess only slight systematic value. For this reason I lay no value on the very special size of the cervical hypapophyses of *Platecarpus* and *Clidastes*, because such modified hypapophyses are also found in *Dasypeltis*, but one does not therefore separate it from the snakes. Then it has not at all been determined how much these specialisations are associated with the teutophagy [JS: SQUID-EATING, OR MORE GENERALLY CEPHALOPOD-EATING?] of *Platecarpus* (cf. Hilzheimer loc.cit.). Also the structure of the cervical vertebrae of squamates, as shown by Siebenrock's (1893-1895) investigations, has only slight value for systematics, for in some forms like uroplatids (Siebenrock 1893) and gerrhosaurids (Siebenrock 1895a) the cervical hypapophyses lie in an intervertebral position, while in other forms (chamaeleontids, lacertids, scincoids, anguids, varanids; Siebenrock 1894, 1895a, Osborn 1899a) they are attached, as in the mosasaurs, on the posterior edge of a cervical vertebra (one could call such an attachment postvertebral), and again in other lepidosaurs such as the agamids (Siebenrock 1995b), the cervical hypapophyses lie prevertebrally.

Also the question whether the epistropheus bears one or two hypapophyses is systematically fairly trivial, for two epistropheal hypapophyses are found in the varanids, chamaeleontids, lacertids, scincoids, anguids and gerrhosaurids; in the agamids and uroplatids one the other hand, there is only one. In some lepidosaurs, such as e.g. the varanids, the anterior hypapophysis touches only this vertebra, while in the scincoids, anguids and gerrhosaurids it also touches the dens [odontoid process] and in the agamids, as in the mosasaurids (Osborn 1899a), it touches not only the dens but also the lower arch of the atlas. As one sees, the relationships of the cervical vertebrae in lepidosaurs are quite variable; and while the persistence of only individual pieces of the two first vertebrae is certainly only conditioned by their aquatic life, in that aquatic life actually often brings with it delays in ossification, so these points are by no means a suitable base on which to build wide-ranging hypotheses. Zygosphenes are also found in the varanids' distant relative *Megalania* and in some (?) Dolichosauridae (Seeley 1865).

To 5 and 6. The shoulder girdle of aigialosaurs, in its semiaquatic adaptations, is exactly intermediate between those of the terrestrial varanids and those of the marine mosasaurs. The same can be concluded for the somewhat shortened feet of these animals, if less pronouncedly. As the investigations of *Conolophus* showed, a reduction of fenestration of the sternum and shortening of the phalanges appear already even in this very slightly aquatically specialised lizard; and then it is also quite an old discovery that on taking to aquatic life the first parts to be affected are the extremities and those parts where the muscles of the extremities insert. If the aigialosaurs were not even different from the mosasaurs in respect of the shoulder girdle, pelvis and extremities, then they would not be aigialosaurs at all but rather, as Abel would have it, mosasaurs. Incidentally the Proplatynota probably had more sternal ribs that the Varanidae, or at least the condition in the Iguanidae would suggest so. These two arguments put forward by Fejérváry lack any weight.

To 7. The question whether differences like those listed in points 2-6 above could arise in an explosive manner or not, is indeed only of a theoretical nature, hence really pointless; but so as not to create the impression that I wish to avoid it, let it be emphasised already at this point that I will discuss it in the conclusion to the whole work.

After careful examination of all of the points brought forward by J.G. v. Fejérváry, I believe that I can with full confidence repeat the statement: **the mosasaurs are descended from the Aigialosaurinae**.

5. Physiological (Arrostia)

Eidolosaurus is interesting physiologically because it so clearly shows a property for which I here introduce the expression "arrostia" [*Arrostie*] into palaeontology. By arrostic phenomena (the word is formed from the Greek αρρωστια = sickliness) I understand such as would have to be described as decidedly diseased based on discoveries in certain recent material, but which occur nevertheless in other, often fossil material in part as nonadaptive, but even in part as adaptive 'abnormalities'.

The first arrostic phenomenon, which I was able to demonstrate years ago, was the gigantism of the dinosaurs associated with an abnormal development of the hypophysis, which is partly accompanied by the same symptoms as observed in humans in the disease of acromegaly; a second analogous change which I would like to show herewith, is the pachyostosis of the ribs of *Eidolosaurus* and some other reptiles.

The cause of pachyostosis and the associated osteosclerosis of marine animals still lies in the dark. Among the reptiles it is only short-legged, more or less long-tailed, newt-shaped, aquatic forms that are affected by it constantly and to a great extent. *Mesosaurus* (McGregor 1908), and *Stereosternum* (Osborn 1899b) from the Permian, *Pachypleura* (Cornaglia [NO DATE]) and *Proneusticosaurus* (Volz 1902) from the Triassic, and *Eidolosaurus* from the Neocomian, although totally unrelated, are however superficially similar forms.

In the naked-skinned *Champsosaurus*, in which the extremities are relatively long, the ribs also show a thickening, but here one can not speak of true pachyostosis. I seem to recall that its compacta is already relatively thick and dense.

The truly pachyostotic, newt-shaped reptiles are all characterised by the lack of armour; in the likewise newt-shaped but non-pachyostotic thalattosuchians (Fraas 1902), armour was originally present which increased the weight of this animal. This is shown by the sculpture of the skull bones. Two other osteosclerotic-pachyostotic water-inhabiting types, which likewise have reduced extremities, are *Zeuglodon* and the sirenians (Abel 1912). In *Zeuglodon*, still provided with rudiments of armour, the pachyostosis is only weak and mostly restricted to the vertebrae, but it is strong in the naked-skinned sirenians. In the primitive Eocene sirenians it was restricted to the chest, while in the later Neogene forms it extends to all the ribs and finally even to the skull. Of the similarly pachyostotic whale *Pachyacanthus* we still know too little to be able to speak of it here (Gervais 1875).

These quite peculiar observations already show that the strength of pachyostosis of the animals mentioned is in correlation with their equilibrium. Observations on newts make it possible for us to better understand this correlation. If one observes a newt in water when it rises to take a breath, one sees how it comes up by swimming movements with the head directed obliquely upward, then fills its lungs with air and next, without changing its position in any way despite its air-filled lungs, however small, it sinks back to the bottom under its own specific weight. The position in which it comes up to breathe thus corresponds to its equilibrium position in water. This observation shows us clearly that in other water-inhabiting animals with larger lungs, such a rising and sinking with upwardly directed head would only be possible if the buoyancy of the lungs is compensated. Naturally such compensation must take place in these cases exactly where the buoyancy of the lungs is brought into action, for in any other case the head would remain under water on rising and obtaining a breath would only be possible by stretching the head out of the water, achieved through exertions by the forefeet (!) and hence only of short duration. Something of this kind would make breathing difficult, but how important it is for an air-breathing aquatic animal to easily stick the nose out of the water, is shown in its frequent prolongation (Abel 1912).

As a result of these theoretical considerations, pachyostosis serving to compensate the buoyancy of the lungs must naturally effect the lung region, and as in reptiles and the specialised sirenians the lungs lie dorsal to the viscera, it must extend to all the ribs; in the more primitive sirenians, where as in all normal mammals the lungs probably lay anterior to the viscera, it must have affected only the anterior ribs; and finally it must be more or less absent, because superfluous, in all such animals as have heavy trunk armour. As all these theoretically demanded premises correspond to the facts, so one can maintain the pachyostosis of all primitive aquatic animals to be a functional increase in weight. Stromer and Babák (Babák 1921) have already shown this for the sirenians in particular.

In general less clear than the pachyostosis of ribs and vertebrae are those isolated cases, especially in the sirenians, where the pachyostosis also extends to the skull, and this should be discussed especially, and particularly in connection with that of the ribs.

Naturally the rather diffuse pachyostosis of aquatic animals is to be separated from that which is traumatic and local, which often sets in with damage to bones or inflammation phenomena, and occurs hereditarily in *Hyperoodon* and *Pesophaps*. In the pachyostosis of this second species, its inheritance is indeed difficult to explain, but its origin is clear; in contrast the origin of rib pachyostosis, which is clearly equally hereditary, remains still to be researched.

Observations on sick humans, recent mammals and on birds throw some light on these questions. In humans osteosclerosis paired with pachyostosis can arise through different causes (Frangenheim 1913), of which those linked with leukaemia should interest us here.

The whole of the literature dealing with leukaemia is to be found in the works of Domarus (1920), Naegeli (1908), and Herz (1920); hence in what follows only the more physiological literature actually made use of will be cited. Diffuse osteosclerosis associated with leukaemia is described by Nothnagel (1891), Neumann (1878), Hammer (1894), Assman ([NO DATE]), Goodall (1912), Nauwerk and Moritz (1905), Schwarz (1901) and others (Jaksch [NO DATE]), but as leukaemia also often occurs without these accompanying symptoms, so in these cases the osteosclerosis appears only, as already emphasised by Assman ([NO DATE]), at the completion of the healing process to form tissues destroyed during the leukaemia. Similar [processes] also occur with carcinomas (Nauwerk and Moritz 1905).

From these relationships it follows automatically, that in order to understand osteosclerosis, first the blood-forming organs must be studied.

A conspicuous accompanying symptom, particularly of chronic leukaemia, is hyperplasy of the spleen and its often myeloid (bone-marrow-like) degeneration (Ehrlich et al. 1901, Hirschfeld 1902). This degeneration also takes place quite often in that kind of carcinoma in which the bone-marrow is destroyed, and hence myeloid degeneration of the spleen can be recognised as a change by which the spleen [which is a blood-producing organ and, at least in the higher mammals, not absolutely necessary (Melzer 1920, Pappenheim 1899)] strives, however unsuccessfully, to vicariously take over the functions of the bone marrow. Leukaemia itself appears more and more as a hyperplasy of those different organs which form the white blood corpuscles. Myeloid and lymphatic leukaemia have the same origin (Ellermann 1921). It is quite clear from the explanations of Domarus (1920) that the incurable hyperplasy of the organs afflicted with leukaemia is only poorly differentiated from true tumour-formation; this is particularly so of the chlorome. In the dark chapter of human neoplasms, one thing now steps clear into the day, that neoplasms can arise in a 'pathological' disposition through different stimuli which initially produce hyperplasies (Bloch and Dreifus 1921, Saul 1920, Yamagiva 1921), and as Herz (1920) determined more or less the same of acute leukaemia, that "it appears in pathological disposition as a special reaction to different infections", so it is worth first of all to explain a part of those processes which provoke the blood-forming bone marrow.

Aschoff (1893) noticed a strong temporary hyperplasy and hyperaemia of the bone marrow on injections of *Parenchymbrei* [parenchyma-porridge?] into the blood (also Arnold 1893), which finally led to a conversion of only those kinds of cells otherwise characterising the bone marrow, moreover with a strong *Verbrühung* ['scalding'] of the body leading to death after a few hours; in [cases?] having a rapid effect these symptoms do not appear (Aschoff 1893). Lengemann (1901) and Schwarz (1901) confirm these findings, add mechanical smashing of the bone marrow, and mention that the hyperaemia appearing in this case even leads to haemorrhage in the marrow (Aschoff 1893); Selling (1911) observed a temporary hyperplasy of the marrow again on low-grade benzene poisoning; strong-grade led to its aplasia (Naegeli 1908, Selley 1911). Ellermann and Bang managed to transfer leukaemia from sick animals to healthy ones in several generations of chickens by over-inoculation with filtered organ-'porridge', whereon it became stronger each time. Sometimes it was more lymphoid, at others myeloid (Ellerman 1921).

What now seems important and in any case indicates a relationship, if not yet a clear one, between quite different processes with different kinds of leukaemia, is the observation already recognised by Neumann (1878) and emphasised by Domarus (1920), that trauma, colds, infection and overexertion are quite often the apparent (?) causes of chronic leukaemia. Perhaps all these kinds of damage to the body are associated with the presence of toxins (exhaustion-toxins, Dale and Landlaw 1919; histamine etc.). With histamine-damage, an expansion of normally closed capillaries is often seen (Rice and Rich 1921).

Of much more interest to us than all this is the information given by Schwarz (1901) that an irritation of the marrow, completely identical to one of these irritations, also enters on artificially produced respiratory distress, and indeed even slight oxygen deficiency induces changes in the blood (Rice and Rich 1921). As it is now fairly clear that animals not yet adapted to life in water, and relatively poor swimmers which still have small lungs, must in any case often come to 'artificial' respiratory distress, and that the marrow-insult thus induced in these animals will indeed never be very intense, but will occur very often, so we may venture the hypothesis that by this means a hyperaemia, then also a hyperplasy of the marrow is produced, which finally leads to degeneration of the marrow. In contrast to the strong and intensely operating marrow-insults in the experiments, the insults in aquatic animals are spread constantly over generations, and that is obviously why the other blood-forming organs have time to replace the marrow. Thus osteosclerosis does not have a deadly effect in these animals. Also in chronic cases of human leukaemia, myeloid alteration of the spleen is stronger than in cases with an acute course.

As interesting as it would now be to learn in greater detail about the spleen of the sirenians, which all more or less 'suffer' from osteosclerosis, I have hitherto, through the kindness of Prof. Foster-Cooper, only been able to study one; that the spleen of young sirenians is relatively large is unfortunately of slight significance, for the spleen of young animals in general is often large (Robertson 1921, Henn 1920). Despite this gap in our knowledge, on this view the state of pachyostosis in primitive aquatic animals can be regarded as the symptom of an illness, but an illness which mostly does the animals no harm (exception: sirenians; more on this below).

If we now compare the grade of pachyostosis in different aquatic animals, we see that the pachyostosis disappears again in parallel with the new development of flippers. The pachyostotic *Mesosaurus* stands to the related, but flipper-bearing and non-pachyostotic ichthyosaurs[2] in the same way as the pachyostotic *Proneusticosaurus* does to the related, likewise flippered and non-pachyostotic *Plesiosaurus*, and exactly as *Eidolosaurus* to *Mosasaurus*. Even in the short series *Eidolosaurus-Adriosaurus-Dolichosaurus* (Owen 1849-1884) the pachyostosis appears in the lower Cretaceous coastal form and is missing in the upper Cretaceous form [which was] found in the *Globigerina* mud and [was] thus pelagic. Also among the mammals the same reduction of pachyostosis can be seen in the pelagic forms, for in contrast to *Zeuglodon*, which shows a modest pachyostosis, it is normally lacking in whales. Among all animals well adapted to marine life, pachyostosis persists in this way only in the sirenians; but that these actually lead a completely different life than the other animals, their exceptional position is conditioned by special factors, as will yet be explained. If we exclude the sirenians, pachyostosis appears constantly in a very particular stage of aquatic adaptation and then seems to disappear again. This disappearance, if one regards pachyostosis as an illness, can only logically be called a recovery. If we now compare the highly marine animals with those which are not, four main points stand out. The long bones of all highly marine animals almost entirely lack a marrow cavity, their bones are mostly uniformly spongy, their lungs are large and wide, and lastly, there are large retia mirabilia on their vertebrae and ribs. The last applies especially to cetaceans and sirenians (Hilzheimer 1913). The spongy bones of cetaceans and ichthyosaurs have been known for a very long time, the reduction of the central marrow cavity in sauropterygians comes from Moodie's works, and the long bones are also dense in mosasaurs. As the central marrow cavity is the first part to suffer in osteosclerosis, this diffuse spongy structure of all the animals mentioned is explained without difficulty in this way: that after an osteosclerotic period the development of marrow in these bones recommenced, but the irreversibility of evolution gives us the explanation why this new development does not return to the destroyed marrow cavity, but was attained by general resorption of the bone.

Now as hyperplasy with marrow damage goes along with hyperaemia (Schwarz 1901), so it can come to such healing in a natural way only when the hyperaemia itself, and also the better swimming of the marine animal allowed by the development of tail fins, displaces the temporary respiratory distress; so one factor in the recovery is already found, and if we take into consideration that the retia mirabilia of marine animals are found in just those places where the blood approaches the bone marrow and that a rete mirabile constantly slows the bloodstream, so we have also in the structure of the blood vessels a further modification before us, which holds back a hyperaemia of the marrow.

As retia mirabilia and large lungs are also present in the sirenians, but pachyostosis still persists as well, and even increases in a manner like no other group of marine animals, we

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[2] I confirmed the previously unknown relationship of *Mesosaurus* and *Stereosternum* with *Ichthyosaurus* together with Prof. v. Huene with the *Mesosaurus* material held in Tübingen. Similarities are present especially in the structure of the shoulder girdle, the rib articulations, the structure of the palate, the quadrate and the lower jaw.

must find a natural cause that only occurs in the sirenians if we are to maintain the correctness of our hitherto developed hypothesis. While all the other marine and previously pachyostotic animals feed on animal food, the sirenians, and especially those living in the northern seas, eat iodine-rich algae (Strassburger et al. 1921). It has been confirmed in experiments with dogs that the iodine content of the thyroid gland depends on the kind of diet and increases with vegetable food (Falta 1913); further, in cases of sporadic cretinism based on defects of the thyroid gland, the ossification of the body is strongly retarded (ibid.), and finally in such cases iodine-containing preparations promote ossification (ibid.); thus a bone-building influence comes from iodine, so the hypothesis seems to be fairly well founded, that the pachyostosis in sirenians and especially *Rhytina* is not only not reduced, but rather further developed, on account of the high iodine content of their food.

Hereby the exceptional position of the sirenians is satisfactorily explained, and so the neoformation of the marrow in the other marine animals can be regarded as a healing process, which occurs as a consequence of numerous specialisations. So a quite significant factor shows itself in evolution, which was not previously known; that is, that such hyperplastically working factors have an effect in evolution, which produce more or less severe illness in the individual.

2ND PART: *PACHYOPHIS*

1. General

The second reptile newly known from the Neocomian is even more important than *Eidolosaurus*. It is likewise known from three individuals, of which one is well preserved on a larger slab, the two others preserved on a neighbouring slab. Since the bones visible on the neighbouring slab show only their cross-section, those of one of the skeletons were carefully removed with a needle, then a cast was made of the cavities, for which I used a new material, namely a mixture of transparent gelatine, glycerine, joiner's lime, and zinc oxide made into a paste with water. This mixture combined the elasticity of ordinary gelatine with the opacity and white colour of a plaster cast, so it is very suitable for photography, which is well known not to be the case for either black gutta-percha moulds or transparent gelatine casts. Such a cast can be kept all day enclosed in thin, dry canvas and covered with a moist towel, without becoming sticky, and hence studied conveniently. If after several hours of examination the edges become a little dry, one has only to cover it with the towel for a while and soon it is flexible again. Since particularly in the study of negative preparations uncommonly much depends on how the positive cast comes out, I can only strongly recommend this method.

In thankful remembrance of Dr A. Smith-Woodward, who has already very often, and again very recently, supported me in my palaeontological studies, I name this important fossil, representing a new genus and new species that will be described here, *Pachyophis Woodwardi*.

Pachyophis is a snake-like reptile about 40 (?) cm long, that possesses neither fore- nor hindlimbs. The fact that all three preserved animals lie on their bellies from the seventeenth vertebra on implies that the original cross-section of the body was at least rounded, and in any case not laterally compressed. Since all the uniformly curved ribs of this region now lie horizontally and in one plane, but corresponding to the curves of the body are directed regularly backward and outward and are more strongly directed posteriorly on the concave side of the curves than on the convex, it will moreover be recognised that the pressure of the rock has displaced all the ribs uniformly, but such displacement after the decay of the soft parts was only possible if it was already prepared by the original position of the bones, so we must reconstruct *Pachyophis* as an animal with the ribs directed outwards, but also posteriorly.

In conspicuous contrast to the trunk's belly-down position is that of the neck, on its side. The ribs of the right side of the body on the main slab lie parallel to each other and are directed almost directly backwards, those of the left side also lie parallel to each other, but are directed almost directly ventrad. The ribs of this second portion are straight in their lower portion, and this state together with the posture implies a laterally compressed neck. While on the other slab the most anterior neck vertebrae as well as the trunk vertebrae do lie dorsoventrally, here several consecutive ribs have been forcibly separated from the vertebrae, and this too indicates that the new arrangement of the ribs and vertebrae was not presaged in the living animal.

The deep-oval neck indicates with some probability a laterally compressed skull, or at least one which was not dorsoventrally compressed, and since osteological details support this inference, we arrive at an animal that differs not only from the habitus of modern snakes, but even more from that of limbless lizards. While the neck region was not only long but, as is still to be shown, was also thin, a certain snakiness was nevertheless recognisable.

Of the better preserved specimen shown on Plate I, there are fragments of the skull and of the most anterior vertebrae, then follows a series of 109 splendidly preserved vertebrae and ribs, which reach their maximum size in the middle of the body. These vertebrae all belong to the neck and trunk, the tail - in any case short - lies buried under the animal itself.

On the neighbouring slab are preserved portions of the vertebral column which instructively show the impression of 33 anterior vertebrae. As the most anterior part of the neck is also missing on the neighbouring slab, the total number of vertebrae of our animal can not be fixed.

Remains of limbs, or any rudiments of shoulder or pelvic girdles, have not yet been found in *Pachyophis*.

2. Description

1. Skull. The only pieces of the skull which have been able to be identified so far, are a well preserved maxilla and the posterior part of a lower jaw.

a) The upper jaw. The upper jaw, visible from the inner side, is an exceptionally important piece and fortunately completely intact. Its total length is 17.0 mm. In shape it is composed of two parts: the anterior forms a long triangular surface, longitudinally concave, narrow, at its highest point just 2.1 mm high, with a blunt tip and a concave posterior outline on the short side; the other half of the jawbone is ca. 1 mm thick, thus rod-shaped, and has a quite blunt end. At the transition between the two regions a small but well-developed lamella projects at the lower edge.

The anterior of these two portions represents the antorbital part of the jaw, the posterior concave outline the orbital opening or the beginning of the lacrimal, the projection formed the connection of the jawbone with the palatine. Posteriorly, the Os transversum attached to the somewhat rounded-off end of the rod-shaped suborbital part of the jawbone. At the anterior tip of the bone one can see at the lower edge a small groove in the somewhat swollen edge, at the upper edge directly above one sees two small grooves with a little blunt lump lying between them, which makes the impression of a suture and probably is one too.

This in any case is the place where the upper jawbone was joined to the premaxilla in the region of the external nasal opening.

The straight linear lower edge of the whole bone bears bowl-like alveoli. Anteriorly one can count several alveoli, further back some teeth attached to the jawbone. The first six alveoli are large and flat and are therefore important, in that one can see that the teeth sat on the basally expanded jawbone in the same way as in *Varanus*. It was possible by careful work with the needle to expose the posterior teeth on one side all the way to the tip. One may best grasp what that means if one considers that here 9 teeth occur in the space of 5.7 mm. The well preserved teeth begin exactly below the palatine process of the jaw.

The three first teeth stand 2.8 mm apart, thus just as far as appears probable, based on the alveoli, for the preceding but missing teeth; the following smaller ones stand more closely crowded, so that the last 6 come in a space of 2.4 mm. They extend to the end of the jaw. The teeth standing further apart are longer and stronger than the others. The attachment of the teeth, seen from the inner side, seems to be thecodont, but because of the groove, already mentioned, in which they sit, externally flat. At the base, especially the more anterior of the nine preserved teeth, they are somewhat swollen, but then they soon become thin. They stand sloping on the jaw ramus, and further up turn strongly and more or less directly backwards. While the longest of these needle-tipped teeth, with a length of 1.6 mm, is scarcely 0.5 mm thick, and the shortest with a length of 0.8 mm shows a width of only 0.3 mm, and all, as already pointed out, are curved strongly backward, they are strongly reminiscent of the teeth of boids. The enamel layer of all the teeth is well developed, the pulp cavity was very large and is also still hollow now, and at the base of several of the larger teeth an opening leads into it - perhaps somewhat enlarged during preparation. Similar foramina are also found in *Varanus*, but here they are relatively smaller.

If we compare the maxilla of our new reptile with those of snakes and lepidosaurs, we see at the first glance that it differs strongly from the normal, mostly dorsoventrally compressed snake maxilla. In the typhlopids the jaw is small and reduced, likewise in the glauconids [leptotyphlopids], in the xenopeltids, boids and colubrids it is flattened (Boulenger 1893-96), and in the viperids strongly modified. The only snakes which have a half-way similar jaw are the uropeltids (Baumeister 1908). Also in these one can differentiate a suborbital and a vertically rising preorbital portion, but in them the part rising anterior to the orbit is sharply set off from the remaining [anterior] part of the jaw.

Our fossil stands much closer to the maxilla of lepidosaurs than to that of snakes. At least in part, one can find a similarly built maxilla already in the varanids. The antorbital part of the jaw of *Varanus salvator* corresponds very well with the same part in *Pachyophis*, though the position of the palatine process in *Varanus* is somewhat different, for there the whole suborbital, tooth-bearing portion, so well developed in *Pachyophis*, is absent: moreover the teeth in this lizard are also somewhat differently built. A long suborbital portion of the maxilla as is *Pachyophis* is found in the scincoids (*Lygosoma*, Siebenrock 1892), and here also the position of the palatine process is the same, though here again the preorbital part of the jaw is short and high. In this way, one can in general say that the jaw of *Pachyophis* is built like a lizard's, but bears snake-like teeth. In an animal of the size of *Pachyophis* its smallness stands out very strongly. Jaw movements of the kind in colubrids or viperids were clearly not present.

The straight course of the alveolar border of the jaw indicates a slender, pointed skull, its height anterior to the orbit shows further that the skull was not flat. While the maxilla of *Pontosaurus* is only badly preserved, it does allow us to recognise that it resembles that of *Pachyophis* in considerable measure (Kornhuber 1871 [cf.] Pl. VIII).

b) Lower jaw. A bone, which for a long time I could not decide what it could possibly be, lies under the fifteenth vertebra. It has a total length of 15.5 mm. The most anterior 2.3 mm are broken off and here the impression shows that the side of the bone lying in the rock is flat, then begins the bone itself with a width of 1.9 mm, somewhat elevated edges and between them a concavity which runs to a point posteriorly and is bounded anteriorly by the broken edge of the bone. This concavity extends posteriorly for 3.5 mm. Behind the concavity appears a bulge in the middle of the bone which was bounded above by the concavity, and runs directly backward, until it ends at a vertical suture 7.8 mm from the beginning of the bone. The shaft of this bone, somewhat twisted in the form of a screw due to this main ridge, is 1.5 mm thick at its thinnest point (some 5 mm from the anterior end) and almost round, then it expands again and at the other end is 2.5 mm wide. This broadening here affects especially the upper border and forms a projecting, flat wing, which is sharply set off from the rest of the bone. At this wing the bone is 8.4 mm long. At the lower border the expansion appears much less marked. The transverse axis of the posterior expanded region forms an angle of approximately 90° with the axis of the expansion of the anterior end.

At the end of the posterior portion, expanded to 2.5 mm, runs a vertical suture which is clearly visible at the upper edge, then runs anteriorly for 1 mm and then down vertically to the lower edge of the bone.

Behind this suture there appear to be two bones. The upper one, 2.2 mm long and 0.4 mm broad, leans diagonally against the winglike process of the anterior bone; the other, which lies on it, is much larger. This larger bone is quite thick, is sharply distinct from the anterior one, is 6.0 mm long, 1.3 mm thick, ends above and posteriorly in a small wing, below and posteriorly in a downward-directed and posteriorly rounded rod, whose rounded end gives the impression as if it was covered by cartilage during life. Its upper border forms a sharp edge. Through the sharp downward inflection of the lower edge and a neck, however indistinct, at which the bone thins to 1.3 mm, the end stands out quite markedly.

In the attempt to interpret the bone described here, one must first think of the possibility that it is a limb rudiment, in which case, on account of the transverse broadening and the torsion of the large bone, it could only be the forelimb, and then on this interpretation the two shorter pieces must be the radius and ulna. [The following points] speak against this interpretation: a) the prominent wing on the upper border of the 'humerus', which would extend further down than the normal articular surface, b) the well-rounded end of one of the two smaller bones, sharply set off by a neck, for it is too well developed to the distal end of a reduced radius or ulna, c) the relationship of the two 'sections of the limb' to one another.

In consequence of the impossibility of the interpretation as a forelimb, imposed by these pieces of evidence, the only possible interpretation of the fragments lying before us is as the posterior end of a slender lower jaw. The rounded, rod-shaped end of the small posterior bone would be, according to this new interpretation, the retroarticular process of the articular; the 2.2 mm long bone projecting behind the articular would be the inner side of the articular itself; then would come a long surangular lying externally between the dentary and the articular, and anteriorly [the bone] lying on the flat triangular 'exception' [*Ausnehmung*, in the sense of a 'piece taken out'?; possible lapsus for *Ausdehnung*, 'expansion, extension, prolongation'] of the surangular would be the dentary itself.

A comparison of our fossil, reconstructed in this sense in Pl. VIII, Fig. A, with the lower jaw of lepidosaurs shows that it is unlike - more slender than - those in the uroplatids, iguanids, agamids, scincoids, lacertids, anguids and teiids, and even more slender than varanids which are particularly slender in this part of the skull, but do show the same torsion of the surangular; and that it looks quite like this part of the dolichosaurids and especially the dolichosaurines (cf. Fig. C). Also, the jaw of dolichosaurines shows a robust articular posteriorly; then a strongly elongate surangular, and then the relatively short dentary attached to this. Also in various species of snakes one may observe a strongly elongate posterior portion and a quite short dentary bone, and in particular the lower jaw of *Rhinophis* illustrated in Fig. B is reminiscent of our form (Baumeister 1908). Even the jaw of boids, indeed even the colubrids, can be compared with our fossil. -- Unfortunately the lower jaw of neither *Palaeophis* nor *Pterosphenus* is known; that of *Archaeophis* indicates, as in the upper jaw of *Pachyophis*, a jaw tapering to a point, and whereas in most snakes the jaws curve inwards somewhat in the fashion of a bow - for this bending facilitates the dilatation of the symphysis - so that this morphology seems, if not in an unambiguous manner, to indicate that the jaw expansion of these two primitive forms was still only slight.

The presence of both of the skull remains of *Pachyophis* described here allows us to calculate its skull length. -- While the lower jaw fragment measures in total 15.5 mm, the upper jaw 17.0 mm, and the process for articulation with the dentary is missing in the lower jaw; while moreover it is probable that the upper and lower tooth rows were equally long; and finally that the toothed premaxilla is missing, which contained at least 2 teeth; which results in a lower jaw length of ca. 36 mm, as is illustrated in the accompanying reconstruction. This indicates a small skull in relation to the trunk. In our animal the skull is at least an eighteenth of the trunk, in *Dolichosaurus* it is a tenth (?), in *Pontosaurus* and *Adriosaurus* already a sixth. In different snakes the skull is even shorter than in *Pachyophis*; here I find the following proportions between the skull and body:

Glauconia	1: 38	*Cylindrophis*	1: 29
Typhlops	1: 38	*Rhinophis*	1: 35.

2. Vertebral column. Although no fewer than 109 vertebrae of *Pachyophis* are preserved in articulation on the main slab, nevertheless one can infer that the first of this series is not the first in the skeleton. Really one must call it 1+x, but for simplicity we call it 1 here. On the adjacent slab one can recognise 33 articulated vertebrae and while it seems that, as will be shown below, the last vertebra here corresponds to approximately the fifteenth of the 109 vertebrae on the main slab, and moreover there are rib remains of another four vertebrae visible before the first one on the adjacent slab, so one arrives at the conclusion that there were at least 130 rib-bearing vertebrae. With the exception of the first cervical of the main slab, unfortunately all of the vertebrae are seen only from the dorsal side.

While the different types of vertebrae distinguishable in the skeleton of our animal pass into each other gradually, and it becomes impossible in this way to distinguish neck from trunk, nevertheless one can recognise the lung region on the basis of the principles observed in *Eidolosaurus*, since a weak pachyostosis of the ribs appears in the vicinity of the twentieth vertebra of the main slab and becomes stronger by the thirty-sixth. The part lying anterior to the lung region, I hence call, in part, neck.

While the last trunk vertebrae are quite small, as will be shown in the detailed description below, so one can conclude there were about 30 caudal vertebrae. The total number of vertebrae in *Pachyophis* therefore rises to somewhat over 160.

Such a large number of vertebrae as in *Pachyophis* is found in aquatic swimming reptiles, such as *Pleurosaurus* (over 106 vertebrae, Nopcsa 1903), *Adriosaurus* (109 vertebrae, Nopcsa 1908), *Eidolosaurus* (110, [this work]), and some varanids, where Gervais (1869), for example, gives 29 presacral and 115 postsacral vertebrae. In all these mentioned fossil forms, as in *Varanus*, the number of postsacral vertebrae is very significantly higher. In

Eidolosaurus there are 36 presacral and 48 postsacral vertebrae, in
Pleurosaurus 47 and 60 + x, in
Adriosaurus 42 and 67, in
Dolichosaurus 57 presacrals [JS: HERE ACCEPTING OWEN'S 2 SPECIMENS AS ONE SKELETON]. We find similar numbers in some terrestrial reptiles. Also in *Ophisaurus* a similar total is observed, here 111 caudal vertebrae stand in contrast to only 54 presacrals (Siebenrock 1895) and in the pygopodids the tail is twice as long as the body. Only in scincoids such as *Scincus tridactylus* (Siebenrock 1895) and the amphisbaenians is the tail shorter than the precaudal portion of the body. In

Chalcides	61 presacral and	43 postsacral vertebrae are present, in
Acontias	77 and	25 (Gervais 1869),
Anguis ['*Augius*']	62 and	65,
Ophisaurus	54 and	111;

since, moreover, the shoulder girdle is more strongly reduced in *Acontias* than *Chalcides*, and in *Anguis* than *Ophisaurus* (Peter 1895), one sees that as in these terrestrial forms living under leaf-litter, a slight shortening of the tail goes with strong reduction of the shoulder girdle and increase in the number of presacral vertebrae.

The same as for these forms above goes for the pygopodids with similar way of life, as is apparent from Werner's (1912) review; here too in those which have relatively small limb rudiments (*Ophioseps* and *Aprasia*) the tail is relatively short. *Anniella* has about 72 presacral and somewhat over 40 postsacral vertebrae (Coe-Kunkel 1907). In the fossorial amphisbaenians, which also have 100 to 200 vertebrae, the truncation of the tail is stronger and it reduces the ratio of the number of pre- and postsacral vertebrae to 5:1 (*Chirrotes* 4:1, *Amphisbaena* 5:1, *Trogonophis* 5:1 to 6:1), moreover the fossorial amphibian Gymnophiona are also distinguished by a high number of dorsal vertebrae and an especially short tail. In them, for 100 to 200 dorsal vertebrae there are only 0 to 5 caudal vertebrae (Peter 1895). The reduction of the tail, already indicated in terrestrial forms which burrow under litter, is thus even more marked in underground forms. In the aquatic, mud-inhabiting, serpentiform amphibians there are relatively many presacral and somewhat more postsacral vertebrae, e.g. (Gervais 1869) in

Siren lacertina	64 presacral and	35 caudal,
Amphiuma	57	18,
Proteus	32	35.

In contrast to this, *Triton* has only 15 and *Menobranchus* 18 presacral vertebrae. In the mud-burrowers there is thus an increase in the number of presacral vertebrae, but a reduction of the postsacrals does not occur; in the burrowing forms of the land a reduction of the postsacrals is combined with the increase of presacrals; and finally in all swimming forms lateral compression makes its appearance together with increase in number, especially in the postsacral part of the body.

While in respect of the rest of its structure, the urodeles do not come into consideration as relatives of *Pachyophis*, our animal can be compared most closely with the scincoids in terms of vertebral numbers, but in distinction from *Pachyophis* and the amphisbaenians these have relatively few vertebrae, and in other respects, like the amphisbaenians, take a different direction of development. A *Pachyophis*-like proportion of pre- and postsacral vertebrae can otherwise be found, among reptiles, only in the snakes. Here the number of vertebrae normally lies between 200 and 300, and exceeds 400 only in some boids and *Dryophis*. In the typhlopids it is as low as 188, in the uropeltids 155, but in these forms, as in the amphisbaenians, the number of caudal vertebrae is certainly reduced. A shortening of the tail can also be observed in the sand-digging *Eryx*. The proportion of numbers of trunk and tail vertebrae of snakes, from Rochebrune (1881) and my own counts, if - not that there should be any doubt - one regards Rochebrune's "sacral vertebrae" as anterior caudals and not, as Janensch (1906) does, as trunk vertebrae (I refer to Cligny 1899), for the individual families, on average, are approximately as follows:

			['average' trunk verts:
in the	Typhlopidae	15:1	160
	Glauconidae	11:1*	130
	Uropeltidae	10:1	140
	Ilysiidae	11:1	170
	Xenopeltidae	6:1	180
	Boidae	4:1	280
	Archaeophidae	5:1	450
	Viperidae	4:1	150
	Colubridae	2:1	170/180/200]

[* The ratio of head-trunk length to tail length can, as Werner states, vary between 20:1 and 5:1. Unfortunately data on the relative number of vertebrae are not available.]

In *Pachyophis* it probably lay between 6:1 and 4:1.

As can be seen from this summary, the typhlopids, glauconids, uropeltids and ilysiids have the shortest tails, probably reduced as a result of a burrowing way of life; the xenopeltids have longer ones, then come the boids, archaeophids and *Pachyophis* (?), next the vipers and finally the colubrids. Thus the last have the greatest number of caudal vertebrae, but it must be remarked that the ratio varies between 2.2:1 in the opisthoglyphs and 2.8:1 in the aglyphs and proteroglyphs, and in some aglyphs (*Dasypeltis*, *Tropidonotus*, *Xenodon*, *Dimades*) can exceed 4:1. The last named forms, on this account, were not included in calculating the average number for the aglypha.

The total number of rib-bearing vertebrae averages 130 in *Pachyophis* and the glauconids, ca. 140 in the uropeltids, 150 in the vipers, 160 in the typhlopids, 170 in the proteroglyphs and ilysiids, 180 in the opisthoglyphs and xenopeltids, 200 in the aglypha, 280 in the boids, and finally in the archaeophids as much as 450. By the number of its trunk vertebrae, *Pachyophis* stands at the beginning of this series. Since all these numbers vary strongly among individuals, we can operate only with averages.

On the assumption that the primitive snakes possessed ca. 140 trunk vertebrae and ca. 30 caudal vertebrae, we can conclude from the above summary that *Pachyophis* probably still retained the primitive condition, that in the glauconids and uropeltids there has been mainly just a reduction of tail vertebrae, in the archaeophids and boids a strong but uniform increase in trunk and caudal vertebrae, and in the colubrids the increase in vertebrae has affected the caudal region relatively more strongly; admittedly these are only **average** results.

A further snake character of *Pachyophis*, which will occasionally be mentioned in the detailed description below, is the very large zygosphene, projecting far anteriorly, and the zygantrum extending deep into the neural arch. Thereby *Pachyophis* is distinguished from the genus *Anniella* which shows 73 rib-bearing vertebrae (Gervais 1875). On the anterior vertebrae the antero-posterior dimension of the zygosphene attains half of the same dimension of the neural arch. In the iguanids the zygosphene is present only in the large forms (Cope 1892, Owen 1877). Together with the number of vertebrae discussed earlier, this zygosphene stamps *Pachyophis* decisively as a snake.

From the form of the vertebrae and ribs, one can distinguish a cervical portion of the vertebral column, a space for the lungs, an abdominal part, and an unknown tail region.

The vertebrae and ribs on the adjoining slab represent a substantial complement to the main slab. There are 33 vertebrae and before them the remains of 4 ribs preserved, and this shows the existence of at least 37 rib-bearing vertebrae. Since on the main slab, of vertebrae 1 to 43 the neural arches of only 19 to 24 are preserved, this fossil in fact fills a serious gap. An exact determination of the numerical equivalence of the vertebrae of the main and adjacent slabs is not possible, but already by the 23rd vertebra of the main slab the width of the neural arch is almost the same as the length (1:1.1), while on the adjacent slab by the 29th the vertebrae are still decidedly longer than wide (1:1.3), so in any case the 29th vertebra of the adjacent slab lies anterior to the 23rd [+x], and indeed the latter must, as a calculation shows, approximately correspond to the not-preserved 36th vertebra of the adjoining slab.

Turning to the ribs, one sees that about the 32nd rib of the adjoining slab corresponds to the eighth rib of the main slab, and this also leads one to the result, that anterior to the first well-preserved vertebra of the main slab, 14 more vertebrae are well known.

The first known cervical vertebra of the adjoining slab is 3.3 mm long, laterally compressed in the middle of the arch and here only 2.3 mm wide. At the prezygapophyses and of course the postzygapophyses the arch becomes much wider. The flanks of the arch, which is longer than broad, fall quite steeply down on both sides. Dorsally there rises anteriorly on the arch a narrow, very low, but quite prominent lamella scarcely 0.1 mm thick, which increases in depth and thickness posteriorly and rises to a 0.9 mm thick, rod-like neural spine which is directed posteriorly. The height of this neural spine can not be determined, because due to its small dimensions the neural spine of none of the vertebrae could be freed from the rock of the counterpart slab. In their present state of preservation the neural spine, which is restricted to the posterior part of the arch, has a height of 0.9 mm. Lateral and parallel to the neural spine, on the neural arch which gently rises posteriad, two very shallow, wide grooves are noticeable, which extend almost to the end of the vertebra and make the ridge [*Leiste*, strip-like moulding in architecture, on cars etc.] of the neural spines especially stand out.

On the following neural arch, which also shows the left side well, it is very clearly visible that the sides of the arch are high and that the prezygapophyses lie quite high above the centrum. From the prezygapophysis to the postzygapophysis runs a prominent, horizontal ridge [*Leiste* again], below which the vertebra is narrower transversely. It cannot be decided whether a second ridge, running downward and somewhat backward from the prezygapophysis, already represents the pleurapophysis.

The third neural arch has a length of 3.7 mm and breadth in the middle of 2.4 mm, its form is similar to that of the first, but the transverse narrowing in the middle is slighter. Already on the sixth, still elongate vertebra a large, prominent zygosphene can be seen, that approximately at its origin shows the considerable diameter of 1.1 mm. Becoming steadily longer, the following vertebrae all show approximately the same build as the third, while all dimensions increase. By the tenth vertebra one can already measure a length of 4.7 mm and width of 2.5 mm; by the seventeenth a length of 5.1 mm and width of 3.3 mm. On the eleventh and twelfth vertebrae the lamella leading up to the neural spine is particularly well preserved, and on the twelfth one can see distinctly that both of the grooves running beside it are reduced to two small flat pits restricted to the upper anterior part of the arch. Between the tenth and seventeenth vertebrae, as already indicated by the measurements given above, an increase in width becomes noticeable. On the nineteenth it is clearly seen that the prezygapophyses still face almost exclusively inwards, and moreover one can splendidly see the zygosphene on this and also the preceding and following vertebrae. It is a good 1.2 mm wide, and visible for a length of 1.8 mm. Its total length probably reaches 2.0 mm. In respect of which, given that the total visible part of the arch is only 5.1 mm long, the zygosphene is very large. Also the following vertebrae show no special change in the arch, only that it becomes steadily broader, and flatter dorsally. In place of the steep flanks meeting above like a roof, by the twenty-sixth arch a bulge is visible dorsally on the anterior part of the neural arch, posteriorly the flanks lead though gradually only up to the neural spine, which is laterally only poorly distinguished from the arch.

Vertebrae of the main slab. Of the more or less fragmentarily preserved cervical vertebrae, which lie anterior to the articulated series on the main slab, there is little to say. On some of these vertebrae the well-developed, high-rising prezygapophysis or the postzygapophysis is distinguishable, others show a fractured centrum, but the conspicuously small size and a very thin and delicate build is common to all.

The **first** better-preserved vertebra of the main slab (= No. 15 of the adjoining slab) shows as its most striking feature a long and narrow neural spine, which with a height of 3.5 mm is only 1.0 mm wide. It is directed obliquely backwards, and somewhat laterally compressed. The neural canal is large in this vertebra, the centrum and arch fully fused, and the centrum and arch together are somewhat higher than wide. The prezygapophysis is in a high position, is narrow and extends far anteriorly.

Vertebrae **two** and **three** are only visible in longitudinal section, so one sees only the wide neural canal. Its floor is divided by a line which corresponds to the line of separation of the two vertebrae; in the middle it projects forward convexly, but is weakly concave on each side. The width of the neural canal measures 1.7 mm.

The **fourth** vertebra is twisted so that its neural spine has the opposite orientation to that of the first; in this case too it is rod-shaped and laterally compressed, so that with a length of 2.6 mm and thickness of 0.7 mm it is very similar to that of the first. Also in this vertebra the prezygapophysis extends far anteriorly and the neural canal is very spacious. Similar, posteriorly directed neural spines are found on the first cervical vertebrae of the amphisbaenian *Pachycalamus brevis* and even better developed in the water snake *Homalopsis buccatus*. Since neither form is closely related to *Pachyophis*, the resemblance among them can only be a case of parallelism.

With the **fifth** begins the series of better preserved vertebrae. Of its rodlike neural spine there is indeed only the imprint preserved in the stone and the centrum and arch are also strongly damaged, so that in its anterior half the 1.9 mm wide neural canal is again visible; but this vertebra is important because its condyle could be split off without damaging it too much, thereby making visible the receptive joint surfaces of the following vertebra. This sacrifice of a small piece was scientifically justified, for on none of the following vertebrae could the articulating surfaces be made visible with such a slight loss.

Of the **sixth** vertebra too, mostly only the right side is preserved, the one turned away from the observer and embedded in stone, so that the neural canal is again visible; but this vertebra shows a fine longitudinal section. Anteriorly the concave articular surface is mostly still preserved, as the cut surface does not pass through the middle of the vertebra. The length of the centrum is 3.0 mm, it is strongly thinned dorsoventrally in the middle and reduced to 1.0 mm; its dimensions increase toward the cotyle and condyle. The cotyle shows a vertical diameter of 1.2 mm; the transverse can not be measured exactly, but the unequal curvature of the edge makes it clear that it was greater than the vertical; so the cotyle shows, as in the anterior cervicals of pythonids and typhlopids, a transversely oval outline. The well preserved postzygapophysis of this vertebra lies quite high up and is directed downwards and outwards. The 0.8 mm-long hypapophysis is also quite well preserved on this vertebra. It is narrow, quite long and lies far anteriorly. It is somewhat anteriorly directed and in this respect differs from the hypapophyses of recent snakes. A similar hypapophysis is found in *Pterosphenus* and *Palaeophis*.

On the **seventh** vertebra, which generally shows the same habitus as the sixth, one sees a small zygosphene projecting 1.6 mm anteriorly, above and behind it the high narrow neural spine, and below and behind it, due to the postzygapophysis being broken off, the zygosphene of the following vertebra, which extends far into the arch of the seventh. At the anterior edge of the centrum and quite far ventrally an expansion, the pleurapophysis, is visible, and on the lower edge of the middle of the centrum sits another short hypapophysis, with a broad base connecting it with the centrum. A second hypapophysis as in *Pterosphenus* seems to be absent, as in the preceding vertebra. On the sides of the centrum at half its height runs a blunt keel, which projects more strongly in the middle of the centrum than at both ends.

The **eighth** vertebra is in most respects the same as those preceding. It lacks the upper end of the neural spine, but the preserved part shows the same shape as on the preceding vertebrae; also the pleurapophysis shows the same position, but is better preserved so that one can see it projects only a little from the centrum and had a high elliptical outline. A roll-joint [?] as in *Python* was not developed. On this vertebra too, a blunt keel is seen running antero-posteriorly at half-height. The zygapophyses show the same position as on the seventh vertebra, but face somewhat more strongly upwards, or respectively downwards.

Unfortunately the **following ten** vertebrae (9 to 18) are all strongly damaged, so that again one sees only cross-sections, but the vertebrae in this neighbourhood complete a torsion, so they are cut differently by the more or less flat broken surface. In the more anterior ones the break runs so that it cuts the left side of the arch dorsally, and ventrally the right half of the centrum, but in the posterior ones because of the twisting of the vertebral column it runs more and more parallel with the base of the vertebra. The extent of the torsion between the ninth and eighteenth vertebrae comes to nearly 90˚. This is the portion of the skeleton where the orientation of the neck, on its side, changes over to the ventral one of the rest of the skeleton. Thus in the living animal, apparently the deep oval neck of the animals changed over to the cylindrical trunk between the ninth and eighteenth vertebrae.

In contrast to the most anterior preserved vertebrae, in which the bone mass is indeed dense, but the bones themselves are thin, already by the sixth [i.e. 14th + x] vertebra an increase in the thickness of the bones is noticeable, so that under the loupe one can already count six concentric layers of bone. Further posteriorly this thickening increases still more, so that on the tenth [18th + x] vertebra already nine, quite thick bone layers can be distinguished.

A detailed description of vertebrae 9 to 18 is not necessary in view of their poor preservation, but it suffices to point out that one can recognise the strongly convex condyle of the fourteenth vertebra which sticks into the cotyle of the following fifteenth vertebra. Between the fifteenth and sixteenth vertebrae a piece has been removed during[?] exposure of the lower jaw.

The **eighteenth** vertebra is so much better preserved than the preceding ones that both of its zygapophyses are preserved on the right side. In contrast to the sixth vertebra their articular surfaces face down and up, and only a little outward or inward. This is harmonious with the body, here no longer laterally compressed. Behind the prezygapophysis the arch is strongly puffed up, the prezygapophysis therefore seems to be sunk into the body of the vertebra and forms a small groove [better than 'pit'?] opening forward and outward. This deep position of the prezygapophysis in front of the swollen neural arch distinguishes *Pachyophis* well from the varanids and partly also from the typhlopids and boids. In the latter, though, a small pit is visible behind the prezygapophysis. A similar pit is found again in *Adriosaurus*, though also more weakly developed.

The **nineteenth** vertebra shows a splendidly preserved arch. Including the visible part of the zygosphene, this is 3.7 mm long, 4.0 mm wide in the middle and 5.3 mm at the prezygapophyses. The articular surfaces of the prezygapophyses also each lie at the bottom of a deep groove, whose medial edge climbs immediately and steeply to the body of the zygosphene, while the posterior edge is formed by the sharply climbing swollen vertebral arch. The outer border of the prezygapophyseal articular facet is formed by a sharp edge, which runs up against the base and flank of the arch. The facet faces upwards and, because it is large, allows a substantial motion of the preceding postzygapophysis. The neural arch has the form of a flat roof, falling off fairly uniformly. The postzygapophyses extend laterally from the posterior part of the roof only as inconspicuous swellings. As the neural spine is broken off at its base, posteriorly to the ridge the roof springs sharply inwards, so that the ride is shorter than the flanks. At the blunt ridge one sees a slight edge anteriorly, which runs up to the broken surface of the neural spine, but begins only in the middle of the ridge. Lateral and anterior to this edge one sees on each flank, in the vicinity of the ridge, a small, shallow, longitudinally oriented groove that lies in line with the posterior edge of the prezygapophyseal groove. The part anterior to this second groove belongs to the zygosphene.

The **twentieth** vertebra is similar in its dimensions and structure to the preceding, but is differentiated from it by the grooves on the neural arch being much more strongly developed. Due to this stronger development the part of the arch between them forms a sharp edge, while it is quite flat on the preceding vertebra. The zygosphene lying anterior to the groove consists of a roughly parallelepiped-shaped body, which disappears under the preceding neural arch and increases in thickness anteriorly. The upper dorsal surface of this parallelepiped-shaped body is traversed by a broad but not deep median longitudinal furrow, increasing in strength anteriorly. This vertebra also lacks the neural spine; to judge from the broken surface, it was limited to the posterior part of the arch and consisted of a thick, posteriorly directed lump roofing the zygosphene.

The four following vertebrae (**21, 22, 23, 24**) are all built like the twentieth, hence a further description is not necessary. The dimensions of the 22nd vertebra are: length 4.3 mm, width at the narrowest point 4.0 mm.

The **twenty-fifth** and **twenty-sixth** vertebrae are unfortunately relatively poorly preserved, for they lack the most part of the ridge of the neural arch and also the preservation of the rest of the arch leaves something to be desired, yet one sees that the neural spine, though broken off, lay still further back than on vertebra 20. The base of the hypapophysis here lay well behind the middle of the neural arch, and the keel between the two [dorsal] grooves becomes pronouncedly stronger against the neural spine.

Vertebrae **27, 28** and **29** are even worse preserved than the preceding; the same goes too for the **thirtieth**, yet on the last, as the posterior part of vertebra 29 is missing, the zygosphene is by chance very well visible. As in the twentieth vertebra, it consists of a parallelepiped-shaped part which gives off anteriorly two divergent short, thick branches. This construction is perfectly that of the zygosphene of some snakes, e.g. *Python*, *Boa.* As far as the dimensions of one of these posterior cervical vertebrae are concerned, it suffices to mention that at the narrowest part, the arch of the 28th vertebra is 5.2 mm wide.

As the posterior part of vertebra **30** and the whole arch of vertebra **31** are missing, the neural canal is here visible again. One sees that the canal, which at the fifth vertebra was still 1.9 mm, is here reduced by the increased thickness of the bone to 0.9 mm [JS: THIS IS TOO SMALL TO BE A GOOD MEASURE OF DIAMETER]. The cross-section of the centrum of these vertebrae shows a drum-like shape.

The **ten following** vertebrae (**32** to **42**), while they show parts of the arch, are all too badly preserved to deserve a detailed description, hence it suffices to say that the length of one of them is 5.2 mm and the width 6.4 mm, that the neural canal is 1.2 mm thick, and that its centrum had an obviously drum-like shape.

With the **43rd** begins a series of well preserved vertebrae, which are different from the preceding ones. The arches of these vertebrae are uniformly swollen and consist of a flattened dorsal part traversed by longitudinal grooves, out of which the neural spine rises, and steeply falling-off flanks, which are joined to the dorsal part by very strong rounded edges. The flanks show on each side a hollow [*Aussparung*, piece taken out] which begins anteriorly at half-height and runs posteriorly and down, increasing in strength. The part anterior to and below this hollow can be counted as part of the prezygapophysis, the part lying posterior and above it is the postzygapophysis. Between the pre- and postzygapophysis the hollow crosses over onto the flank of the centrum. The neural spines of all these vertebrae have the form of a longitudinal, low lamella, increasing significantly in thickness posteriorly, which attains its highest point at its posterior end. In general the arches of these vertebrae are all broader than long, in particular the following differences can be recognised:

The arch of the first of these vertebrae (43) is 4.6 mm long and 6.8 mm wide. The neural spine does not reach the beginning of the arch and is relatively little developed in the longitudinal direction. At the thickest part of the base it is 2.9 mm wide, it thus takes up transversely a large part of the flattened, 5.5 mm wide upper part of the arch. Laterally the neural spine is bordered against the arch by two deep, narrow, sharply incised grooves, against which it is hence sharply discontinued. Caudally the neural spine does not extend further than the arch itself, the vertebra therefore looks like it has been cut off in a straight line posteriorly. Corresponding to this form, the anterior edge of the following vertebra is also almost straight.

In contrast to the anterior edge, the posterior edge of vertebra 44 is posteriorly convex in the middle, as its neural spine extends far caudally, and correspondingly a deep anterior median concavity is present on vertebra 45. This strong median convexity of the posterior edge of the trunk vertebra of *Pachyophis* is again reminiscent of *Adriosaurus*, then too somewhat of *Pontosaurus*, and does not appear in recent snakes. The neural spine, which on the 44th vertebra reaches the anterior edge of the neural arch, on this vertebra has the shape of an anteriorly narrow, posteriorly thick ridge gradually rising posteriorly. As on this vertebra several of the concentric bone lamellae, already mentioned in the cervical vertebrae, have been flaked off on the left side, one sees that the uniformly swollen shape of the arch of all these vertebrae comes about by the pachyostosis, especially in the different hollows of the arch, so that the grooves running parallel to the neural spine stand out particularly strongly, and hence these grooves are also made visible on the left due to the flaking off, while they are missing on the right. On the anterior side of this neural arch one can recognise the base of the large, strong zygosphene, which disappears under the arch of vertebra 43.

Vertebra 45 is also built like vertebra 44, but the grooves lateral to the neural spine are completely absent, and its base shows a longitudinally elliptical cross-section. I think I can count about 12 concentric white to grey bone layers on this 2.9 mm thick cross-section under the loupe, which surround a less distinctly concentrically built, dark, coffee-coloured core of diameter 0.6 mm - obviously the original neural spine. The pachyostotic part is more than three times thicker than the original bone. The prezygapophyses are well preserved on the left, on the 44th as well as the 45th vertebra, they lie deep ventrally and face directly upwards. This shows that the vertebral column in this part was capable only of exclusively lateral motions.

On **vertebra 47** the two lateral furrows beside the neural spine can again be clearly seen, but here their maximum development is at the posterior edge of the arch.

A perfectly preserved neural spine is retained on the **fiftieth** vertebra. A cross-section through its base would show the form of an elongated egg with the anterior end sharply pointed. The neural spine itself consists of a keel rising from the anterior edge of the neural arch, which posteriorly climbs at first somewhat more steeply, further back less steeply, and attains its highest point behind the intersection with a line drawn vertically from the posterior edge of the arch. Beyond this point a small facet is noticeable on the tip of the neural spine. Below and anteriorly the keel leading to the neural spine is sharpened, further up is becomes gradually more blunt, and it is rounded at the highest point. This rounding is of course related to the caudal increase in thickness of the neural spine base. As implied by this description, the neural spine of each vertebra projects quite significantly backward, and thus pushes itself above and between the lateral parts of the following arch.

On **vertebra 54** one sees, on the blunt and steeply falling-off rear edge of the neural spine, a small vertical notch, becoming stronger towards the base, which serves to accept the keel of the following vertebra. The anterior lower part of each neural spine is thus flanked by two bone lamellae developed, particularly at the base, on the preceding neural spine. The same can also be stated for the preceding vertebra, but here the posterior side could not be correspondingly freed from the rock. Otherwise vertebra 53 is built just like the preceding ones. Lateral to the neural spine the arch on both sides is swollen like a cushion, and separated from the spine by a furrow. The flanks of the cushion fall off steeply; the upward-facing prezygapophysis lies anteriorly deep below the cushion; it is separated from the upper part of the flank of the cushion by the shallow, broad hollow which crosses to the centrum of the vertebra between pre- and postzygapophysis.

Vertebrae 54 to 61 are built exactly the same as vertebra 53, but they are now missing the neural spine from the fifty-sixth on. On vertebra 60 the arch has a width at the narrowest point of 7.5 mm, and length in the midline 5.4 mm. The concavity at its anterior edge for the neural spine overhanging its zygosphene is strongly developed, and correspondingly forces the base of the neural spine of vertebra 60, above the zygosphene, far into the arch of vertebra 61. The connection of individual vertebrae in this manner is indeed mobile, but very tight.

The entire arches of the **following eight vertebrae** (**62 to 69**) are missing, but this is of use in so far as one can again follow the course of the neural canal. This is approximately circular in section, has a diameter of 1.0 mm and expands only insignificantly at the ends of the vertebrae. The length of one of these vertebrae comes to 4.1 mm, the outline again indicates a drum-shapes centrum.

Also the **following vertebrae** (including **70**) are generally built like the preceding, but the upper flat portion of the arch, still elevated into a cushion shape, is transversely narrower, measuring only 5 mm on vertebra **73**, while the furrows separating the neural spine from the arch becomes stronger again and duplicate, so that two parallel longitudinal furrows run on each side beside the base of the neural spine. Also the anterior concavity of the middle of the neural arch is again more weakly developed than in vertebra 60.

As the neural spines of all the vertebrae from 70 to 90 are missing and a perfect neural spine is not preserved until vertebra **90**, all that can be said about their proportions is that within this series of vertebrae their anterior ends again become restricted to the posterior part of the vertebra, so that eventually again only the posterior half of the arch bears the neural spine. It climbs steeply but gradually from anterior to posterior, then falls off posteriorly, overhanging the following vertebra, and culminates in a rounded thick knob.

The prezygapophyses are first visible on vertebra 73, then especially on **82**, **83**, **84**, **85**; in all these cases though, only on the right side. The prezygapophysis of vertebra 73 is distinguished from those preceding by its articular facet no longer facing directly upward, but rather obliquely upward and inward, which is achieved by an inward and upward bending of the prezygapophysis. Thereby arises a deep and spacious hole between the articular facet, the zygosphene, and the arch rising high behind them. Where the upper edge of this hole meets the lateral edge of the zygosphene, it is more sharply developed.

The same characters, but even more pronounced, are found on vertebrae 82 to 85. Due to the upward and inward bending of the prezygapophysis, its outer edge lies at the same height as the parallelepiped-shaped part of the zygosphene, while the articular facet descends from this edge and faces more inward than upward. Rising again posteriorly and medially, it is connected by curved surfaces on one side with the lateral facet of the zygosphene, on the other with the neural arch which lies at the same height as the body of the zygosphene. Thus the articular facet of the zygosphene forms the outer surface of an anteriorly open pit climbing against the zygosphene, neural arch and prezygapophysis.

The reduction of the flat upper part of the arch lateral to the neural spine, which was already noticeable by vertebra 70, has proceeded even further by vertebra 82, for the flat upper lateral parts of the arch are reduced to a very narrow zone and the flanks of the obviously very thick arch meet the neural spine almost immediately. By vertebra 84 one can no longer speak of an upper flat area at all.

The arch of **vertebra 89** consists of two less steeply sloping surfaces next to the neural spine, and two steeper ones further below, hence close to the centrum, In this way the vertebra has the form of a doubled roof, blunt above, from which the neural spine rises on the posterior half. The zygosphene is also well developed on this vertebra, flattened above and as always, reaches under the arch of the preceding vertebra. The length of this vertebra is 6.5 mm, its width 4.5 mm. The transverse thickness of the neural spine is 1.5 mm, its brown core 0.9 mm. Unfortunately the direction of the postzygapophyseal articular facet of this vertebra is not recognisable, but it seems to have had the same orientation as in vertebra 84, where it is a vertically rising knob over the zygosphene of the following vertebra.

Due to the still greater reduction in width, the vertebrae yet more posteriorly seem to become more slender while the shape [otherwise] remains the same; so vertebra 97 is now only 4.2 mm wide, but still 4.2 mm long; vertebra 101, on which the neural spine is incidentally again well preserved, just 3.7 mm wide and 4.8 mm long; and the next-to-last vertebra visible from the dorsal side (108) only 3.8 mm long and 3.2 mm wide. An indication of the orientation of the prezygapophyseal articular facet is visible on vertebra 95, and shows that the orientation itself was as on vertebra 83.

On **vertebra 97** one can well see that the anterior part of the neural arch shows a dorsally elliptical cross-section, and that the neural spine only rises behind the middle of the arch; on **vertebra 102** there are again two shallow grooves on the part of the arch anterior to the neural spine, as we already knew on the cervical vertebrae. An overhang by the neural spine, still quite thick, over the arch of the following vertebra is also recognisable on vertebra 102; on the other hand on those vertebrae where the neural spine is missing the zygosphene still reaches far under the arch. As the next-to-last vertebra 108 only differs in its slighter width from those already described, its detailed description is not necessary, and a more detailed description of the arches in this region can hence also be done without, for they vary to some extent in their fine structure. This variation, combined with the reduction in size, shows that despite the presence of true ribs we are approaching the end of our animal's tail.

3 [lapsus '2' in original]. Ribs. The ribs of the most anterior portion of the body of our animal are only preserved on the adjoining slab. They are extremely delicate structures. Unfortunately nothing further can be recognised apart from their generally needle-like shape. The length of the third rib on the right side comes to 8 mm, its thickness even at the proximal end not much more than 0.3 mm, and at the distal end it is correspondingly thinner. Approximately its upper third is almost straight, then the rib bends relatively quickly through an angle of 120 degrees and then becomes straight again. Its articular facet is a round bowl with swollen borders.

The twenty-second rib shows almost the same structure, but its angle of bending comes to about 140˚, moreover its proximal end is 0.9 mm thick, and finally the rib itself (measured along its curve) is already almost 17 mm long. On the rib of the thirty-second vertebra the proximal thickness comes to about 1.0 mm, but its length is unknown.

The circular bowl-shaped articular facet can also be seen well in negative on the 23rd to 25th ribs.

In addition to the description of these ribs, that of the ribs on the main slab can now be given, but it is to be noted that, as said before for reasons of convenience, I have begun again from 'one' in numbering these, to facilitate finding the individual ribs in the figure of the specimen.

Fragments of badly preserved ribs are already present by the first remaining cervical vertebra of the main slab, but they only begin to be better preserved at the first vertebra of the whole series to be preserved with its neural spine. The left-side rib of this vertebra (No. 7 = No. 21 of the adjoining slab) is straight in its first third, circular in section, 0.5 mm thick and ends proximally as if cut off. As seen in the photograph, the straight part is very slender. Its proximal third is somewhat curved and thickens towards the unfortunately missing head.

On the tenth rib of the series the head is preserved, and there one sees distinctly that is was cut off straight and showed one presumably concave articular facet. Unfortunately it does not seem advisable to remove the matrix from the facet. The rib length amounts to about 15 mm. Between the seventh and seventeenth vertebrae the ribs are poorly preserved. By the seventeenth vertebra a rib head is again preserved, but it belongs to the eighteenth vertebra. One sees quite distinctly how the body of the rib (=33 of the adjoining slab), gradually thickening dorsally, at the upper end simply stops straight. This rib too, which must be called a transitional rib, was gently curved in its upper part, straight below. The cross-section of this rib is circular, its diameter at the head comes to 1.0 mm. It can be determined that all ribs up to the 82nd lack any marrow cavity.

The left rib of the twenty-first vertebra is distinguished from the eleventh in that one sees a slightly developed thinning of the rib distal to the articular facet, adjacent to it and again disappearing towards the middle of the rib, a kind of collum. On the twenty-third rib, certainly representing a trunk rib, this collum extends scarcely 1.5 mm [but] is already distinctly visible and quite well bordered against the rib. Unfortunately the upper ends of both ribs of the **twenty-third** vertebra hidden under its centrum, hence their length is not exactly measurable. At the twenty-fifth rib the length, measured along the outer edge of the rib, comes to 17.7 mm, the thickness of the collum 1.0 mm; the thickest part of the rib has a diameter of 1.3 mm. At the distal, well-preserved end this rib is 0.4 mm thick. This end, as one can see especially well on ribs 27 and 28, is somewhat thickened and cut off straight at the beginning of the costal cartilage. On the thirtieth rib the collum is 1.1 mm, the rib at its thickest point 1.5 mm, and the distal end 0.6 mm thick. As the swelling of the rib sets in fairly immediately ventral to the collum, this seems even more sharply set off against the rib than in the preceding ribs. The curvature of the rib, which on the twenty-fifth scarcely reached below the first third of the rib, on the twenty-ninth already reaches the middle.

On the thirty-fourth rib the proportions are approximately the same as on the twenty-ninth, but the cross-section of the rib, as the bone-thickening of its middle does not increase uniformly around the periphery, is not round but a high ellipse; in addition it is flattened on the posterior side. The antero-posterior thickness - unfortunately the only one measurable - comes to 2.2 mm at the thickest point. The ribs of the **thirtieth** show distinctly that the flattened part is somewhat rougher than the convex upper and anterior parts, and on the following ribs this roughness increases rapidly and quite significantly. It forms strongly projecting, quite irregularly distributed, small bumps of various sizes, which join up on the more posterior ribs into irregularly shaped, elevated parts, out of which the tips of the individual ribs still project. Every aspect of these structures allows them to be recognised as periosteal growths. Thus periosteal growths are added to the osteosclerosis of the ribs already mentioned earlier. On the **thirty-ninth** rib these periosteal growths are already quite strong, [while] they become really conspicuous from the **fifty-first** rib on.

Constantly bound to the flattened posterior side of the ribs, the growths persist up to the **sixty-ninth** rib, then they gradually reduce again. On the **seventy-ninth** rib they have nearly disappeared. On the ribs which show these periosteal growths on the posterior side, one can see numerous round pores on the smooth surfaces, but not at all close together, which lead to the interior of the bones, as in the pachyostotically and osteosclerotically changed ribs of the halitheres.

Of course a significant increase in thickness goes hand in hand with the development of the periosteal growths of the thoracic ribs of *Pachyophis*. At the **fifty-first** rib its greatest diameter is 3.5 mm, at the **fifty-sixth** it falls to 3.1 mm. Their lengths are about 40 mm.

As implied by the position of the collum with respect to the hyperostotic part, the hyperostosis affects principally the dorsal part of the ribs. On the **forty-fourth** rib the collum still lies in the continuation of the rib axis, [while] on the following ones it retreats gradually below the axis. This deep position of the collum makes it difficult on the strongly hyperostotic ribs to free it from the rock, for the upper hyperostotic part of the rib retreats close to the vertebra. Only on a few of the more strongly hyperostotic ribs was is possible to expose the collum. On the **thirty-seventh** right rib it is shown that the bone growths affect not only the dorsal, but also the ventral side of the collum, and here form a narrow plate, 0.5 mm wide, projecting in front of the collum and becoming wider toward the proximal end of the rib. At the end of the collum this plate is joined to the thickened part of the rib, hence forming a longitudinal notch in front of the collum and equal in length with it.

One obtains approximately the same picture on observing the **sixty-first** rib, but one sees clearly on this that the hyperostosis here also extends onto the collum. The anterior notch on the **forty-seventh** rib has almost completely disappeared, to a slight trace, and the collum, which on this rib had a diameter of 0.7 mm, is thickened to 1.2 mm.

A similarity, not to be undervalued, with the structure of the forty-seventh rib appears again with the **sixty-seventh** rib; but on this one, besides the ventral, the sharp posterior edge of the rib creates the impression that the ventral surface of the rib were completely flat.

Between the sixty-seventh and seventieth ribs the hyperostosis, as already mentioned, reduces significantly, and correspondingly the collum again projects clearly and on all sides. From the seventieth on, the less hyperostotic ribs, about 18 mm long, also differ from the preceding ones in their straighter shape and their once again round cross-section. The maximum thickness of the **seventy-third** rib comes to 2.1 mm, at rib **96** 1.4 mm, and on rib **103** only 0.8 mm. From the ninety-eighth rib on, the collum disappears completely and correspondingly the thickness of the rib decreases uniformly from the proximal articular facet out distally. From rib 82 on the ribs, which until this point were massive, become porous proximally and hollow at the distal end, and in part completely hollow from 94 on.

The fact that only a part, and indeed only the more anterior trunk ribs, shows the enormous pachyostosis, also speaks in favour of the hypothesis that pachyostosis is conditioned by the lungs; for otherwise the lack further posteriorly, where the lung-sacs no longer reach, is absolutely incomprehensible.

The form of the articulating surfaces of all the different types of ribs could not be investigated on the main slab.

4. Scales. While exact knowledge would be very important, unfortunately only little can be said about the scalation of *Pachyophis*.

Among recent snakes one can distinguish **a**) those in which the belly as well as the whole rest of the body is covered with undifferentiated cycloid scales (glauconids and typhlopids), **b**) those in which broader scales occur on the belly, which somewhat or conspicuously exceed the lateral rows (most snakes), and **c**) those in which the median ventral scale row is only a little or not at all broader than the other rows, but in which these scales are somehow distinguished, e.g. by two keels, and thus show that they derive from previously broadened scales (uropeltids, ilysiids, *Enhydris*, acrochordines). On the bellies of such snakes scale-anomalies are not at all rare (Jan and Sordelli Vol. **3**, fascicle [*Lieferung*] 39, Pl. 4 fig. 41; fasc. 40, Pl. 3 fig. 57, Pl. 4 fig. 35; fasc. 41, Pl.1 fig. 47, Pl. 2 fig. 33). Among fossil snakes only the scales of *Archaeophis* and some modern types have hitherto been known and illustrated. Janensch described the scales of *Archaeophis* as oval. A development of true ventral scales could not be recognised. The scales of the other fossil snakes connect with those of the modern types. To this restricted number of fossils known from their scale structures, *Pachyophis* is now added.

In *Pachyophis*, at several places close to the body and in part also under the ribs, a layer can be recognised filled with a brown, sometimes blackish, somewhat granular substance, along which the stone easily separates from that below. Under the loupe it gives the impression of a very thin layer of coal. It shows clearly an impression of the skin of the body. Unfortunately the whole skin is extremely thin and mostly badly preserved, so that almost nothing can be said about the form of its components, for it is mostly seen only as multiply interrupted granulation. There is an exception in the vicinity of the 6th to 12th ribs, where under the loupe one can see some parts where the brown substance is built up into short, straight bulges [JS: SAME WORD USED FOR E.G. 'ROLLS OF FAT']. Observed under good lighting, the course of these bulges is seen to run parallel to each other and at right angles to the cervical vertebral column. The length of one such bulge is approx. 2.2 mm, the distance between two of them 0.8 mm; their thickness is of course minimal. Unfortunately there are only about 10 bulges altogether which are even half preserved, covering a length of 10.9 mm. At one of the places where one could expect a well-preserved bulge, lies the 8th cervical rib; and the 3rd, 7th and 9th bulges are very poorly preserved.

Despite all these restrictions I believe that we are dealing with more than just an accidental accumulation of the organic substance into rows, and that one has to recognise these bulges as the borders of scales. Since they do not run diagonally but parallel to each other, we cannot be dealing with the remains of imbricate scales in diagonal rows, but only with scales arrayed in transverse rows.

Through this arrangement and shape of the scales, *Pachyophis* can be differentiated from the glauconids, typhlopids and archaeophids, but whether these transversely arranged scales are to be interpreted as a snake character must remain undecided for the time being. In the apodous lacertilians there are even considerable differences present between closely related forms (*Ophisaurus* and *Anguis*). In some apodous lizards one can find round scales arranged in diagonal rows, in others rectangular ones lying in transverse rows, in others again expanded ventral scales reminiscent of the ventral shields [*Bauchschienen* , *Schienen* = 'rails' or 'runners'] of snakes. In this manner, the scale remains of *Pachyophis* are in any case systematically worthless. That the locomotion of this animal was not accomplished as in recent snakes by means of the ventral scales, is also shown by the structure of the ribs.

From the combination of the description of the main slab and the adjoining slab it can be stated with certainty, that a thin-necked, legless animal over 40 cm long lies before us, whose 46 anterior vertebrae lie before the lungs, the following 49 correspond to the broadened pulmonary space, while the digestive tract lay under the following 28. To these 123 vertebrae were added in any case still some caudal vertebrae, conjecturally some 30. The heavy stout trunk stands in conspicuous contrast to the slender, long neck.

3. Biology

After the habitat, form and the toothed jaw of *Pachyophis* are known to us, we can deduce its biology.

As Katzer suggested in the first volume of his work on the fossil coals of Bosnia and Hercegovina (Vienna 1918 p.37), the properties of the Bilek Plattenkalk, in which *Pachyophis* was found, indicate a shallow and, I would add, probably coastal sea. As three skeletons of *Pachyophis* were found at once in quite a restricted area, so we are forced to the conclusion that *Pachyophis* lived in this shallow sea, probably in swarms. The calcareous mud, in which *Pachyophis* is present, indicates little water movement. The thickening of the bones of our animal indicates definitely that it led a benthic way of life, and the orientation of the pre- and postzygapophyses show that it moved with undulating movements of the body. In contrast to the stout trunk, which could probably only move slowly, the neck was capable of faster movement; and in contrast to the body, which was principally undulated horizontally, the neck was capable of vertical movement; the head would thus often be held above the bottom while creeping.

The lateral motion of the trunk separates *Pachyophis* well from the amphisbaenians, in which vertical movements of the trunk occur, and places it closer to the anguids. Locomotion with the help of broad ventral scales was absent, and would also have been impossible in soft mud.

The erection of the most anterior portion of the body in *Pachyophis* is a somewhat anguid and still more snakelike character; but it is naturally associated with the conspicuous smallness of the head and slenderness of the neck. The tail would move freely and easily in any direction.

The conspicuously small, sharply tapering mouth and the delicate but unusually sharp teeth indicate feeding on animals, but very soft and slippery ones, or in any case such as could only be gripped but not bitten. The posterior elongation of the jaw makes it possible that the jaws were considerably blocked up [*macht ein erhebliches Aufsperren des Rachens möglich*, i.e. prevented from opening widely], but regardless of the blocking-up the cross-section of the gripped prey was quite small in proportion to the body volume.

As the jaws of *Pachyophis* would hardly have been advanced alternately during the swallowing of prey as in recent snakes, for this contradicts the form of the maxilla, but the teeth are nevertheless conspicuously curved posteriorly, one is forced to the conclusion that it had to withstand a constant forward pull during the swallowing act; now this indicates the gradual swallowing of quite elongate, but still living and desperately fighting prey.

If one investigates the bottom of a shallow sea for such animals, which have a soft and slippery, elongate body and which could still make escape attempts with part of their body while another part was already swallowed, one finds them especially among the worms. Strange as it may seem, in this way we are able to know quite well that *Pachyophis* lived on marine worms: obviously it crept slowly up to these animals, grabbed them with a sudden strike by the head, and dragged them out of their burrows while swallowing. This explains the structure of *Pachyophis* harmoniously in all features.

It is not to be thought that *Pachyophis* was a fish-eater, because the ichthyophagous dentition as seen in mosasaurs, some mesosuchians and also the gavials, has a completely different structure.

4. Systematics

In a comparison of *Pachyophis* with the other reptiles which are clearly closely related to it, the following points stand out:

1. The upper jaw is reminiscent of the varanids, scincoids and dolichosaurids, the lower jaw of the dolichosaurids, but also somewhat of the snakes.

2. The dentition is snakelike and indeed reminiscent of the ilysiids and boids, less of the uropeltids. A comparison with more highly specialised snakes, such as the aglyphous colubrids, does not seem necessary in view of the jaw structure.
3. The smallness of the skull and slenderness of the neck are snakelike.
4. The great number of rib-bearing vertebrae is a snake character.
5. Snakelike is the articulation of all vertebrae and the form of the anterior cervical vertebrae, though these are found also in *Dolichosaurus*.
6. The construction of each vertebra is in most respects un-snakelike, in particular: the posteriorly directed neural spines of the cervical vertebrae; *Dolichosaurus*-like posterior production of the base of the neural spine in trunk vertebrae and the consequent concavity in the anterior edge of the following vertebra; the pit accommodating the prezygapophysis of trunk vertebrae; their cushion-like swelling; and the inward rotation of the prezygapophyses of the cervical and posterior trunk vertebrae.
7. The pachyostotic trunk ribs are dolichosaurid. The lack of a tuberculum costae is seen in dolichosaurs and primitive snakes (Janensch, 1906a, b).
8. The lack of developed pectoral and pelvic girdles and of sacral ribs distinguishes *Pachyophis* from the dolichosaurs, but this is a character of slight significance.
9. The rather short, but hardly truncated, round tail distinguishes *Pachyophis* from the dolichosaurs and from many legless lepidosaurs, and places it close to snakes and scincoids.
10. The presence of transverse ventral plates also seems to be snakelike or anguid. This last point is important in respect of the cycloid scales present in typhlopids and glauconids, and the elliptical scales of *Archaeophis,* but is otherwise without phylogenetic significance.

The points set out here show that the snake-like properties expressed in *Pachyophis* (2, 4, 8, 9) are mixed with decidedly un-snake-like ones (1, 6, 7). Other noticeable properties of *Pachyophis*, such as the shape of the vertebrae, are present also in the dolichosaurs, or are common to these and the snakes (1 in part, also 3 and 5).

In a comparison of *Pachyophis* with the amphisbaenians, it is shown that in *Pachyophis* the lung lay further back than in the amphisbaenians, further it had a long slender neck, a different skull and different vertebrae. The amphisbaenians thus do not come into consideration as relatives. On account of the neck the scincoids and anguids are also ruled out straight away by a comparison. *Pachyophis* differs from the long-tailed pygopodids by its probably short tail, which is obviously primary in *Pachyophis*. That it does not also in this case, as in the scincoids and amphisbaenians show an adaptation to a burrowing way of life, is supported by the slender neck, otherwise a thicker neck would be expected. The anniellids, as Cope states, lack the zygosphene.

This short and quite cursory overview alone already shows that as the forms most closely related to *Pachyophis*, apart from the snakes, only the Dolichosaurinae come into consideration; but as a large oar-like tail is constantly present in the Dolichosaurinae, but this is absent in *Pachyophis*, so the latter must descend from a group in which the oar-like tail was not yet present. In this respect *Pachyophis* stands closer to the relatively weak-tailed Aigialosaurinae than to the long-tailed Dolichosaurinae, but the number of cervical vertebrae separates it from this group.

Pachyophis must thus be regarded as a form descended from *Aigialosaurus*-like forms, but in which an increase in the number of cervical vertebrae had occurred as in the Dolichosaurinae, but as in mud-inhabitants the development of an oar-like tail did not occur.

Despite all oddities of its structure, its teeth and the number of its ribs speak for regarding *Pachyophis* as a true snake.

This form belongs to those rare types, which connect together groups which are now sharply separated. If one tries to refer it to the Dolichosaurinae on account of the shape of the jaw and vertebrae, one must unduly expand their definition. But one can not well refer *Pachyophis* to the snakes, although the general structure of the teeth and the number of vertebrae stamp it as such, and so one must create a new systematic unit for it. This unit must be called Pachyophidae, it is indeed to be referred to the snakes, but as an extremely primitive group.

The definition of this new Family Pachyophidae is as follows : Skull small, upper jaw not snake-like but lizard-like; lower jaw as in Dolichosauridae and Uropeltidae; jaw region small; teeth needle-shaped, snake-like; about 160 to 180 vertebrae, of which 123 are known including 46 cervical and 77 (?) trunk vertebrae. Cervical vertebrae elongate, somewhat laterally compressed, neural spines remain slender. Trunk vertebrae square, neural spines broad and short, anterior trunk pachyostotic and osteosclerotic. All ribs without tuberculum costae, anterior ribs curved only proximally and thin, trunk ribs uniformly curved. Shoulder- and pelvic girdles at most rudimentarily present. Ventral scales developed as small, narrow transverse shields. A single species: *Pachyophis woodwardi* Nopcsa. The total number of teeth (15) and the smallness of the 5 posterior teeth can serve as specific characters. Locality: Selisca quarry near Bilek (Herzegovina), Age: Neocomian. Type specimen of the family, genus and species in the Naturhistorisches Museum in Vienna.

The discovery of *Pachyophis* brings us somewhat closer again to the understanding of the origin of snakes. That the snakes have no close relationship with the mosasaurs seems finally proven (cf. the works of Janensch and most recently of J.G. von Fejérváry) [JS: NOTE THAT 'NOT CLOSE' COULD BE MISLEADING IF TAKEN OUT OF CONTEXT! - SEE BELOW]. Less clear until now was the position of the snakes with respect to the dolichosaurids. Owen (1849-1884) and Seeley (1865) have already demonstrated the snake-like form of the cervical vertebrae of *Dolichosaurus*, and in agreement with Boulenger I also, in 1908, held the dolichosaurs to be those animals which among all the lepidosaurs had the most connections to the snakes; Janensch (1906b) and Fejérváry (1918) however believe that it is even now necessary to reject any relationship between these groups. For Janensch it is especially rather biological factors which force him to this conclusion, while Fejérváry is silent over his grounds.

If one considers the different types of snakelike animals, one sees that these forms develop on land and in the water. Janensch's conclusion that all aquatic animals constantly retain traces of their limbs can not be accepted. The eel is indeed a water animal, descended from finned forms, and yet it has no fins.

For serpentiform animals of the land, as Janensch emphasised well, it is without exception the case that they lead a more or less burrowing way of life; some only under leaf litter, others even in the ground. Not uncommonly in these animals, in relation to their digging way of life, even the skull is modified, and in agreement with the skull structure it is again generally the case, for all these animals, that the cervical portion of the vertebral column is shortened. In the burrowing terrestrial amphibians (Gymnophiona), where no long neck region exists, this shortening can not of course be established, but in the snakelike terrestrial reptiles, the anguids, the scincoids and similar forms, the truncation of the cervical vertebrae constantly appears. In these forms the neck-shortening gives the head-borers (Peter 1896-98) a firm hold and this is again especially important as long as projecting forelimb-rudiments exist immediately behind the neck, hindering burrowing. As in contrast to all the forms just mentioned, neck-shortening is absent in the snakes, they have obviously never passed through a burrowing stage. For determination of the neck length the presence of hypapophyses is important in these animals, though they also extend secondarily to the trunk, but even more important are the positions of the heart and lungs.

If we now consider, after the terrestrial anguinidiform [JS: 'anguiform' better; Nopcsa used 'Anguinidae' throughout] animals, the aquatic anguilliform ones, so we must first of all establish to our regret, that today no anguilliform reptiles live apart from the water snakes. Since the watersnakes must cursorily remain out of consideration for the discussion of the origin of snakes, and the anguilliform fish and amphibians can also not be brought in for a judgement of the eventual elongation of the neck, we unfortunately lack recent material to solve the question whether life in water allows stretching of the neck in anguilliform animals; but we can obtain an answer to this question indirectly.

Merely considering that the loose mud at the bottom of a body of water gives no more resistance to an animal burrowing in it than the water itself brings us to the thought that the mechanical demands on the head, and hence naturally also the neck of such an animal, must be decidedly slighter than in one which burrows in not-so-loose earth. Should one succeed in proving, according to this notion for aquatic reptiles, that during life in water an elongation of the neck occurs concurrently with reduction of the extremities, then one might also assume, without the danger of being exposed to error, that such an aquatic animal would also retain the neck elongation, once present, as an inhabitant of land. As the dolichosaurs, neusticosaurs and the mesosaurs show that aquatic life easily allows elongation of the neck with simultaneous partial reduction of the extremities, so one may also, it seems to me, expect an elongate neck in such mud-burrowers as have completely lost the extremities.

As an increase in the number of postsacral vertebrae is always present in the long-tailed swimming forms, and further the swimming forms always use their extremities as balancing organs in turning their bodies, as a result of which their complete disappearance always fails to occur; so naturally an anguilliform animal can come from a swimming form only by giving up a direction of development to which it is already committed, that is by the radical alteration of its way of life, which seems hardly probable; hence to explain the appearance of an anguilliform species of animal in a natural way, one must suppose the basic form of anguilliform animals to be newt-like ones, which had not as yet gone through a pronounced swimming stage.

According to Janensch, the main difficulty in the derivation of snakes from aquatic animals supposedly lies in that all aquatic animals also have a laterally compressed body, which then makes creeping on dry land difficult. This objection is not convincing. In part it is deprived of force by what has already been said above, moreover still further counterarguments can be found.

If we are speaking of aquatic animals, one must naturally think first of fish, of which most are in fact laterally compressed and hence, on solid ground, just lie there; but if one considers the mud-burrowing forms, one sees that these also move relatively well on land. To begin with the best known, I would mention first the eel, of whose wanderings many stories have been told and which, by its life in mud, has even gained an adaptation which is also of some use for living on land (gill-covers). Then secondly I would mention no less a conspicuous example than *Amphipnous* and as third *Lepidosiren.* These three unrelated fish all show clearly that precisely in the anguilliform animals, the merely weak lateral compression of the body is relatively easily compensated during forward locomotion on land by the lateral undulation of the trunk. Naturally, locomotion was worse in the semi-aquatic snakes, still clumsy on land, than in the snakes now living, indeed the lack of a tuberculum costae in the primitive snakes points in the same direction. Janensch's assertion that the biological effects of aquatic specialisations in apodous animals were directly opposed to those by which the land snakes became mobile and swift animals, indeed hits the mark for swimming forms, but cannot be accepted for the mud-burrowers. Even *Siren* and *Amphiuma* are not entirely helpless creatures in dry conditions.

As a consequence of this reflection, no grounds can be found why the snakes should not be descended from mud-burrowing, anguilliform animals, though initially they would still have crept poorly on land.

Also the early appearance of very primitive, but yet in other respects (pelvic reduction) already highly specialised watersnakes in the Eocene, speaks for the aquatic origin of snakes; and finally also the specialisation of the skull of all snakes seems to indicate, if not unambiguously, in any case in a quite remarkable manner, that the snakes descend from reptiles which lived as *Pachyophis* did.

Only with the adoption at one time of an extraordinarily reduced skull are those jaw modifications affecting the quadrate and squamosal, which we meet in most snakes, made explicable. These peculiar modifications appear, on the adoption of this premise, as the secondary enlargement of the mouth of such an apodous form which once showed jaw reduction. Despite the monstrous mouth, the maxilla and dentary of all snakes are really quite small and the gigantic opening of the mouth is not, as in some other reptiles, achieved by the growth of these parts, but rather by the bringing in of elements which do not otherwise function in forming the jaws. This shows a compensation of formerly reduced jaws which were no longer able to secondarily increase in size.

These reflections all lead back indirectly to regarding *Pachyophis* as a form extremely closely related to the ancestor of snakes, indeed almost the ancestor of snakes itself, and as we can now recognise that this form represents a distinct type, we must now also fix its position in the system of snakes. The systematics of a group without knowledge of its direction of evolution is of course perfectly worthless, but the direction of evolution of snakes now shows itself more clearly for the first time, and hence snake systematics deserves a revision.

The individual families of recent and fossil snakes have actually already been fixed by Boulenger and Janensch, so here we need only deal with their respective grouping.

The glauconids, despite their tooth reduction, are still very primitive in respect of their firmly ingrown maxillae and their pelvis (Boulenger 1893-96), and the typhlopids and glauconids still retain a high coronoid process with the small to very small jaw apparatus, but have toothless or weakly toothed palates. Further, *Simoliophis* and *Palaeophis*, without being typhlopids, are yet distantly related to the typhlopids (Rochebrune 1880, Sauvage 1880) (for *Palaeophis* this has yet to be proved in detail), while *Pachyophis* has the thickened neural spines in common with *Simoliophis*, and the structure of the ribs separates the palaeophids, pachyophids and the archaeophids from the typhlopids and glauconids. [Hence] I believe that one has to bind the pachyophids, *Simoliophis*, the palaeophids and possibly also the archaeophids together in one primitive group, and most of the recent snakes (Boulenger 1893), namely the boids, ilysiids, uropeltids, xenopeltids, colubrids and viperids, in a second [JS: THIS PARAGRAPH SO FAR ORIGINALLY ALL ONE SENTENCE]. The first of these groups must, in my opinion, comprise those snakes in which the jaw is not yet distensible, where the tuberculum costae is absent and correspondingly locomotion does not take place with the help of the ventral shields, for which reason I name the animals of this group **Cholophidia** (____ς = lame); the second group must then of course include the forms in which these properties are present. I would like to name the second group **Alethinophidians**, as it includes the true snakes. According to the presence of the coronoid and, in parallel with it, the greater or lesser solidity of the skull, one can differentiate primitive alethinophidians (Xenopeltidae, Ilysiidae, Uropeltidae and Boidae) from specialised alethinophidians (Colubridae, Viperidae and Amblycephalidae). To these two groups Cholophidia and Alethinophidia, a third unit of equal rank is joined which has already been recognised by Boulenger as in some respects a very specialised, but in others a particularly primitive group, which combines a small, non-distensible jaw with the presence of a tuberculum costae and the absence of ventral shields. This group comprises the typhlopids and glauconids and one can retain the name **Angiostomata** for it. *Typhlops* stands in relation to *Glauconia* somewhat as *Ornithorhynchus* to the echidna among mammals. As a strong tuberculum costae is also found outside the snakes, in *Amphisbaena* and *Lepidosternum* (Cope 1892), one can suppose that it also arose independently in the alethinophidians and angiostomes.

In this new systematic arrangement of the snakes, the complete lack of a pelvis is ignored, in contrast the presence of the coronoid is emphasised.

The Angiostomata and Alethinophidia must both in any case be regarded as direct descendants of the cholophidians, and indeed it seems that the split leading to these two groups already takes place within the cholophidians. It seems to me that *Archaeophis*, on account of its skull structure, is decidedly closer to the alethinophidians, but *Simoliophis* and *Palaeophis* closer to the angiostomatans.

From a charming communication by letter from Prof. Boule, I gather that the teeth of *Simoliophis* mentioned by Rochebrune, which he compared with the teeth of *Odontomophis*, probably do not belong to *Simoliophis*; Sauvage and Rochebrune have already commented on the similarity of the vertebrae of *Simoliophis* to *Typhlops*, it does not need to be discussed more closely here; the likeness of *Palaeophis* to *Typhlops* has not yet been emphasised, and thus remains still to discuss.

As Andrews (1906) already mentioned, and Janensch demonstrated in his monograph on the palaeophids (1906b), the palaeophids are distinguished from all other snakes by the development of the pterapophyses, which project above the postzygapophyses; but as I convinced myself, there are just in the typhlopids, in the anterior part of the trunk, small bumps above the postzygapophyses which obviously correspond to the pterapophyses of the palaeophids. While these bumps in *Typhlops* are minimal in comparison to *Palaeophis*, they are nevertheless systematically important, because their conspicuous smallness in these burrowing animals is obviously conditioned only by those factors which (as in the amphisbaenians) also reduced the neural spines. The palaeophids are recognisable as extreme swimmers by their enormous neural spines, the typhlopids as extremely adapted burrowers, but otherwise the type of vertebra is identical. [JS: ANTERIOR CERVICALS OF MADTSOIID AND ALETHINOPHIDIAN SNAKES ALSO HAVE PROCESSES IN THE 'PTERAPOPHYSIS' POSITION, SO THIS ARGUMENT IS FALLACIOUS EXCEPT AS IT APPLIES TO A LARGER GROUP.]

As zoologists erecting new species of reptiles in recent forms mostly do not pay attention to the skeletal structure, which moreover shows sex and age differences, while palaeontologists on account of their material can only pay attention to the skeletal structure, the consequence is that even if one ignores the resulting possibility of error, the zoological and palaeontological concept of a species do not coincide.

A palaeontological species very often possesses the value of a genus of the zoologists, but sometimes not even that of a local variation, and out of the total of the palaeontologist's good species, it is again self-evident that a palaeontological genus often equals a zoological subfamily.

As unimportant as this divergence is as long as the two disciplines do not come into close contact, it naturally emerges as disruptive if the palaeontologist classifies material of which there are few fossils but many recent forms. That applies among others to the snakes. On account of the abundance of recent material, it is quite impossible to degrade the families of recent snakes to subfamilies, but yet the diversity of fossil reptiles prevents the palaeontologist from giving the snake group as a whole more than the value of a **suborder** (cf. also Boulenger), for he must join them with the lepidosaurs as an order, so as to be able to form a superorder with the Araeoscelida and pleurosaurs and Squamata together; and so it is self-evident that the newly created Cholophidia, Alethinophidia and Angiostomata can only be superfamilies.

This new expansion of our knowledge of primitive snakes reinforces the old view which I also supported, that among all lacertilians **the dolichosaurs are the reptiles which come closest to snakes**.

In a phylogenetic tree of the dolichosaurs and related animals which was reproduced, though inexactly, by Fejérváry in 1918, I placed the dolichosaurs close to snakes, without actually joining them. Today we are far enough, as a consequence of our new discoveries, to be able to carry this connection through. Also the Proplatynota, which on the phylogeny of 1908 were still hypothetical forms, have taken firmer shape (cf. section on *Eidolosaurus*), and so a more exact phylogeny can be given, which essentially coincides with that given by Boulenger (1891).

- Proplatynota (1) J--T (terrestrial)
  - Varanidae (5) T--R (terrestrial)
  - **Aigialosaurinae** (2) N (terrestrial and littoral)
    - Mosasauridae (3) K (pelagic)

- **Mesoleptinae** (2) N (littoral and benthic)
    - **Dolichosaurinae** (2) N--K (pelagic)
- ? **Cholophidia** (4) N--T (marine, partly benthic)
    - Angiostomata (4) T--R (terrestrial underground)
    - Alethinophidia (4) K--R (terrestrial and secondarily aquatic)

[JS: THIS INDENTATION SCHEME FULLY CAPTURES BRANCHING PATTERN OF ORIGINAL FIGURE: TAXA SHOWN INDENTED TO SAME EXTENT ARE SUPPOSED TO BE DERIVED INDEPENDENTLY FROM THE STEM-GROUP ABOVE.]

In this phylogeny R means 'Recent', T 'Tertiary', K 'Cretaceous', N 'Neocomian' and J 'Jurassic'. (1) indicates the varanoid families Proplatynota; the family Dolichosauridae is signified by (2); (3) is the sign for the Mosasauridae; (4) that of the different ophidians and (5) the sign of Platynota, as whose representative the Varanidae was put in.

The 'aigialosaurid' forms theoretically to be expected as ancestors of the cholophidians, with elongate necks, slightly shortened tails and strongly, that is dolichosaurid-like, reduced limbs, indeed has not yet been found, but it is to be expected in the Neocomian of Istria-Hercegovina. The forms printed in bold type are all found in the Neocomian of the *Dinariden.*

If the snakes were not, as they are shown in this phylogeny, a relatively new group, but rather as Fejérváry thinks an old group of squamates, it would have to be considered a riddle why many of their older representatives, even in the Eocene, still had no tuberculum costae, whereas the assumption represented here explains this.

If we now review once again, before concluding the work, the diversity of Neocomian lepidosaurs of the *Dinariden,* something else remarkable stands out. In a relatively restricted area, at a very specific point in time (Neocomian), and indeed - which is very important - at the beginning of a marine transgression, two groups of terrestrial lizards began to adapt to life in the water. The first stimulus of evolution thus lies in a geological process. After this first step the animals varied enormously and quite heterogeneous forms appeared, which are characterised by the mosasaur-like aigialosaurs, the dolichosaurs and the pachyophidians. Here we have typical explosive 'genotypic' species-formation: it is tied to a new environment. As has been discussed in detail in the section on arrostia, aquatic life brings profound biochemical changes, so we could quite well expect an influence on the germ cells in animals whose blood and hormones are changing radically, and this can explain the lability of these aquatic forms.

The lineages of dolichosaurians, owing to this lability, did not follow a one-sided, mechanically determined direction of development, and thus they have the form of a bush;

but two groups of forms shoot out of this bush, which each shows a quite specific direction of adaptation, namely mosasaurs and snakes. In conspicuous contrast to the lability of the primitive group, both of these groups seem fixed, and indeed this can be recognised particularly in the mosasaurs. The Mosasauridae adapt themselves to mechanically conditioned necessities, we know numerous phenotypic forms: there are diving forms and swimming forms, then appear forms which feed on larger animals, on fish or on crustaceans; but the type stays the same. Once adapted to aquatic life the Mosasauridae are not plastic, at any rate in comparison to the Dolichosauridae. All this can now be understood. An increase of individual parts conditioned only by mechanical use surely affects the germ plasm much less strongly, and also much less directly, than a biochemical process.

In the snakes, while there is still very little known about them, this fixity appears exactly as it does in the mosasaurs. In comparison to the primary variability, coupled with poverty of species, of the relatively primitive snakes (I refer to the deep differences of archaeophids, palaeophids, pachyophids, typhlopids and uropeltids), the later alethinophidians despite their species richness seem to be quite uniformly constructed, hence the difficulty of their classification. This shows that even while some new specialisations still appear (increase in vertebral number, venom fangs), the germ plasm remains the same from a given moment on. Should this coincide with the return to land? Observations of this kind lead spontaneously, as we have seen, ever further and to the question of phenotype and genotype; and as the same features as here in vertebrates, also appear in invertebrates, they seem to be extremely important. In invertebrates the cause of genotypic variation was hitherto unclear, as also recognisable from Dacqué's last works (1921), whereas in one of the two cases before us here it is apparently clear. This fact seems important, for Joest (1921) has developed similar views in a very interesting recent work, which assumes an influence on the genes through the hormones of the body.

APPENDIX

Whereas, one the one hand, counting the vertebrae of limbless reptiles is among the less agreeable and [more] time-consuming occupations, and to my knowledge a summary of vertebral numbers of these animals has not yet been presented, but on the other hand that the knowledge of the so-called and (quite unjustly) slightly regarded "individual variations" is of the highest importance for the understanding of evolutionary processes, since they are best able to demonstrate the lability of incipient and rudimentary [organs]; so I believe that it will be widely appreciated that I give in the following a summary of the vertebral numbers of different serpentiform reptiles.

Apart from those marked "G" for "Gervais", "R" for "Rochebrune", or "S" for "Siebenrock" [also "J" for "Janensch", omitted], the data derive from my own counts of numerous skeletons identified through the Naturhistorische Museum in Vienna and the Nationalmuseum in Budapest. Deviations are shown. In some skeletons quite significant deviations from Rochebrune's data are noticeable, such as in *Platurus laticaudatus* and *Bitis arietans.* Where nomenclature is concerned, that used by Boulenger was well adjusted. In the following list the terrestrial forms, the *burrowing forms*, the **aquatic animals** and the ***arboreal*** animals are distinguished by special printing for the sake of blogical deductions.

The first number in the list shows the total number of vertebrae, those located in the brackets show the proportion of trunk vertebrae to caudal vertebrae.

[Tables omitted]

The numbers brought together in the above lists are, though still sparse, nevertheless extremely informative especially in the case of snakes. If one keeps in view the average numbers for individual genera, it is apparent that in the fossorial forms of the angiostome type one can count ca. 160 trunk and 13 caudal vertebrae (=12:1), that in the less fossorial-adapted ilysiids these numbers then climb to 194 and 14 (=13:1), in the exclusively fossorial uropeltids they fall to 148 and 14 respectively (=10:1), and that in the fossorial aglyphous colubrids they also come to only 153 and 18 (=8:1).

Among the terrestrial snakes the surface-inhabiting ilysiids have on average 226 trunk and 37 caudal vertebrae (=6:1), in the more or less ground-living aglyphs one can distinguish one group with 175 trunk and 64 caudal vertebrae (=2.7:1) and a second (*Spilotes*, *Zamenis*) with an average of 232 trunk and 100 caudal vertebrae (=2.3:1). The slightly venomous ground-living opisthoglyphs have almost the same average vertebra numbers as the aglyphs, namely 170 trunk and 66 caudal vertebrae (=2.5:1), while the numbers sink in the more or less venomous proteroglyphs to 158 and 51 (=3:1) and in the constantly venomous viperids to 150 and 38 (3.9:1). The viperids thus have almost as few vertebrae as some burrowing forms, though the proportions are different.

Aquatic life has no great influence on the absolute number of vertebrae in snakes. The aglyphous acrochordines have 184 trunk and 63 caudal vertebrae (=2.8:1), the opisthoglyphous water-snakes 140 and 69 (=2:1), and finally in the proteroglyphs one can recognize one group with 133 trunk and 40 caudal vertebrae (=3.3:1) and a second with an average of 244 trunk and 58 caudal vertebrae (=4.2:1).

With arboreal life the number of vertebrae and especially the number of caudal vertebrae increase strongly in every group of snakes. In the arboreal, aglyphous colubrids there appear 182 trunk and 170 caudal vertebrae (=1:1), in the opisthoglyphs one one can calculate an average number of vertebrae in the arboreal forms of 228 trunk and 150 caudal vertebrae (=1.5:1) and in the proteroglyphous tree-snakes one can still count on average of 220 trunk and 100 caudal vertebrae (=2.2:1).

It is very remarkable that the phylogenetically old boids show great variation in respect of the vertebrae: in *Eryx* there appear 186 truk and 35 caudal vertebrae (=5:1), in *Boa* and *Eunectes* 241 trunk and 55 caudal vertebrae (=4.3:1), in *Corallus* 271 trunk and 125 caudal vertebrae (=2.1:1), and in *Python* 308 in the trunk and 86 in the tail (=3.5:1). The cause of these differences is found only to the extent that, as in *Eryx*, a certain amount of tail-reduction enters in association with the fossorial way of life; but otherwise it is still unclear whether the primitive proportion of trunk and tail vertebrae was indeed originally about 4:1 (cf. the preceding work).

LITERATURE CITED

[omitted]

CAPTIONS

[There are unfortunately none in the original, though obviously intended to be included]

[See also:
Lee, M.S.Y., M.W. Caldwell & J.D. Scanlon. 1999. A second primitive marine snake: *Pachyophis woodwardi* from the Cretaceous of Bosnia-Herzegovina. *Journal of Zoology, London* **248**: 509-520.]