ON *ARCHAEOPHIS PROAVUS* MASS.,

A SNAKE FROM THE EOCENE OF MONTE BOLCA

by

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Über *Archaeophis proavus* Mass., eine schlange aus dem Eocän des Monte Bolca.
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Introduction

The geologisch-paläontologisch Museum der Berliner Universität a short time ago came into possession of a fossil snake that came from the Eocene limestones of Monte Bolca, well known to be rich in fossils, especially splendid fish, and had been in the collection of Herzog of Canossa. In a work which was not widely distributed and which, as a consequence, until now had not been cited in our usual textbooks of palaeontology, Massalongo (Specimen photographicum animalium quorundam plantarumque fossilium agri Veronensis, 1849) already more than half a century ago described this snake as *Archaeophis proavus*, and together with it the fragments of a second, much larger form which received the name *Archaeophis bolcensis*.

Massalongo then spoke in favour of both species belonging to a single genus, in spite of certain differences, especially in size. He also stressed that they had nothing to do with the fossil genera *Palaeophis* or *Paleryx*, so that a new generic designation was appropriate. In individual points it was supposed to be well in accordance with recent genera, but considering all characters together, no relationship to living snakes would be apparent.

The author [Massalongo] now gives two photographic representations of *Archaeophis proavus*. The first shows the whole animal at two-thirds size, the other only the head and the anterior section of the trunk at natural size.

Apart from the conditions of measurements and shape of the body we learn that the small, straight jaws are set with numerous teeth, ca. 24, and that the palate shows two rows of conical, pointed teeth of $1^1/_2$ mm in length. Further, Massalongo was able to make out the traces of very small scales measuring $^1/_3$ mm, which were arranged in extremely numerous rows. The vertebrae were supposed to be similar to those of *Natrix*, showing a weak, straight, upward projecting - thus probably dorsal - keel, slightly developed lateral apophyses (articular processes?) and articular facets, which according to their development would allow easy bending and rolling-up. From the round form of the vertebrae, including those of the tail, it was concluded that the snake lived on the land.

The number of vertebrae, of maximum length 3 mm and width 2 mm, Massalongo gives as approximately 507, of which over 80 were to be accounted to the tail. The ribs were supposed to be very small, posteriorly curved, and furrowed.

These are the most essential data which Massalongo supplies on *Archaeophis proavus*, which in any case already lets it be known that we are dealing with a strange type of snake. After a detailed investigation and careful preparation with the help of a **Zeiß** binocular preparation microscope of 24x magnification, it was possible to make Massalongo's findings considerably more complete and in part correct them. In particular the jaw apparatus together with the dentition, the form of the vertebrae and the ribs could be quite well seen, and it stands out with great clarity that in *Archaeophis* we have a type of snake which is absolutely strange with respect to all others known. This result, together with the well-known fact that rather complete fossil snakes are among the great rarities, may well justify dedicating a new, detailed monographic treatment of *Archaeophis.* A short preliminary communication already appeared some time ago (Zeitschr. d. deutschen geol. Ges. 1904 and Sitzungsberichte d. Ges. naturforsch. Freunde 1904, no. 6).

There yet remains to me the welcome duty of expressing my most devoted thanks to Herr Geheimrat Prof. Dr. Branco, for most kindly permitting me to work on this valuable specimen.

I likewise thank Herr Geheimrat Prof. Dr. Möbius in a friendly manner for permission to use the rich reptile collection of the zoological department of the Museum für Naturkunde in Berlin.

I am bound to give extra special thanks to Herr Prof. Dr. Tornier, curator of the Museum für Naturkunde in Berlin, who supported me many times with his expert advice and most obligingly made recent comparative material available to me.

A. The Skull.

Description of the parts present.

The skull lies with the upper side on the slab, and thus offers the observer the view from below. Consequently it is pleasingly possible to examine the important conditions of the jaw apparatus and the dentition. The actual braincase is compressed, the individual bones themselves, at least those of the underside, are broken in pieces and hence not to be determined in their form and outlines. The bones of the jaw apparatus and the toothed ones of the palate, on the other hand, are relatively slightly compressed and filled internally with calcite as clear as water. However, parts of these bones are also missing. They may have remained attached on the unavailable counterpart, or perhaps have been removed by earlier attempts at preparation. At the places where pieces of bones have been broken out, frequently there are still parts of a more or less hollowed-out lamella of bone of still lying attached on the rock, which in part is further covered by crystalline [*späthigen*, as in *Kalkspäth* translated 'calcite' above] filling-material. Some of the gaps where bone material is completely missing yet show at least its impression, so that here too some information on their form can be gained.

The skull has been affected by a small disturbance in that on the right side of the head the individual bones have their posterior parts displaced towards the middle along a break passing through them. In the left half of the skull, however, this displacement can no longer be perceived.

The total length from the premaxilla to the posterior end of the squamosal comes to 28 mm, the greatest measurable width between the outer edges of the maxillae 14 mm. The overall shape of the skull is thus narrow. The posterior half may have been approximately limited by nearly parallel lines. The form is clearly somewhat disturbed by the lateral displacement mentioned. In the anterior half of the skull there is a narrowing, which continues regularly anteriorly and results in the formation of an extraordinarily pointed snout.

Both **quadrates** are distinctly visible (Pl. II, Fig. 1, Qu). They lie at the posterior edge of the skull to right and left and are separated by 5 mm; they diverge from each other anteriorly. Their while form is only slightly differentiated. They represent flattened strips of bone 4.5 mm long, which ave a width of about 0.4 mm in the middle, but broaden uniformly to about three times this amount at each end. Both ends are chopped off very slightly crookedly.

At the posterior end of the quadrates lie two curved bones (Fig. 1, Sq), which from below project out of the rock upwards and laterally, applied to the skull and hanging down from the skull roof. Here no doubt we have the **squamosals**, to which the quadrates articulate. The left could be exposed somewhat further, but it was not possible to determine how the attachment to the skull takes place.

The **maxillae** (Fig. 1, Ma) are for the most part preserved on both sides. The most posterior part of the right one is separated from the anterior part by the transverse break discussed above, and fragmented, so that only dark traces of it are still recognisable on the rock. Otherwise the right maxilla shows itself to be a bones that is broad and flat in its posterior half, and somewhat concave dorsally, but anteriorly narrows to a thin, somewhat laterally compressed strip of bone. The teeth sit fairly exactly in the midline of the bone in the anterior part, posteriorly as it becomes increasingly flat they shift ever more distinctly to the inner edge. Some 5 mm from the incompletely preserved anterior end there appears, close above and outside the tooth row, a narrow groove, and immediately above it a second one. They can only be followed a little further back, however, as further back a part of the bone has been split off. Above the upper groove the alveoli project outwards as bulges separated by narrow in-sinkings. The lower edge of the anterior end of the right maxilla is missing, the middle part is preserved, but only the impression of the posterior part is present. A small gap can be seen between the maxilla and premaxilla; it can also be distinctly seen that the anterior tip of the former does not lie completely in line with the lower edge of the premaxilla, but is set a little further laterally. Both grooves can also be observed on the left maxilla, though here too only for a short stretch. Here only the impression of the posterior part is preserved as a convex swelling, which thus corresponds to a concavity of the bone itself. Posteriorly the maxilla ends in a point. The total length can here be determined precisely as $18^1/_2$ mm. The width attains its greatest extent at around $^2/_3$ of the length and here measures some 2 mm, but diminishes at the anterior end to less than half this.

The **premaxilla** (Fig. 1, Pr) takes up the extreme end of the extraordinarily sharp snout. Laterally it forms a sharp edge of some 2 mm in length, which passes into a broad plate anteriorly. The form of this bone posteriorly can not be determined. Apparently another small plate of bone which has broken loose belongs to it; it would seem from this that the premaxilla extended further posteriorly in the middle than its edges. The premaxilla was clearly not toothed. The lateral edges are too narrow for one to assume that they could have borne teeth. And here, just as on the anteriorly positioned broad plate, there are no indications of dentition to be seen.

The **pterygoid** and **palatine** (Fig. 1, Pt and Pa) are recognisable on both sides. Fairly exactly in the middle of the whole skull lies a short bone on its side, which bears four teeth turned to the left. It is laterally, i.e. at right angles to the direction in which the teeth are attached, somewhat compressed, and is barely 1 mm high anteriorly, 4 mm further back $1^1/_2$ mm. Then the bone, interrupted by a gap which does not quite extend all the way across it, sets off at a small angle more strongly laterally, in a piece which is clearly laterally compressed, that lies against the mandible and ends 3 mm from the articulation of the latter with the quadrate. One almost obtains from this the impression that it originally reached to the quadrate itself, as a few further traces of bone seem to indicate this.

From the dentition and orientation it follows indubitably that the whole bone described represents the pterygoid. It originally ended not with a break, but with a regular curve. This would speak for this being in fact the place where the pterygoid attached to the palatine. By an oversight during preparation this part was subsequently somewhat damaged and suffered an irregular appearance. The length of the pterygoid would then have been 7 mm, and 10 mm if it extended to the quadrate.

Only a part of the anteriorly contiguous left palatine can be identified, of which the whole lower, toothed part of the length has split off and been lost, so that only the upper edge is preserved as an elongated. narrow strip of bone. The latter can be followed anteriorly to a distance of 7 mm from the tip of the snout. Traces of the external impression extend somewhat further anteriorly in the same direction.

On the right side of the skull little can be seen of the pterygoid. With some probability one can ascribe to it a very short fragment of bone bearing two laterally directed teeth. The break already mentioned several times, here running straight across, has separated it [the fragment] from its posterior continuation. The right palatine is likewise only partly preserved. A fragment representing approximately the middle section of the palatine, however, is still preserved with its laterally directed complement of teeth.

Of this toothed part of the palatine itself it can here only be determined that it shows on the medial side a flat, smooth, tooth-bearing expansion. Anteriorly the palatine forms a narrow, laterally compressed *Spange* ['clasp' etc.] of bone. With a width of some $1^1/_2$ mm, this can be seen for about 3 mm anteriorly from the broad section as mostly preserved bone, and for a further $2^1/_2$ mm as an impression. Only indistinct traces of the most anterior section are present. Only indistinct remains of bone are still preserved of the toothed part posteriorly.

The traces of the **vomer** which are preserved are too unclear to be worth describing further.

On the right **mandible** (Pl. II, Fig. 1, Uk) there is certainly nothing recognisable of the most anterior part to a distance of 9 mm from the tip of the snout. Only some teeth, which are imbedded in the rock with the teeth directed more or less steeply ventrally, can be allocated to this part. It can not be determined, though quite probable, that a very thin, vertically oriented ridge of bone beginning 7 mm from the tip is one of the bones of the mandible. Between 9 and 16 mm, measured from the tip of the snout, only the upper toothed edge of the mandible is preserved, which one naturally sees from below and inside as a lamella of bone, concave towards the observer. The remains of the mandible are preserved as a complete bone for a length of 10 mm, which is divided by the break across the skull already mentioned several times into an anterior section of 3 mm and a posterior one, displaced medially relative to it, 7 mm long. The anterior piece of 3 mm has, in the part projecting above the slab, that is ventrally, a cross section in the form of a crooked segment of a circle $1^1/_2$ mm wide and perhaps half as deep. The posterior part offers essentially the same view, but seems to pass medially into a thin, lamelliform, strongly fragmented expansion, which in the uncompressed skull one supposes was directed upwards. Probably we are here dealing with an expansion of the articular serving for insertion of muscles [coronoid?]. The individual elements composing the mandible can not be differentiated. The articular surface against the quadrate lies diagonally, medially and posteriorly, corresponding to the posteriorly convergent orientation of the quadrates, so that the sharp end of the articular lies on their outside. Otherwise the ossification of this articular facet seems to have been rather imperfect, as, apart from a small hollow close before the tip of the articular, no sharp contours are present.

On the left mandible there is likewise nothing preserved of the most anterior parts - up to 6 mm measured from the tip of the snout -, only one single tooth is seen in this place which can be accounted to it. There follows then a fragment 5 mm in length that lies close against the inner side of the maxilla, then again there is a gap of $5^1/_2$ mm, then a second fragment of ca. $5^1/_2$ mm, and from here to the beginning of the quadrate there can be seen mainly just the impression of the upper side of the mandible for a distance of 3 mm. Exactly as was observed on the right side, this also shows that the articulatory surface is so oblique to the articular that the line in which it meets the quadrate runs diagonally laterally and posteriorly.

The total distance from the tip of the snout to the joint with the quadrate measures 25 mm. The length of the mandible may probably have been somewhat slighter, probably about

23 mm. What kind of symphysis the two mandibular rami formed, whether it was ossified or not, can unfortunately not be observed, as neither of the anterior parts is present.

Reconstruction of the jaw apparatus.

Plate II, Fig. 2 represents a reconstruction of the jaw apparatus of *Archaeophis*, as far as this arises from the parts present and visible. The restoration of bones which are only incomplete is made by comparison with Fig. 1. A reconstruction of the skull capsule is done without, as there are almost no clues at all to be gained for its form. The postpalatine [=ectopterygoid], that in the normal snake skull goes across from the posterior end of the maxilla to the pterygoid and connects these bones together, is completely covered by the mandible in our snake, so that nothing can be recognised of its form and more precise position. It is therefore also omitted. It was, however, with high probability present in a similar manner to the snakes now living, as it is indispensable for the fact that it essentially holds the maxilla, transfers the motion of the pterygoid to the maxilla when the jaws are opened, and pushes it laterally. The left mandible is not shown, so that the posterior part of the pterygoid remains uncovered.

The following reflection may make it probable that the two jaw rami were not joined to each other by a bony symphysis. The mobility of the bones of the jaw apparatus typical of the normal snake skull is also present to high degree in our form. That shows the mutual independence of the maxilla and premaxilla and the free position of the quadrate. But the resulting mobility of the upper elements of the jaw apparatus is then only justified and comprehensible if both mandibular rami were mutually freely movable, thus had no bony attachment. We also find this independence of both jaw rami in living snakes, thus too in the narrow-mouthed, burrowing typhlopids and glauconiids as well as in the ilysiids and xenopeltids, in which the quadrate is very short and the maxilla is immobile against the premaxilla. Such a comparison with the recent snakes also raises the probability of the assumption that the two mandibular rami in *Archaeophis* also possessed no bony attachment to each other.

It can likewise be made probable that the quadrate was pronouncedly forwardly oriented, thus that it also had in life the position that it shows now, and which is also assumed in the reconstruction. It would be thinkable that the posterior part of the skull including the squamosals had been displaced posteriorly by compression in the rock, and the quadrates brought out of their original, somewhat laterally or even posteriorly directed, orientation into their present position by a rotation of the lower jaw joint. But it would then be quite striking that these [the quadrates] had, during this complicated displacement, almost completely retained ['almost not at all lost'] their connections with the mandibular rami and squamosals. That the present position must on the contrary be close to the original arises from the orientation of the articular facets of the quadrates. Particularly the posterior ones lying against the squamosals must have had a very much more diagonal orientation, and in the opposite direction to that which is in fact the case, if the quadrates had been normally oriented posteriorly. In life the anterior ends of the quadrates may well have been inclined somewhat ventrally, as they did indeed connect the squamosals, lying on the dorsal side of the skull, with the deeper mandibles. From this somewhat inclined position, the motion resulting from compression of the skull into the horizontal stratification level of the limestone could perhaps have strengthened the forward orientation a little, but in any case not significantly.

The dentition.

Teeth are present or demonstrable on the following bones: on the maxillae, the palatines, the pterygoids and the mandibles. As far as the teeth themselves are preserved, they are always directed posteriorly. Those of the maxillae lie on their inner sides, specifically those of the right side approximately in the level of the slab, are also clearly moved laterally by the compression of the skull, while those of the left stand more steeply, and thus have better retained their original orientation. The teeth on the palatines and pterygoids are directed laterally, they lie facing upwards on the right, those of the left on the other hand face diagonally downward - transferred to the orientation of the animal, diagonally towards the skull roof. As they are still fixed tightly to these bones in their original positions, it must be assumed that this part of the left pterygoid has undergone a subsequent change of orientation, a kind of twisting. The teeth of the mandible one can of course not see directly fixed to this bone. They can only be perceived where the bone itself is no longer preserved. On sees them here from the underside, with their tips sticking into the rock.

To determine the shape of the teeth in every aspect, it was attempted to extract some of them. This succeeded, after long efforts, in one case. The teeth are actually so fragile and brittle that they mostly broke apart with even the lightest touch of the preparation needle. The broken tip of a second tooth crown provided a good useful cross-section. In addition, the teeth in their different orientations on the slab provide good information about their external form.

If one compares the fully developed teeth of the different skull bones, a great similarity in form and size is apparent (Pl. II, Figs 3-6). The colouring is mostly dark brown, deeper than that of the bones. Mostly the base is tinted a little darker than the somewhat translucent tip. The surface of the teeth shows a lively gloss all over. The length measures fairly exactly 1.1 mm, and to judge from the visible teeth it is uniformly fairly equal. On a 0.4 mm wide, basal, plinth-like thickening, the crown rises almost straight, barely curved, only a little inclined posteriorly. The tapering towards the tip is somewhat more gradual in the lower half than the upper.

The sculpture of the teeth, and the cross-section produced by it, are also very peculiar. In glancing at the bones of the jaw apparatus one sees, of the teeth, either flat surfaces or extremely sharp edges, which also still appear as absolutely sharp blades with the 24x magnification of the big **Zeiß** binocular microscope. The one cross-section obtained, mentioned above, which lies some $^1/_2$ mm from the tip, shows distinctly a pentagonal outline (Pl. II, Fig. 6). At each of two adjacent edges the two surfaces meet at right angles. The three other angles, on the other hand, are obtuse. The three flat surfaces forming the two right-angles of the cross-section are somewhat broader than the two others. On the first three there lie, almost exactly in their midlines, narrow and quite shallow elevations, which are also visible in side view. Otherwise the surfaces are flat, [but] a slight concavity is indicated adjacent to the edges, whereby these are made somewhat sharper [receive a certain sharpening]. The cross section shows, incidentally, that the tooth is not exactly bilaterally symmetrical, rather that one edge is moved a little out of the plane of symmetry, whereby naturally a recognisable inequality of the sides of the pentagon is produced.

The isolated tooth which could be investigated, and on which except for a part the sculpture is perfectly preserved, shows that the edges, partly, do not run totally straight in the direction of the tip, but describe a bend which, though quite insignificant, is in any case sufficient to explain the weak asymmetry of the cross-section. The edges can be followed down to the base. The shallow elevations in the midlines of the three broader surfaces extend just as far down, though at the same time they broaden significantly and are more distinctly distinguished from the edge zones by furrows which become deeper, increasing the sharpness of the edges. The tip is not very sharp.

In cross-section there can be seen a narrow hole somewhat behind the middle, that represents the pulp cavity. That it is not the canal of a fang is clear from the fact that on none of the teeth can an indication be seen of an outer opening connected with this cavity.

Unfortunately it can not be determined, due to the tiny size of the tooth, whether an enamel layer is present, as the lively outer gloss could lead us to suppose.

Apart from the fully developed teeth there are also still-unfinished replacement teeth present (Fig. 7). They show themselves even just by their different coloration. In particular, the smaller and less developed the replacement teeth are, the matter is their brown coloration, and indeed the smallest are almost white. It was not possible to extract such a replacement tooth. But it could also be seen that the smaller they are, the blunter a shape they possess. The outer sculpture however, particularly the formation of edges, could be observed even on the smallest of scarcely $^1/_2$ mm in length.

From the completely free position of the replacement teeth beside the jaw bones on the slab it is clear that the replacement must have taken place in just the same way as in the living snakes, namely by new formation in folds of the mucous membrane surrounding the tooth-bearing bones.

Of course nothing more exact can be said about the number of teeth that were originally present. If the whole maxillae were set in the same manner as the parts preserved, they must have borne 26-29, approximately as shown in the reconstruction (Fig. 2). How far the dentition extended anteriorly on the palatines, how far posteriorly on the pterygoids, and how they were distributed on the mandible, is thoroughly uncertain. The restorations of these features in the figure correspond somewhat to the average proportions in living snakes.

B. Vertebrae.

Preservation.

While the body of the animal is visible on the slab of rock for its whole length, and while the vertebrae are all physically present with the exception of a small number, only a few actually allow their forms to be examined with precision. This is due to the fact that the vertebrae were clearly only truly ossified in a thin outer layer, which was the only substance of the vertebra able to be preserved, while the whole inner space has been filled with crystalline calcium carbonate. With the splitting apart of the slab by which the snake first came to light, and possibly also during the first attempt to further expose the animal, the breaks almost always occur either through the middle of the calcite filling of the vertebrae, or at least separated the thin preserved layer of bone from the core lying below it, which of course shows none of the finer features and can only give an approximate picture of the vertebra.

At some few places, on the other hand, vertebrae remain preserved more favourably, particularly those which were still covered by rock and could be prepared out. With the uniformity of the vertebrae of the snake skeleton, however, these few well-preserved parts are thoroughly sufficient to recognise the form and structure of the vertebrae with some exactitude. To completely prepare out and free a vertebra was not possible due to the easy fragility of the skeletal parts of the snake.

More complete preservation is found in the region of the 46th vertebra, at vertebrae 90-92, and 116-117. The general outlines and size proportions can also be determined at a series of further places in the whole vertebral column. The preservation of the dorsal arch and particularly the articulatory connections is very deficient, but on the other hand, the hypapophyses and haemapophyses are distinctly visible at a number of places in the vertebral column. However, with the uniformity [*Gleichartigkeit*, qualitative] of the vertebrae of a snake, it is safe to give a reconstruction of a whole vertebra based on the different details shown by neighbouring ones. If moreover, as in our case, information can be obtained on those points which vary most in proportions, namely the ratios of height to width and the form of the hypapophyses and haemapophyses, we can finally derive a picture of reasonably satisfactory completeness.

The picture of a complete trunk vertebra (Pl. II, Fig. 8) results from the combination of features preserved on neighbouring vertebrae, or at least not far apart. On another trunk vertebra, in addition, a view is available of the underside (Fig. 9). On a third, sticking fairly vertically into the rock in the plane of the slab, a cross-section could be obtained by carefully shaving it off (Fig. 10).

Number of vertebrae and length of the vertebral column.

As the first thing concerning the number of vertebrae, the original label states that over 500 of them are present; more precisely, Massalongo in his publication reckoned them at about 507. In any case it is not possible to determine their number absolutely correctly, as the articulation is disturbed at a number of places and also vertebrae are missing. First, at the beginning of the neck the vertebrae can not be counted with certainty, and further, in particular a part about 6 cm long, in the strong curve behind the middle of the animal, no longer shows any vertebrae. Moreover, there are also some short interruptions of articulation. At such unfavourable places, the number of missing vertebrae could either be concluded from the number of ribs present, or it could be estimated with approximate correctness from the length of the gaps. The uninterrupted impression of the body continuing over such places gave certainty that vertebrae had been present here and had only been lost subsequently. It could well be maintained that the error in careful counting would not surpass 15. Thus was obtained the **extraordinarily high number of 565 vertebrae**. Of these, as indicated by the presence or absence of ribs, **452 are presacral** with the deduction of two cervical vertebrae (atlas and epistropheus), **111 postsacral**.

The numeration used here corresponds to the number obtained in the count. As is clear from what has been said, these could not make a claim to absolute accuracy, but are to be regarded only as approximately correct.

Regarding the total length of the vertebral column, this measures about $92^1/_2$ cm, of which more than $10^1/_2$ cm belong to the tail; the presacral part consequently measures some 82 cm. The total length of the snake, including that of the head, amounts to about $95^1/_2$ cm.

The size proportions of the vertebrae.

On the length and height of the vertebrae a number of impeccable values were able to be obtained. For length, that of the vertebral centrum was chosen, as this could be determined more surely than that of the dorsal arch. For height, firstly the distance from the underside of the centrum to the upper side of the dorsal arch, and secondly this together with the hypapophysis, were taken. As the latter shows strong variation in its length, its inclusion in the amount of the height influences the latter to a varying extent, according to the body region.

The adjacent table of measures makes known that the vertebrae of the trunk are somewhat higher than long, and it also shows that those of the most anterior trunk region, e.g. no. 46, were somewhat smaller than in nos. 117-257, and differed from these particularly in their relatively shorter shape. In the posterior part of the trunk they become gradually smaller, but without the ratio of height to length significantly changing (cf. nos. 383 and 452). In the tail the size steadily decreases further. But at the same time the vertebrae become relatively more elongate, to be precise, at a rate such that in no. 525 the length noticeably surpasses the height.

Table of measurements of vertebrae of
***Archaeophis proavus* Massalongo (in mm):**

Number of vertebra	Length of centrum	Height of vertebra:		Width of vertebra
		without hyp- or haemapophysis	with hyp-or haemapophysis	
46	1.8	2.3	2.9	----
78	2.5	----	----	2.2 (centrum width 1.9)
117	2.5	2.8	----	----
257	2.5	2.7	3.0	----
383	2.0	2.2	2.4	----
452	1.8	2.0	----	----
489	1.5	1.5	2.4	----
525	1.1	0.9	1.3	----

Presacral vertebrae.

The **vertebral centrum** possesses, as can be clearly seen in a number of places, a pronouncedly procoelous structure, which indeed is otherwise constantly present in the snakes. In its middle part, as shown in ventral view (Pl. II, Fig. 9), the centrum is narrowest, and it thickens anteriorly and posteriorly to receive the broad surfaces for the articulation. A narrow ventral flattening is set off, not very sharply, from the flanks by blunt ridges. The cross-section (Fig. 10) is overall - apart from both ends, of course, where it is rounded - approximately triangular. Seen from below, at the anterior end an arch-shaped bulge can be seen. But it is evident that this appears as a result of a part of the rim surrounding the cotyle being broken off.

The condyle is not very spherical in proportions, but rather flat, and not set off from the rest of the centrum. In vertebra no. 117 its diameter measures 1.3 mm, its outline is fairly exactly circular. It is set straight, not obliquely, on the posterior end.

In the figured cross-section, incidentally, it can also be seen how extraordinarily weak is the ossification of the centrum. Specifically, this is formed only by a very thin outer layer of bone. The inner, on the other hand, remained unossified apart from a few extremely thin bony lamellae crossing it, and during fossilisation it was filled with crystalline calcite.

The illustration also shows that on the dorsal side of the vertebral centrum, in the midline, there ran a tiny groove, on whose significance, however, nothing can be said.

The **upper arch** is lowest approximately above the middle of the centrum, its upper contour rises somewhat anteriorly and posteriorly. Both anteriorly and posteriorly it projects a little out beyond [the centrum]. Over the anterior end of the centrum the dorsal arch forms a projection, while over its posterior end it shows a cut-out, arch-shaped below and angularly bordered above. The cross-section in Fig. 10, which lies somewhat anterior to the middle and hence no longer meets the hypapophysis, shows that the arch encircles the rounded, pentagonal lumen of the neural canal as a bony roof, and that it is extremely thin in its lower half but substantially stronger above. A sharpening appears dorsally, which further posteriorly bears a low, but extremely delicate, blade-like keel. In particular, there was one visible more posteriorly before the cross-section figured here was obtained by careful further shaving-off of the limestone, in which that extremely sharp keel was distinctly visible. It was, incidentally, a little curved over to the side, which speaks for it being somewhat flexible. Clearly it is to be regarded as an indication of the spinous process.

The cross-section also allows one to notice that the upper arch too was only ossified in an extremely thin outer layer, while its inside contained only a few delicate bony lamellae, but between them simply calcite crystal.

The **zygapophyses**, which are very developed in the vertebrae of living snakes and lend them their distinctive character, are extraordinarily indistinct in *A. proavus*, so indistinct that one is forced to investigate very closely whether the articulation of the post- and prezygapophyses is present at all. However, it can be determined with certainty by closer examination of the figured vertebrae (Fig. 8) that the arch of the anterior vertebra projects a little over a process of the following one. Thus, a postzygapophysis with a short and, as the figure shows, approximately horizontal contact surface, lies on the prezygapophysis (Fig. 8, Pr) of the following vertebra. Actual articular facets could not be observed and are clearly only indistinctly developed. Also, the cross-section (Fig. 10), which is to be assumed anterior to the middle of the vertebra, yet shows no projections worth the name at the level of these anterior zygapophyses, as we would have to expect if they were strongly developed.

With respect to the articulation of the **zygosphene** with the **zygantrum**, proof of this is even harder to produce than that of the zygapophyses. That comes about due to the hidden position of the articular facets, which are not perceivable at all on articulated vertebrae and can only be recognised on isolated vertebrae or uncovered ends of vertebrae.

The fact can, however, be determined that the posterior [part of the] dorsal arch covers the anterior edge of the arch of the following vertebra on both sides above the zygapophyseal articulation. At the same time, as shown by vertebra 46 (Fig. 8, Zy), an inner projection of the overhanging posterior edge lies in a furrow-like hollow in the anterior edge of the following vertebra [lapsus, 'posterior edge of the preceding' in original]. One would thus have to seek in the projection the articular surface of the zygantrum, and in the furrow that of the zygosphene. Distinctly bounded articular facets are thus no more present than they are on the zygapophyses.

The **transverse processes** serving for attachment of the ribs are weakly developed throughout. One can see distinctly on vertebra 89, on which they are not broken off, immediately before the anterior end of the centrum, to be precise, notably at the place where the somewhat flattened underside of the centrum passes into the lateral surface at an indistinct ridge, a projection which emerges gradually from the surface from above and behind, but falls away steeply below and is bordered anteriorly by a semicircular concavity.

A standard, ossified transverse process was thus clearly not present. Apparently it was only cartilaginous, as indeed the proximal ends of the ribs show no sharp contours either, and thus were probably cartilaginous too. The low position of the transverse processes is notable for the important [*wichtige*; lapsus for *richtige* = 'correct'?] assessment of the rib attachment.

In the lateral view of vertebra 46 (Fig. 8, Tr) the indication of the transverse process described above is restored, which can probably be done without danger as these usually remain the same in the whole presacral vertebral column of snakes.

The **hypapophysis** is clearly recognisable on various vertebrae. Its form is not always the same. In the anterior part of the trunk it forms a blunt-ending, posteriorly directed, saw-tooth-like, thin lamella of bone (Fig. 8, Hy) with a height of about 0.6 mm. It sits ventrally, only on the posterior two thirds of the vertebral centrum, though in such a way that the condyle remains free. In the posterior half of the trunk, on the other hand, the hypapophysis begins anteriorly just under the cotyle of the centrum and extends, becoming only slightly and slowly deeper, to the condyle (Fig. 11, Hy). Its anterior and posterior ends are rounded, the greatest height comes to 0.2-0.3 mm.

Postsacral vertebrae.

In the skeleton of the snakes the trunk and caudal regions differ in that the vertebrae of the former possess free ribs and possibly a hypapophysis, while those of the tail do without free ribs, but on the other hand show two so-called haemapophyses. In our specimen the last, very short rib can be clearly recognised, it belongs to vertebra 454 and is, as may yet be remarked incidentally, a little displaced anteriorly. Vertebra 455 in contrast is provided with distinctly developed haemapophyses, though they are broken off and have got into the wrong position, but yet belong to this vertebra without doubt. Hence, the tail begins with vertebra 455.

The distinguishing character of the caudal vertebrae, the ventral **haemapophyses**, is distinctly developed. They show the form of narrow, thin rods of bone which are somewhat inclined posteriorly and make up about $^{1}/_{3}$ of the total height of the vertebra, as is clear from the Table (p. 9 [=11 here]) and the illustration (Fig. 12, Hae). It could be determined that the haemapophyses were in fact present in pairs, on some vertebrae on which one could be seen lying over the other.

The dorsal arches are unfortunately only badly preserved due to their delicacy and small size, particularly their anterior and posterior contours, and as a result the articulations are also only very indistinctly recognisable or not at all, while naturally the dorsal contour is often clearly visible. So far as can be concluded from what is recognisable, the arches of the caudal vertebrae correspond essentially with those of the trunk in their form, as may also seem probable in any case, given the uniformity of vertebrae in the snake skeleton. In any case it can be determined with certainty that the dorsal contour has a similar simple course to that of the presacrals, thus that spinous processes were not, or extraordinarily weakly, developed.

The ribs.

The first preserved rib already shows itself very soon behind the skull and may belong to the fourth vertebra. The most anterior part of the vertebral column is, however, as already mentioned, especially badly preserved, so that it can not be surely decide whether that rib is the first. If we assume the latter, we obtain with the 454 presacral vertebrae the unusually high number of 451 pairs of ribs. The proximal ends of the ribs mostly lie in natural position against the vertebral column. Only in two places, about in the middle of the trunk, where the articulation of the ribs is strongly disturbed, and at the beginning of the last third they are disarticulated and have become irregularly arranged.

The length of the ribs is very variable according to the region of the trunk. But overall, the extraordinary delicacy and fineness, the weak curvature, and the strong posterior inclination are characteristic. While a very large majority of them are visible, yet it is only possible to measure their total length exactly on very few, because the strongly posteriorly inclined ribs lie so close together and in part also across each other, that it is only rarely that any single one of them can be followed to its ends.

In the most anterior part of the trunk the ribs at first possess a slight length. In the region of the 17th vertebra it comes to about 6 mm, with a thickness of about 0.15 mm not far from the proximal end. The curvature is very weak and restricted to about the first third. They are very strongly directed posteriorly, and lie with the greater part of their length nearly parallel to the axis of the vertebral column. At vertebra 35 one disarticulated rib lies at some distance from the vertebral column and shows the proximal end especially distinctly (Fig. 13). It begins with a weak knob-like expansion, though it lacks a recognisable articular facet and is strongly compressed, and possesses a thickness behind it of 0.25 mm, narrows further by a distance of 3.5 mm [lapsus '35'] from the articular end to about 0.1 mm, and then retains a fairly constant cross-section to the end. The curvature is restricted to the anterior half of the total length, which comes to 7 mm. At vertebra 62 the rib length is 8 mm, the thickness remains the same. Towards the proximal end the cross-section of this rib is approximately egg-shaped, as longitudinal compression sharpens somewhat ventrally. At vertebra 123 the length of the rib has grown to 11.5 mm, about $4^1/_2$ times the vertebral length, and the maximum width to 0.4 mm. The proximal end is strongly compressed. This compression can be followed for about half the total length. In the middle of the latter the diameter comes to about 0.15 mm and diminishes yet further towards the end.

At vertebra 177 the length of the ribs reaches 22 mm, thus about nine times the vertebral length. Their thickness in the initial part behind the swelling of the articular end comes to about 0.4 mm, but 10 mm from the proximal end it has already diminished to 0.2 mm and reduces further towards the end. The curvature of the rib is also very weak in this region of the trunk. At vertebra 240 the measurements of the ribs are the same, but the curvature seems to be a little stronger. At vertebra 340 the length was determined to be 18.5 mm. Vertebra 408 bears ribs of 15 mm and somewhat slighter thickness than the preceding. At vertebra 436, thus not far before the beginning of the tail, the rib length comes to only 9 mm, thus about five times the vertebral length. The last ribs, finally, were somewhat shorter still.

As already mentioned, a distinctive, but at the same time also important, character is the slight curvature of the ribs. Their second half is mostly quite straight. The figures (Figs 13-15) reproduce three ribs from different regions of the trunk and also show, at equal magnification, the proportions of their lengths. In detail, the form of the ribs is not absolutely constant for any particular part of the trunk. We must conclude from the extraordinary delicacy of the bony walls, soon to be discussed, that they were not rigid but rather flexible to a considerable extent. It could thus come about that their extremely thin distal parts are often a little bent. The remarkable change in degree of curvature can also be traced back to the same cause. The ribs disarticulated from the vertebral column, and lying free, without question show the normal form best. One part from the middle of the trunk, roughly between vertebrae 220 and 250, shows disturbances of the articulation of the vertebral column which may have occurred during embedding in the mud, perhaps due to the development of gases in the putrefaction of the animal's body. The pressures thus arising, and possibly the weight of the body itself or of the overlying mud, have at this place produced a somewhat stronger curvature of the delicate ribs. The more correct picture is without doubt that of a very weakly curved rib, as presented by much the greatest part of the trunk and especially the ribs which lie completely free. Their length, particularly in the middle of the body, is proportionally great. They are in the proportion to the height of the vertebrae (without hypapophysis) as 22 : 2.7 = 8. Further anteriorly and posteriorly this ratio is substantially smaller.

As in respect of the lengths, nor are the ribs all alike in respect of their cross-sections. In the anterior portion of the trunk the latter, on vertebra 35 about 1 mm behind the proximal end, is in the form of a right-angled triangle with an acute angle of 30˚-40˚; the shortest side is directed medially (Fig. 16a), $1^1/_2$ mm further it has taken on the form of an oval with the narrow side directed medially (Fig. 16b), and then soon passes into a circular form further towards the tip, which rules for more than half the total length (Fig. 16c). Pl II, Fig. 17 a-c depict the cross-sections of the ribs of the middle of the trunk, specifically those between vertebrae 160-180. Fig. 17a is the rib cross-section at a distance of about 2 mm from the proximal end, which here shows the form of a somewhat unequal-sided triangle, whose shortest side was directed obliquely anteriorly and medially, and the somewhat concave side posteriorly and medially. The cross-section changes quickly, though, and 4 mm further (Fig. 17b) has attained an only slightly sloping, rectangular character, whereby two opposite sides show distinct concavities. This form persists for somewhat longer, but eventually passes into a regular circular form (Fig. 17c) which is characteristic for more than the distal half of the ribs. The concave structure mentioned of part of the sides of the cross-section comes from superficial longitudinal out-throatings [*Auskehlungen*, another obscure synonym for hollows or grooves] of the ribs, which stand out with great distinctness in the view [*Aufsicht*, 'supervision']. It may be expressly pointed out that this we are not dealing with something like a consequence of possible compression. This interpretation is excluded by the **constant** appearance and uniform extent of the longitudinal out-throatings, as well as the lack of fracture lines on well-preserved ribs. In the most posterior part of the trunk the ribs vary somewhat again from the just-described type. No concavity is present in the cross-section. At first the proximal end is of the same triangular character, then soon becomes oval and later circular in the posterior half.

As the cross-sections show, the ribs also, like the other bones of the skeleton, are formed only by a thin outer layer of bone, while the inside is filled by crystalline calcite as clear as water. The proximal part, where this inner space is especially large in proportion to the thickness of the bone, is often compressed, while this is more rarely the case at the distal end.

A distinct formation of a distinct articular surface for the corresponding transverse process is not to be observed on any rib. Always the proximal [lapsus: 'distal'] end represents a thickening, which is chopped off either fairly straight or irregularly. A knob-like projection at the anterior end, which is found in recent snakes and is designated by Hoffmann (Reptilien III: 425) as a "tuberculum costae", is not present. The anterior end of the ribs was, as is clear from its external formlessness as well as from its very pale colour in comparison to the whole rest of the rib, extremely weakly or not at all ossified, thus essentially cartilaginous, as indeed also applies for the transverse processes of the vertebrae.

As was already detailed in this chapter, the slenderness and the relatively great length are distinguishing characters of the ribs of *Archaeophis.* By their extraordinarily thin and delicate form, especially too at places in the middle part of the trunk where they lie about on the slab somewhat confused and irregularly arranged, they quite give the impression of very fine hairs. The most posterior portion of the trunk also, part of which is shown at $2^1/_2$ x magnification in Pl. I, Fig. 2, and which stands out by the particular delicacy of the ribs, provides this picture quite especially developed. The likewise remarkable, strongly posteriorly directed arrangement of the ribs, already several times stressed, will be discussed below in the section on the presumed body form and way of life of *Archaeophis* in connection with these questions.

Extremities.

No traces of the extremities were discerned, nor any of the shoulder or pelvic girdles. Certainly, it is indeed not absolutely impossible that remains of them, by an unlucky accident, are no longer preserved or visible on the slab. However, probability speaks decidedly more for such not having been present at all. For with the completeness in which the ribs are clearly preserved, it would be peculiar if precisely those parts had gone missing. With respect to the hindlimbs and the pelvic girdle, by the way, their absence can be determined with certainty, as the transition from the trunk to the tail is preserved clearly and distinctly. This evident total reduction of the pelvic girdle, besides, would in itself make it probable that nothing was present of the shoulder girdle either. In any case, there are certainly forms with rudiments of the pelvis among the living snakes, but not with any of the shoulder girdle.

Incidentally, the snake type is indeed developed to such a high degree in *Archaeophis* that the complete reduction of remains of the extremities and their girdles, as is assumed here with the highest probability, can not stand out in the slightest.

The squamation.

The well-preserved impression of the body shows, as Massalongo already stated, unmistakable indications of scales. They can be noticed in the most anterior section of the trunk, at around vertebra 35, then again in the middle half of the loop formed by the snake's body at vertebrae 85-125, in the posterior part of the trunk at vertebrae 380-410, and in the anterior half of the tail. Besides, the impression of an isolated scrap of the body skin, with traces of scales, lies at vertebrae 160-170 on the ventral side of the body. The form of the skin is most favourably recognisable on the second part named, to be precise on the external, ventral side of the loop (at vertebrae 100-110). Here the borders of the scales are distinctly recognisable as fine dark lines, which stand out clearly against the pale rock. The individual scales show oval outlines with diameters of about 0.5 mm for the long and 0.3 mm for the short axis (Pl. II, Fig. 18). The wider end is the anterior one.

That only the outlines have been preserved is probably to be explained by the fact that the overlapping edges of neighbouring scales formed a layer twice as thick as the rest of the surface and could more easily preserve a trace of their substance. At the concave dorsal side of the part just discussed, and also at all the other places offering indications of scales, the whole outlines are not preserved, rather just short dark streaks running longitudinally, but anyway they allow the individual transverse rows to be distinctly distinguished.

Corresponding to the tiny size of the scales, there is a quite high number of transverse rows. At the first of the sections of the body given as showing the scales, four longitudinal rows of scales come in a width of 1 mm; no variation in width worth mentioning can be determined. The squamation is preserved over about half the width of the body impression. The total width here comes to 9 mm, so 36 scale rows would come in. The impression of the body, which naturally only depicts one of its sides, can also only allow at most half their number be seen, probably somewhat less. Therefore, for the total circumference of the body about 75-80 scale rows would result. These numbers result with the assumption of approximately equal-sized scales on all sides of the trunk.

At the second part, between vertebrae 100-110, where the squamation can be seen over the whole width of the impression, on the ventral side the width of the scale rows comes to about $^{1}/_{4}$ mm, and apparently somewhat less on the rest of the part. The width of a transverse row is naturally somewhat slighter than that of the individual scales, as these always mutually overlap somewhat at the edges. With a total width of the body impression of 10 mm, there thus results a total of about 80. The ventrally located loose scrap of skin mentioned above, at vertebrae 160-170, likewise shows a scale width of about $^{1}/_{4}$ mm. At about vertebra 385 there are traces of scales over the whole width of the impression, especially distinct at the ventral boundary. Here too the width of a scale row, as above, comes to $^{1}/_{4}$ mm and the total number to be assumed is at least 80.

At vertebra 400, where the total width comes to 8 mm, the scale rows have also become noticeably narrower. Here too, the parts of the impression located quite ventrally show this particularly distinctly.

The observations which have been given now allow a judgement as to whether the assumption made in the calculation of the total number of scale rows was correct, that the width of the scales was nearly the same all over, on the ventral as well as the dorsal side. The fact that in most - though not in all - recent snakes the ventral side is covered with large, broad shields (ventral shields), while the sides and the back bear small scales, in fact makes it necessary to test this assumption. It is now of decisive significance that we have, fortunately, well-recognisable traces of the squamation just especially at the ventral borders, which in the generally present lateral orientation of the body would have to show large ventral shields or at least larger scales, if such were present. It is precisely the parts just discussed, showing scale impressions, which would have to show them, as we are here without doubt dealing with an exactly lateral orientation. It follows from this that the scales on all sides of the trunk were of approximately the same size.

In the chapter following below on 'Degree of specialisation of *Archaeophis* and comparison with living water snakes', incidentally, yet further information will be given which, on other grounds, make this conclusion seem thoroughly probable.

The number of scale rows can be estimated, if we assume that the whole half of the body surface has been compressed, at about 80, though as that was surely not completely the case, 85-90 may come nearer to the truth. That is, as we will see more precisely later on, an unusually high number.

The external body form and way of life of *Archaeophis*.

To gain an idea of the external body form, first of all two points must be taken into consideration, namely the impression of the body on the slab of rock, and its orientation, and these must be combined with the results from the portions of the body described above.

That the skull possessed an extraordinarily sharp snout, but otherwise was compressed fairly flat in the manner of those of the living snakes, was already stated above.

The impression of the trunk is so clear and sharp, for a great part of its extent, that it is not to be assumed that the body underwent any strong flattening and wide-squashing [*Breitquetschung*] through the pressure of overlying calcareous mud. If, on the other hand, one must probably reckon with a slight broadening, yet this may well not be considerable. A compression of the body may not have taken place until after it was covered by a layer of mud to a certain thickness and was contained laterally. But the lateral orientation of the corpse would then have stood in the way of a *Breitquetschung* worthy of the name. One can thus quite well conclude the original diameter of the body from the sharply bordered parts of the impression. This of course does not hold for parts where even the articulation of the ribs with the vertebral column is disturbed, or the borders of the impression have not been sufficiently clearly exposed by preparation.

As a general result on the shape of *Archaeophis*, it was extremely slender. The thickness was at its greatest in the middle of the trunk, from there it decreased uniformly posteriorly to the end of the tail, without a break being noticeable at the transition to the tail. Regarding details, it demands a more precise examination.

Let us begin with the most anterior portion of the body. The first semicircular curve up to about the 40th vertebra shows a fairly exactly lateral orientation, as is clear from the position of the vertebral column at the outer border of the impression, and the inward-directed ribs. The sharply bordered impression of the body shows a width of 8 mm, and at the point of greatest curvature a slightly greater one of 10 mm. There is then a kink in the vertebral column, and it switches more over to the other side. Here, and already for a short distance anteriorly, the ribs show on both sides of the vertebral column. One vertebra shows a distinct lateral orientation, such that its ventral side faces the convex side of the bend in the trunk. As the ribs of both sides do not lie ventrally from the vertebral column, as would have to be the case in an exactly lateral orientation, but rather on both sides of it, we see here a somewhat disturbed position of the vertebrae, although at this place the contours of the 9-mm-wide body impression still run quite straight and uninterrupted. The following point, where the impressions and skeletal parts of two parts of the body lie across each other, naturally gives no clear picture. The loop that comes next, comprising the section of the trunk from vertebra 50 to about 150, offers peculiar positional relationships. Namely, the vertebrae lie right on the outside of the loop throughout, but in the first part, as one vertebra shows clearly, the ventral side is turned toward the observer, while in the middle section, comprising at least a third of the loop, the ventral side faces nearly exactly to the outside. In the first section the ribs of one side lie inwards, and only short proximal portions of those of the other can be seen on the outside of the vertebrae, while they [ribs] are mostly covered by them [vertebrae]. In the remaining segment comprising two thirds of the circle the left and right ribs lie on the inner side of the vertebral column, though those of one side, lying more deeply imbedded in the rock, also remain with their anterior ends covered. Fairly exactly in the middle of the loop both contours of the impression are sharp and undisturbed. The width here comes to 10-11 mm, that of the zone outside the vertebral column about 1 mm, that on the inside 6-7 mm - outside and inside reckoned from the centre of the loop. The ribs do not extend to the inner contour, but leave a free strip about $2^1/_2$ mm wide. This positional relationship of the ribs and impression remains the same for as far as the inner contour is sharp, i.e. for about $^2/_3$ of the whole circle, only the inner zone remaining free of the former [i.e. ribs] is in places considerably wider still. An explanation will be sought further below for the conspicuous fact that the vertebrae thus for the most part have their dorsal side turned toward the ribs.

The section following now, comprising about 50 vertebrae, is strongly disturbed, and thus is not taken into account for the question before us. The nearly straight-running part from vertebra 200 to 250 shows the ribs of both sides directed to the same side of the respective vertebrae. The few somewhat distinctly preserved vertebrae of this part have the ventral side facing the ribs. The body thus lies in the normal fashion on its side. The impression possesses no distinct contours, its width is thus not measurable. Here too the impression extends for a considerable distance ventrally beyond the ribs.

Between vertebrae 250 and 270 the vertebral column shifts from one side of the impression to the other. At the same time the ribs appear on both sides and to the same extent, [and] as the vertebral column shifts to the other side the previously distinct ribs disappear from one, except for their proximal ends which remain visible beside the vertebrae. The body of the snake thus turns over from one side to the other, and in a short turn at that. The vertebral column in the next portion of the trunk, curved in a semicircle, is only partially present. Where it is, it lies on the convex side, and the ribs are directed to the concave one. Thus the vertebrae here again turn their ventral side outwards, that is to the dorsal contour of the impression. Behind this semicircle the vertebral column shifts, between vertebrae 365 and 385, from its position at the edge of the impression into its middle, and retains this position to the end of the tail. The ribs remain lying on the same side of the body; indeed at first, here and there their proximal parts are visible on the other side of the vertebrae, but from vertebra 385 on they can all only be discerned on the one side. The ventral side of the vertebrae also faces in the same direction from here on: the orientation of the body is a normal lateral one. The impression is very clear in this whole posterior section of the trunk and in the tail, and sharply outlined on both sides almost throughout. Very remarkable here is the very slight width, taking the vertebrae and ribs reckoned together. Namely, it comes to less than, or only very slightly more than half the width of the impression, so at about vertebra 388 it is $4^1/_2$ mm of the total width of 10 mm; at vertebra 408, $4^1/_2$ mm of $7^1/_2$ mm; at vertebra 450, $3^1/_2$ mm of $6^1/_2$ mm. This striking phenomenon comes about from the fact that the ribs, which were already described above, are directed posteriorly to an extraordinary extent, so that they snuggle close up against the vertebral column and lie nearly or quite parallel to it.

In the middle of the tail, at about vertebra 385, the width of the impression comes to 5 mm, of which 1 mm is covered by the vertebral column (counting the haemapophyses). At vertebra 513 the width is determined to be $3^1/_2$ mm, at 532, $2^1/_2$ mm.

It arises from the detailed description above that the body of the snake is mainly found lying on its side. That this is the preferred orientation is shown especially clearly at the place where the trunk turns over from one side to the other. This transition is completed in a very short stretch; it is also clear from this that a ventral position is, as it were, avoided. The explanation for this could be seen in the body being strongly laterally compressed, and thus the ventral side was only narrow. It is obvious that, with this shape, the trunk had to take up a lateral orientation as it sank together on the sea floor. It is striking that at the places with strong curvature the vertebrae have their ventral side turned toward the dorsal line. It can now be considered that a strongly laterally compressed body, under considerable curvature, would offer a picture similar to a curled ribbon or strip of paper, i.e. the dorso-ventral line would stand roughly vertically on the plane in which the curvature lies. In this position, those strongly curved parts may have sunk to the sea floor with the venter or the dorsum directed downward, and only then have been laid down on the side. It can be imagined that thereby the ribs of one side, under the weight of the body, although in the water that can not have been great in any case, or of the overlying mass of mud, somehow worked as a lever, which twisted the vertebrae about their own axis as they hung loose in the rotting corpse. In this or a similar way one can perhaps explain the peculiar orientation of the vertebrae in the places with strong curvature.

However, the form of the trunk is also associated with the structure of the ribs, which we must again briefly go into. The ribs, as was shown above, are strikingly delicate, long, weakly curved and strongly directed posteriorly. These properties distinguish *Archaeophis* to a high degree from the snakes living on land. In the latter the ribs play an important role, namely in locomotion, as they are used as levers together with the broad, flat ventral shields covering the ventral surface, by means of which the animal braces and pushes itself forward against irregularities of the ground, plant-stems etc. It is not possible to accept this manner of function for the ribs of *Archaeophis.* They are here too delicate to be able to be used as such levers. Also their posteriorly directed position, especially in the posterior part of the trunk where they are almost horizontal, makes them seem thoroughly unsuited for it. It is also relevant here that the ribs, as can be concluded from the impression, did not support the body wall down to the ventral surface at all, but left quite a wide zone free here. Thus, if one would think of *Archaeophis* set down on the land, then if the body didn't lie on its side, the ends of the ribs would not even touch the ground, and creeping would thus hardly be possible. The considerations already put forward above, and especially the conditions in the posterior part of the trunk, speak against the part of the body impression lying below the ribs on the slab being entirely, or even substantially, spread out by subsequent compression of the snake's body. Here, for the most part, the ribs cover a space not wider than the vertebrae; thus if one wished to interpret the part of the impression lying ventral to them as an expansion due to compression, there would result far too low a value for the height of the cross-section of the body. Even including the whole impression one arrives at an extremely slender shape. It is thus to be accepted that in fact a ventral portion of the wall of the trunk was not supported by ribs. Whether the narrow ventral side of the laterally compressed body was rounded, or perhaps formed a sharp angle, and bore a fold of skin as it exceptionally does in living snakes, can not be gathered from the impression. Even this latter assumption would not be excluded, as the absence of ventral shields can make it possible.

The interpretation of *Archaeophis* as a land snake living on solid ground is forbidden, as we have seen, by the form and structure of the ribs together with the cross-section of the trunk. Still less does a burrowing way of life come into question, as this demands especially strong ribs, as e.g. the living genus *Typhlops* shows. Also we may not ascribe to *Archaeophis* the life of the tree-snakes, despite the slenderness common to both, as those generally possess much longer vertebrae but only short ribs, as is so typically to be seen in the skeleton of e.g. *Dryophis*. On the other hand the features in question speak absolutely for **aquatic life**. The ribs have no burden at all to bear in swimming locomotion, can thus be delicate, but by their length, their dense succession, and strong posterior inclination may allow especially uniform antero-posterior undulatory movement, somewhat as the fin-rays in the fins of an eel, with which they were probably comparable in their form. That comparative considerations of *Archaeophis* and the living forms of snakes adapted to aquatic life also speak for the habits assumed, will be shown further below.

It should here only be pointed out in this respect, that the geological deposit in the limestone sediments of Monte Bolca supports the interpretation expressed and makes it more probable that *Archaeophis* is a marine form, not one living in fresh water. For those limestones represent a marine deposit, as evidenced by the fish and worms present. Certainly there are also often frequent impressions of tree-leaves; but these could just as well have been blown or washed in. In any case, land animals seem not to have been reported yet from these deposits. Besides, all highly specialised living water snakes are also pronouncedly marine animals.

Comparison with *Archaeophis bolcensis* Mass.

If we compare *Archaeophis proavus* with other fossil snakes, the first to come into consideration are naturally the two fragments of a large snake, likewise coming from Monte Bolca, which Massalongo figured under the name *Archaeophis bolcensis* (1849, Pl. III, IV). Massalongo states that he had three specimens available, which were 48, 33 and 27 cm long and 50-60 cm wide. None of the fragments fit with another. As those three fragments of *A. bolcensis* did not also arrive in the possession of the Berlin collection and it was consequently not possible for me to examine them personally, only the information and plates in Massalongo can be used for comparison.

Both of the illustrated fragments come from the trunk region and, as can be concluded from the length of the ribs, either from the most anterior or the most posterior sections. With respect to the general size proportions of the vertebrae, Massalongo states that the length comes to 8 mm, the thickness at the ends 10 mm. What he means by the term 'thickness' is not clearly apparent, perhaps he understands by it the greatest width, thus that of the dorsal arch. The vertebral centrum ('corpus') is supposed to be somewhat concave in the middle, thus probably constricted, and correspondingly to thicken towards the ends. Measurement on plate IV results in a length of the centrum - without the condyle, which in every case is covered by the following vertebra - of 8 mm, a width of circa 4 mm in the middle and circa 5 mm at the ends. In *Archaeophis proavus* at vertebra 78 the length of the centrum comes to 2.5 (the condyle included), the width 1.9 mm [not cm]. If one considers that at vertebra 78 the vertebral length already shows the highest value found, it is beyond all doubt that in *A. proavus* the vertebrae are proportionally significantly shorter and broader than in *A. bolcensis.*

The author further states that four blunt projections ('eminentiae') were present, which produced a nearly rectangular character. What is meant by this is not apparent, and also the further statements about these 'eminentiae' provide no clarity. Possibly it is only the state of preservation that induces these remarks. Namely, the vertebrae are perhaps compressed so that the thin outer bone layer is broken apart into several pieces by longitudinal breaks, and these then pressed into such a position that longitudinal grooves and keel-like rises are produced. As far as one can decide from the illustration, the vertebrae in the fragment represented in plate III are in fact strongly compressed in this manner. More important is the statement that the apophyses, which were broken off to be sure, seem to have been pointed but very short. To be sure, this too really need to be checked on the object itself, as the unfavourable preservation can easily produce deception even in the most careful observer. If what is said on the apophyses corresponds to the facts - and the illustrations seem to justify this, especially in the somewhat more clearly reproduced parts of the vertebral column -, in this point there would be thorough agreement with the vertebral form of *A. proavus*.

The ribs, as in our form, are strikingly long, as far as one can conclude from the illustrations, not less than 7 cm, perhaps even longer in reality. They thus had quite probably nine times the total vertebral length. That ratio is also the same as we found as the maximum value in *A. proavus*. The ribs, moreover, are only curved in their upper parts, and here too only quite weakly, while they are otherwise stretched straight. They are oriented diagonally backward. If this shape of the ribs, as was explained above for *A. proavus*, indicates a considerable lateral compression of the body, a glance at pl. III in Massalongo will make this view appear quite indubitable in this case too.

In the lower part of this illustration one sees the body of the snake lying laterally, or mainly laterally pressed on the slab, then the body shows a sharp rotation to lie on the other, right side in the upper half of the picture. The body of the dead animal thus lay with its high, flat flanks on the bottom, but not on the ventral side, which was clearly too narrow to allow the body to come to rest in this position. At the place where the twisting occurs and one thus sees the snake from the back, despite the vertical pressure which was in any case active during deposition, the ribs are not now pushed apart, but remain in their natural position and consequently allow the slight thickness of the body to be recognised, which can not have come to much more, in maximum, than half of the height.

The fragment reproduced on plate IV shows a strongly curved portion of the body lying flat on its left side. At the places where the ventral border of the body impression is preserved in a smooth line, it shows clearly that the ribs, as in *A. proavus*, did not reach to the ventral side but left a fairly wide zone unsupported by ribs.

The question is now to be answered, whether *Archaeophis proavus* and *bolcensis* really belong to one genus, as Massalongo thought. There are in fact fully consistent relationships, namely affecting the ribs and the body form. To be sure, the ribs in *A. bolcensis* make a quite different impression, in so far as they lie in regular arrangement, than in *A. proavus*. However, that is surely just caused by the fact that the ribs of the much larger form are also correspondingly stronger and also have been displaced to a smaller extent during the deposition in the marine mud. After all it can only be considered probable that both forms in fact belong to one genus.

But now there arises the further question, whether we really have two different species before us, or whether both specimens should not even be counted as one and the same species. The only recognisable objection that can be given is that the vertebrae of *A. proavus* are proportionally shorter than those of *A. bolcensis*. But this is a difference which is very pronounced between juvenile and adult individuals in the recent snakes. In a just-hatched specimen of *Tropidonotus natrix* that was made available to me for study through the kindness of Herr Prof. Dr. Tornier, I could personally convince myself of the strikingly short shape of the vertebrae. It can hence not be indicated as improbable that both specimens even belong to one species, as the only recognisable difference does not speak against such a unification, but allows it. One must then, on the assumption of an equal number of vertebrae, decide on a length of about 3 to $3^1/_2$ m for the large specimen. Meanwhile, as long as no real proof has been produced that both forms belong together, it may be best to retain both species names. Should specific identity be shown later, such as by a new investigation of *A. bolcensis*, it would be best for the name *proavus* alone to remain valid, as the specimen so named by Massalongo is the better known, and besides its description precedes the other in his work.

The undeniable possibility that both specimens belong together raises yet another question, whether the extremely weak development of the zygapophyses and transverse processes in *Archaeophis proavus* is to be seen as something of a juvenile feature. Apart from the fact that Massalongo seems to have recognised the zygapophyses as small points in *A. bolcensis* too, the findings on that juvenile specimen of *Tropidonotus natrix* also speak against this assumption, as here zygapophyses as well as transverse processes are quite sharply and distinctly developed. The slight development of these parts is perhaps also only a consequence of life in water, where indeed, due to the elimination of the effects of body weight, the articulations of vertebrae and ribs need to be much less strong and firm than in land forms.

Degree of specialisation of *Archaeophis* and comparison with living water snakes.

After we have already learned above that we have to see *Archaeophis* as a genus living in water, in this section some considerations of the degree of its specialisation and a comparison with living water snakes should be given. In the lack of special summary accounts, the factual documents for the comparison were first obtained and brought together from the study of material of the zoological collection of the Museum für Naturkunde at Berlin, as well as from the use of the available literature.

Firstly, as far as the skull is concerned, in *Archaeophis* we are dealing with a true snake skull. The quadrate is freely mobile on the squamosal, the pterygoid probably contacted the quadrate or the lower jaw in the region of the joint of these two bones and took part in their motion; the maxilla was not grown-together with the premaxilla, thus clearly likewise somewhat mobile; we can also assume, as was explained above, that the two mandibular rami were not bound together in a bony symphysis. The jaws of *Archaeophis* were thus clearly capable of considerable expansion. However, this was certainly slighter than in the overwhelming majority of recent snakes. If we leave aside the families with a burrowing and digging lifestyle, the typhlopids, glauconiids and uropeltids, in which, probably due to their lifestyle, a more or less profound alteration and reduction of the skull has taken place and the capacity for expansion of the jaws is very slight, the latter is almost always significantly greater in the living forms than in *Archaeophis*. In most, especially by strong development of the squamosal or by the more or less conspicuously pronounced posterior inclination of the quadrates, the joint of the latter with the mandible is moved more or less far posterior to the occipital condyle, with corresponding elongation of the mandibular rami. This is especially strikingly developed in certain colubrids, namely proteroglyphs and viperids, where the mandible, e.g. in *Bitis arietans*, can surpass the skull by $^2/_3$ of its length. In *Archaeophis proavus* on the other hand, the quadrate is directed anteriorly and the mandible consequently considerably shorter than the skull. The illustration of *Nardoa boa* from the family Boidae in Boulenger (1893: 75, fig. 4) shows a weakly anteriorly directed orientation of the quadrate, but on the other hand the squamosal is here more strongly developed than in *Archaeophis*, so that the mandibular joint comes to lie only very slightly anterior to the occipital condyle. Generally, the posterior extension of the squamosal seems to be relatively little developed in the boids. In any case Boulenger's representation of *Enygrus asper* (1893: 104, fig. 6) also shows an anterior inclination - though very slight - at the same time as a huge development of the squamosal. In the Ilysiidae, in *Xenopeltis*, the only representative of the Xenopeltidae, and in *Furina occipitalis* [=*Vermicella annulata*]

(Boulenger 1896: 405, fig. 28), an insignificant capacity for expansion of the jaws is produced by the shortness of the quadrate at the same time as slight development of the squamosal. In all these cases, however, the lower jaw joint still lies somewhat further posteriorly than in our snake, while on the other hand the latter is beyond them in the more considerable size of the quadrate. The Ilysiidae and Xenopeltidae are incidentally less highly specialised, as in them the maxillae are not at all or only very slightly mobile against the premaxilla. In any case it can be asserted that *Archaeophis* is less specialised in the capacity for expansion of the jaws than the great majority of living genera.

If we further compare the dentition, [but] ignore the quite divergent form of the individual teeth, this is truly snake-like in that they are present on the maxilla, palatine, pterygoid and mandible, as is also the case in the majority of living snakes. Also the substitution of the teeth by replacement-teeth is absolutely the same. The stronger posterior curvature of the teeth of snakes now living, compared to *Archaeophis*, is certainly to be regarded as a more advanced adaptation to their function of holding prey. Venom fangs, distinguished by furrowing or the formation of a canal, naturally represent a much higher specialisation.

In the skeletal structure of the snakes the tendency becomes more pronounced, with reduction of the limbs, to allow the greatest possible flexibility and mobility of the trunk. The latter is attained by means of the numerous articulations of the vertebrae and the high number of the vertebrae themselves.

In regard to the first point, in the complete reduction of the limbs as well as the shoulder and pelvic girdles, *Archaeophis* stands at the same level as the overwhelming majority of living snakes, thus higher than the families Typhlopidae, Glauconiidae, Boidae and Xenopeltidae which still sow pelvic rudiments. The same articulations are found on the vertebrae of *Archaeophis proavus* as we know in all living and fossil snakes, thus pre- and postzygapophyses, zygosphene and zygantrum. With respect to the number of vertebrae, our form surpasses all [others] known by a considerable amount. The accompanying Table may serve for comparison, whose data are taken from Rochebrune's (1880: 219) compilation, with the exception of those marked with *, which come from my own counts on specimens in the Zoological Department of the Museum für Naturkunde at Berlin. In the choice of the listed species consideration has been taken to offer examples from different families which are the upper and lower extremes in regard to vertebral number. It is also to be remarked that the **vertèbres thoraciques**, **pelviennes** and **sacrées** are here put together under the heading "**presacral vertebrae**".

Summary of vertebral numbers in different snakes.

Name	Cervical	Presacral	Postsacral	Total
Typhlopidae:				
Typhlops lumbricalis Dum. Bib.	2	176	10	188
Boidae:				
Python sebae Gmel.	2	306	62	370
Python molurus Gray	2	372	61	435
Liasis amethystinus Gray	2	330	92	424
Boa constrictor L.	2	256	44	302
Xenopeltidae:				
Xenopeltis unicolor Schleg.	2	188	20	210
Colubridae:				
a) Aglypha:				
Tropidonotus natrix Schleg.	2	211	45	258
Elaphis aesculapia Daud.	2	226	68	296
Zamensis viridiflavus Wagl.	2	239	73	314
Dendrophis picta Boie	2	196	87	285
Acrochordus javanicus Horus	2	191	55	248
b) Opisthoglypha:				
**Dryophis prasinus* Boie	2	237	176	415
Homalopsis buccatus Fitzing.	2	171	58	231
Dipsas annulata L.	2	182	71	255
c) Proteroglypha:				
Platurus fasciatus Daud.	2	147	42	191
Pelamis bicolor Daud.	2	158	32	192
**Enhydris hardwickii* Gray	2	130	32	164
Viperidae:				
Pelias berus Merr.	2	150	51	203
Cerastes aegyptiacus Schleg.	2	120	16	138
Crotalus horridus L.	2	184	24	210
Archaeophidae:				
Archaeophis proavus Mass.	2	452 ca.	111 ca.	565 ca.

One can see from this table that the highest total numbers found in living snakes, those of *Python molurus* Gray, *Liasis amethystinus* Gray, and *Dryophis prasinus* are surpassed by that of *Archaeophis* by 130 to 150. The number of trunk vertebrae, and thus at the same time the ribs, exceeds the highest figure obtained, of *Python molurus* Gray, by about 80. The ratio of the number of caudal vertebrae to those of the whole body, of about 5 : 1, may come close to the average.

With respect to the number of vertebrae, *Archaeophis proavus* is thus hence significantly further advanced in specialisation than any known living species, and is in that respect superior to any known vertebrate whatsoever.

As in *Archaeophis* we are dealing with a snake living in water, a short discussion may here next be dedicated to the **living water snakes**, on the basis of which the level of organisation and specialisation of our snake should then later undergo a special comparative consideration.

According to their organisation, the water snakes the most pronouncedly and furthest adapted to life in water must without doubt be the hydrophines from the group of proteroglyphs, i.e. the colubrids with furrowed teeth on the anterior portion of the maxilla. In these hydrophines the nasal openings are remarkable by their position on the dorsal surface of the head as well as by the fact that they can be closed by flaps, peculiarities that one finds only in lung-breathing aquatic vertebrates. The trunk, apart from the most anterior portion, is more or less strongly laterally compressed. Especially strongly compressed is the tail, which represents a pronounced oar-tail and whose considerable height usually exceeds that of the trunk.

The genus *Enhydris* [=*Lapemis*] can count as an especially outstanding example of a hydrophine. Through the kindly cooperation of Herr Prof. Dr. Tornier, I was able to study a skeleton of *Enhydris hardwickii* Gray from China. The ribs in this form, corresponding to the deep, narrow cross-section of the body, are very long, only curved in their anterior portion, but stretched almost totally straight in their distal half or even two-thirds. The considerable length of the ribs is also caused by their being very strongly inclined posteriorly, so that they form an angle of 50 to 60˚ with the vertebral column.

Such ribs are very suitable, together with the musculature belonging [to them], for propagating the undulating motion of the trunk antero-posteriorly, and can do this the better the longer they are and more obliquely they are set. On the other hand they have been relieved of the function to which those of land snakes are devoted, to serve as a lever in creeping, a function which can only be well fulfilled with a steeper, normal orientation.

In the most anterior part of the trunk, where the lateral compression is not present at all, or only to a slight extent, the ribs do not yet show that characteristic character. Thus, the rib belonging to the 25th vertebra measures 25 mm, with a vertebra length of 5 mm. The greatest rib length of 49 mm is found at vertebra 100, with 5.3 mm vertebra length. The strong development of the oar-tail is brought about by the powerful extension of the spinous processes and the haemapophyses. [ERRATUM p. 33: On pages 22 and 23 the formation of an oar-tail, as shown in the hydrophines and especially *Enhydris hardwickii*, is attributed to the strong development of the spinous process and haemapophyses. This view is to be corrected to: that the oar-tail obtains its greatly expanded surface through the strong development of the spinous processes and of the ventrally directed transverse processes.] In the middle of the tail, where the total height of the vertebrae reaches its greatest value at 12.5 mm, the length of the high spinous process comes to 5 mm, of the haemapophyses 4 mm, with a length of the vertebra of 4.4 mm. In association with the strong lateral compression of the trunk also stands the fact already stressed by Rochebrune (1880: 215), that the transverse processes are moved quite ventrally, so that the ribs can go out from the vertebra only at a slightly divergent angle.

Of interest and importance is also the squamation. In the overwhelming majority of living land snakes the ventral side is covered with a row of very broad ventral shields or '-rails'. These, as was already remarked above, play an important role together with the ribs in locomotion on the surface of the earth. In contrast to this, in the hydrophines adapted to aquatic life the ventral shields are developed only to a very slight degree. In *Hydrelaps darwiniensis* they have, as is clear from Boulenger's (1896, pl. XII, ff.) illustrations, only about twice the width of the scales on the sides and the back, and they are just about as large in *Disteira grandis* and *Hydrophis melanocephalus.* In *Hydrophis latifasciatus* and *Hydrophis cantoris* they exceed the other scales in width only very insubstantially, and in the genera *Hydrus*, *Thalassophis*, *Acalyptophis*, as Boulenger also states (1896: 267 ff.), ventrals are not developed at all, in *Enhydris* and *Enhydrina* only very weakly. This slight development of the ventral shields in these forms living in water is without doubt associated with their way of life. While the land snakes lie on the ground with their broad, flat ventral side, the trunk of the water snakes is laterally compressed and their ventral side more or less sharpened. Broad ventral shields are at least useless for swimming; consequently they are so weakly developed in the highly aquatically adapted forms enumerated.

But there are two genera in this group of almost exclusively marine hydrophines, *Aipysurus* and *Platurus*, in which broad ventral shields are present. In the former genus they are keeled; only investigation could prove whether they thereby express the tendency to sharpening of the ventral side. In *Platurus* such a keel is present only in some species and only in the posterior part of the body. Moreover, in this genus the nares are lateral, not placed on the dorsal side of the head as in the rest. *Platurus* can hence count as the least strongly aquatically adapted genus of the hydrophines. This stands in accord with what Boulenger reports precisely of it, that it has been repeatedly found on land at some distance from water.

In the group of opisthoglyph colubrids, whose maxillae bear furrowed teeth in their posterior parts, the subfamily of homalopsines encompasses, without exception, forms living in the water. The adaptation is here much slighter than in the hydrophines. The vertebral column seems to have undergone no modification, at least neither Boulenger nor Hoffmann mentions anything of it. On the other hand, the nares have taken their position on the dorsal side of the head. With respect to the squamation, the homalopsines do not behave uniformly. In most of them well developed ventral shields are present. Only in three of the enumerated ten genera does Boulenger state that these are very narrow, thus that they show the character which predominates in the hydrophines.

A small, third circle of aquatic snakes belongs to the subfamily Acrochordinae from the group of aglyphs, i.e. colubrids showing no furrowed teeth at all. Here the two genera

Acrochordus and *Chersydrus* are known as forms inhabiting rivers and coastal waters. On *Acrochordus javanicus* Hornstedt we find, for example in Hoffmann (1890: 1828), the information that this snake never leaves the water and can only move slowly on dry land. In the genus *Acrochordus* the body is only very weakly, in *Chersydrus* on the other hand the trunk and tail are strongly compressed. The vertebral column shows no distinctly noticeable adaptations to aquatic life. In both the nares lie on the dorsal side of the head. But again, the squamation is very remarkable. The knobbly scales are very small and arranged in extraordinarily numerous rows, about 120 in *Acrochordus* and 100 in *Chersydrus*. Ventral shields are not developed at all, indeed in *Chersydrus* the sharpening of the ventral side has led to the formation of a ventral skin-fold, which runs along the underside for the greatest part of the trunk and tail. The three other genera of the subfamily of acrochordines, clearly land forms - Boulenger makes no particular remarks on their way of life, just as for land forms in general - have well-developed ventral shields.

From the above, the following turn out to be phenomena of adaptation to aquatic life: position of the external nares on the dorsal side of the head, compression of the trunk, deep position of the transverse processes, great length of the ribs, formation of a deep oar-tail by strong development of the spinous processes and haemapophyses, small size or total absence of the ventral shields, skin-folds on the underside of the trunk and tail. These properties are, as explained above, distributed differently in the individual groups, and their presence or absence determines the height of their specialisation. Of the groups discussed, the hydrophines are highly specialised water snakes, *Chersydrus* less so, and the homalopsines the least specialised.

But besides the genera mentioned, there are also many others whose members, while land snakes, are yet accomplished swimmers, as e.g. the universally known grass snake, but show no distinctly pronounced adaptations to locomotion in water. In these, such could not become more pronounced so long as they have not completely given up life on land, for with the possible exception of the position of the nares, all the other mentioned adaptations are directly disadvantageous for creeping on the ground.

Of these named, different adaptive properties distinctive for water snakes, several are found in *Archaeophis.* Unfortunately nothing can be said about the position of the nares, as nothing can be determined about this in *Archaeophis proavus*. The transverse processes have a quite deep position. The ribs are very long and strongly inclined posteriorly. In *Archaeophis bolcensis* Mass., the illustrations of the trunk fragments given by Massalongo are reminiscent of *Enhydris* in a very striking manner. In *Archaeophis proavus* they are also correspondingly developed, but here in addition, especially noticeable in the posterior half of the trunk, appears the extraordinary delicacy and almost horizontal position. In both points our form, as far as I can judge from the skeletons I have examined, is unmatched, and is in this respect more highly specialised than the living water snakes. The lateral compression of the trunk was clearly considerable and may have come close or equal to that of *Enhydris* and also *Chersydrus*. *Archaeophis* does not show an oar-tail such as that of the hydrophines, thus stands behind these as a consequence of this lack, like the homalopsines and acrochordines which also lack it. In the lack of the ventral shields *Archaeophis* stands with *Hydrus*, *Thallassophis* and *Acalyptophis* from the family of hydrophines, and in the small size and high number of scale rows agrees even better with the group of acrochordines. Indeed, as remarked above, it is not excluded that a ventral fold in the manner of *Chersydrus* was present.

It must here incidentally be pointed out, that the lack of ventral shields does not absolutely speak for aquatic life. This is also found in the typhlopids and glauconiids, and also in the uropeltids the ventral shields are only very small. Now these three families contain forms which burrow in the ground. That no well developed ventral shields are found in these groups - whether they are reduced, or that they have not been developed if their ancestors also did not possess them - the reason for this is certainly also here their way of life. In burrowing in the soil the animals would not be able to use broad ventral shields as levers to shove the body forward, for the simple reason that the necessary clearance for the body, tightly enclosed by the ground, would be lacking. But that *Archaeophis* does not represent a burrowing form is certain, as was already said above, from the strong lateral compression of the trunk and the delicacy of the ribs. The presence of a long, slender, laterally compressed tail also speaks against that view, for in each of the named fossorial groups the tail is, as also in the limbless, burrowing lacertilian genus *Amphisbaena*, formed only by a very short stump. Here too an adaptation is clearly to be seen, perhaps in so far as this short, strong tail-stump also serves in pushing the body forwards in solid soil. Thus the view that *Archaeophis* had a burrowing way of life is hence to be totally rejected out of hand; we must see it as a pronounced water snake, which in respect of grades of specialisation did not quite reach the hydrophines, but is rather to be compared with the acrochordines, but in the formation of the ribs is even more adapted for swimming than all of the latter.

Systematic position of the genus *Archaeophis*.

As the System of the snakes, in view of the rarity and incompleteness of the remains of fossil forms, is simply based on knowledge of the living ones, the determination of the systematic position of the genus *Archaeophis* depends especially on investigating whether a relationship of our genus with recent ones can be made probable. First, though, let the prehistoric ones be drawn briefly into the circle of our considerations.

Answering the question whether genealogical relationships to such are recognisable depends basically, as more or less complete remains are found only very occasionally, on a comparison with isolated vertebrae, on the knowledge of which alone almost all the extinct species and genera have been based. This question is now without further ado to be answered in the negative, as far as the forms described in the German, French, English, Italian, and to a large part the American literature come into consideration*.

The above negative determination applies equally to the land forms as to those whose vertebrae, by the deep position of the transverse processes, betray adaptation to aquatic life, such as *Palaeophis*, *Pterosphenus* (=*Moeriophis*) and related genera. In no case is such weak development of the zygapophyses observed as in *Archaeophis*. The differences, in this respect, are too great for any closer genealogical connection to be assumed with any other fossil genus.

The enormous palaeophids, in which the zygapophyses are at any rate weaker than in our recent large forms, show a further fundamental difference with respect to *Archaeophis* in the development of strong, very high spinous processes.

The beautiful snake, preserved with the skull, which von Meyer (1860) described from the Braunkohle of the Siebengebirge as *Coluber* (*Tropidonotus*) *atavus*, apparently belongs to one of these recent genera. *Coluber kargii* von Meyer (1845) from Oeningen, a completely preserved form, which Rochebrune more correctly regards as a probable viperid, likewise has nothing to do with *Archaeophis*, and the same applies for *Python* (*Heteropython* Rochebrune) *euboicus* F. Roemer from Kumi, of which a lower jaw is known along with the dentition.

The other known remains of cranial parts, extremely rare, are too insignificant to allow certain judgement. It can only be stated categorically with respect to the "palato-pterygoid" of *Palaeopython sardus* Portis, that the description of the available remains of the dentition allow no similarity to be recognised with that of *Archaeophis*.

We now turn to the recent snakes, whose enormous number of genera fortunately have been dealt with in summary works, among which especially the recent ones by Hoffmann and Boulenger allow those not intimate with this group of animals to obtain an overview with relative ease.

With regard to the tooth form, nothing similar is mentioned in recent genera, at least as far as I was able to survey the relevant literature, and as far as can be gathered from the great systematic works of snake lore. We can immediately exclude the venom fangs from our consideration, as no evidence of perforation is noticeable in *Archaeophis* - the pulp-cavity can not be confused with such - and also the sculpture can in no way be compared with the formation of a groove. The solid teeth of the non-venomous snakes never seems to possess a strong external sculpture.

Leydig (1869) mentions only that in species of *Tropidonotus*, *Coluber* and *Coronella* the posterior, larger teeth of the upper jaw show a sharp cutting ridge posteriorly, as well as that on each side of the tip of all teeth, a fine ridge visible only with the microscope runs

* A part of the American literature was unfortunately not available to me.

down for some distance. But all this is of course not comparable with the conditions in *Archaeophis*.

The structure of the skull, at least in the parts that we have become acquainted with, likewise can not be used to determine relationships with any form. *Archaeophis* possesses a true snake skull, which is mainly distinguished by the shortness of the lower jaw. The latter property, however, would allow connection with equal legitimacy to may living genera, and this can not be used for our purpose here. It may incidentally be proposed that the great shortening of the lower jaw in the typhlopids and glauconiids can not be used as grounds for assuming phylogenetic connections between these and *Archaeophis*, as that property in the named fossorial genera simply represents a consequence of, or adaptation to, their way of life, which has been secondarily acquired and, at least in the forms now present, does not show the original structure.

Nor can anything be found in the formation of the vertebrae which would allow connection with any living form, as far as they have been dealt with in the monograph of Rochebrune and the other large summary works, and such as I myself was able to examine, through the kind assistance of Herr Prof. Dr. Tornier, from the zoological collection of the Berlin Museum für Naturkunde.

In relation to the formation of the ribs, the scales, and the overall body form, it was already pointed out above that similar conditions can be met with in certain aquatic groups, the hydrophines and acrochordines. But as we are here dealing simply with adaptations to the way of life, these characters can also not be regarded as signs of phylogenetic relationship unless other properties, independent of them, as e.g. the tooth structure, were also to speak for it. But the latter is not the case.

Further, apart from that it does not seem justified to derive land snakes from water snakes, as will be represented in the next chapter, it can be asserted with undisputable correctness that at least all of the now-living forms with pelvic vestiges, thus the typhlopids, glauconiids, boids and ilysiids, can not be regarded as descendants of *Archaeophis*, as in this genus the pelvis had already disappeared.

As phylogenetic relationships between *Archaeophis* and living families are not recognisable, also with only slight confidence, but our genus is far distant from all recent groups in the tooth form, and as relationships to the only very incompletely known fossil forms can also not be made probable, the necessity arises to erect a family **Archaeophidae**. A classification in a system based essentially on certain bones of the braincase not preserved in *Archaeophis*, such as Boulenger's, is not possible, however, while it easily possible in one such as Duméril and Bibron's based principally in the kind of dentition. The diagnosis of the new family Archaeophidae goes as follows: **Snout pointed, lower jaw relatively short; quadrate slender, directed anteriorly; teeth slightly curved, with sharp edges, pentagonal in cross-section; number of vertebrae extraordinarily large, zygapophyses**

and transverse processes weakly developed, hypapophyses present in whole trunk region; ribs delicate, long, weakly curved and strongly directed posteriorly; limbs and their girdles completely absent; scales very small, arranged in very numerous rows; trunk strongly laterally compressed; aquatic, probably marine.

On the descent of snakes.

Two views have been expressed on the descent of snakes. According to one the pythonomorphs are supposed to be their ancestors. Thus Kornhuber (1901: 151) has recently expressed the opinion that from the pythonomorphs, on the one hand the ophidians, on the other the lacertilians seem to have developed. Already earlier, Cope had also stepped into a dispute with Owen over the probability of close relationships between ophidians and pythonomorphs. Of another view is Boulenger (1891), who presents a scheme in which the ophidians are descendants of the Dolichosauria. A critical consideration of both these points of view requires, beside a detailed discussion of the named groups of reptiles, also a setting out of the nature and causes of the specialisation of the snake body. Out of practical considerations, this latter question will here be dealt with next.

The peculiarity of the external body form of snakes consists, as is well known, in the extraordinary elongation, the smallness of the head, and the lack of extremities. It shows itself to be an adaptation to an environment in which locomotion can best be managed simply by undulation of the trunk. This is the case for burrowing in the ground or creeping in dense plant growth, in undergrowth, shrubs, grass etc. Here, for more rapid locomotion a suitable body is as flexible as possible, elongated lengthways, and its cross-section remains as constant as possible or only varies gradually, thus offering no hindering resistance. Limbs are of only slight usefulness or direct hindrances. The adaptation to such a way of life must therefore be expressed in their reduction or even complete disappearance.

Especially instructive for our consideration here are also the numerous living lizards with strongly or completely reduced limbs. With respect to the grade of reduction we find very different stages. Thus the genus *Seps* has weakly developed fore- and hindlimbs, in *Pygopus*, *Ophiodes*, *Pseudopus*, *Lialis* the forelimbs, in *Anguis*, *Ophisaurus*, *Acontias* and the amphisbaenids both have disappeared. Now all these genera are pronouncedly land animals and as far as information is available to me - the richest in biological observations is still Brehm's Tierleben - these lizards with reduced limbs in fact live in an environment such as indicated above, thus in thick vegetation, grass, moss etc., and for the most part generally seek their hiding-places [*Schlupfwinkel*] under the earth. The genus *Amphisbaena* is even supposed to lead a completely underground way of life and to inhabit termite nests.

If we thus see that the living snake-like lizards are exclusively land animals, we must assume that their predecessors gained their body form on the land, but not in water.

Among the fossil forms, it could be mentioned that some of the stegocephalians, *Dolichosoma* and *Ophiderpeton* did without feet and extremities, and likewise had a snake-like body form. With the greatest probability one may ascribe to them as similar way of life to the limbless lizards, but probably moister habitats. In any case nothing speaks against this view, or more in favour of another.

In the overwhelming majority of land snakes, of which alone we will be speaking for now, the formation of broad ventral shields represents a specialisation of the coat of scales which is of not insignificant significance. This plays a role especially, as was stated earlier, in locomotion. Functioning together with the ribs, their posterior edges are braced against the irregularities of the substratum and thus, serving as it were as levers, allow the use of slight roughnesses of the ground for creeping. Thus locomotion on relatively smooth, unvegetated ground is also made possible. In general, the well-developed type of snake body allows quite versatile locomotion without further adaptation. One observes, e.g. in the boids [*Riesenschlangen*] and ordinary snakes [*Nattern*], that many times they also know perfectly well how to swim and to climb. This versatility is made possible by the flexibility and suppleness of the true snake body, it is hence also present to a much weaker degree in the snake-like lizards, and was certainly also slight in the ancestors of snakes so long as they had not yet attained their marked, typical structure.

Of the forerunners of snakes, it may hence with great probability be assumed that the acquisition of the snake type is to be attributed to adaptation to residence on ground covered with thick vegetation, perhaps also a burrowing way of life, or both conditions at once. However, we certainly do not have to think of such marked fossorial forms as today's typhlopids and glauconiids, which are quite extremely differentiated in this direction; not even if Rochebrune (1880) should have been right when he classified *Symoliophis* with the typhlopids. From the similarity, incidentally by no means great, of the isolated vertebrae (all that is known) of this genus with those of *Typhlops*, no further conclusions at all can be drawn regarding its organisation and way of life. The possibility may also not be ignored that the these recent fossorial groups could have developed secondarily from snakes living above ground.

If we thus assume, first for the land snakes and further for the snake-like lizards, that they developed to their present form on the land, the fact that we also know a number of fossil lizards with noticeable reduction of the limbs, but which are absolutely to be regarded as aquatic, requires more detailed discussion. These are certain *Varanus*-like lizards of the Cretaceous, the Dolichosauridae. A somewhat more detailed consideration of these forms is appropriate here, because Boulenger's (1891) scheme mentioned at the beginning of this chapter, allows that the pythonomorphs, the varanids and the ophidians developed as three independent branches from the group of Dolichosauria. The dolichosaurians, which are thus seen by him as the ancestors of snakes, are lacertilians which have been known from the upper Cretaceous of England (*Dolichosaurus*), but especially in a series of splendidly described finds from the Neocomian of Istria described by Kornhuber, H. von Meyer, Gorjanovic-Kramberger and Seeley. But according to Gorjanovic-Kramberger (1892) and Franz Baron Nopcsa jun. (1903) two sharply different families are to be separated among the dolichosaurians now known, the Aigialosauridae and Dolichosauridae. Baron Nopcsa places in the first the genera *Dolichosaurus* Owen, *Actaeosaurus* Meyer, *Pontosaurus* G. Kramberger, *Adriosaurus* Seeley, to the latter *Aigialosaurus* G. Kramberger, *Carsosaurus* Kornhuber, *Opetiosaurus* Kornhuber, ?*Mesoleptos* Cornalia.

Let us first consider the first family, Dolichosauridae Nopcsa in the stricter sense, which Boulenger principally had in mind when he let the ophidians descend from the Dolichosauria in his family tree.

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

There are in fact several features present in these dolichosaurids which call for an external similarity with snakes, such as the smallness of the head, the elongate body form, and the reduction of limbs, especially the forelimbs.

Owen (1851) proposes repeatedly in the discussion of *Dolichosaurus longicollis* that the way of life may probably have been predominantly aquatic, though visits to dry land were perhaps not to be excluded. He cited in favour of this interpretation that the humerus was strikingly broad, and further that the compression of the ribs and the slight curvature in their middle parts would lead one to decide on a strongly laterally compressed body form, somewhat as in water snakes. To what extent the compression of the ribs speaks for such a body form may remain to be seen. In their overall form they do in fact seem to express a certain, if not very extensive, adaptation to aquatic life.

For *Pontosaurus* one must assume a decidedly aquatic way of life, as Kornhuber also strongly emphasised. The formation of a long, powerful oar-like tail, whose strong lateral compression is proved by the considerable development of the spinous processes and hypapophyses, especially speaks for this [interpretation].

Standing close to *Pontosaurus*, the genus *Acteosaurus* described by H. von Meyer is clearly likewise, as was clearly accepted by its founder, an inhabitant of the water. The oar-like tail, however, is less pronounced than in *Pontosaurus*; on the other hand one may well conclude from the weak curvature of the ribs, and perhaps also by their not-spread-apart position, that the trunk was laterally compressed.

Seeley's *Adriosaurus*, of which the anterior part of the trunk, the neck and head are not known, was also placed in the genus [just] discussed by Nopcsa, who was able to demonstrate strongly developed spinous processes on the caudal vertebrae, so that we may also probably assume an aquatic way of life for it.

The family Dolichosauridae thus shows without any doubt that the inclination towards the snake type can also be strongly expressed in water-inhabiting lizards.

Incidentally, *Pleurosaurus* from the Upper Jurassic of Solnhofen and Cerin, regarded by most as a rhynchocephalian, shows a similar external body form.

Also in this genus there is a distinct reduction of the extremities, especially the forelimbs, an elongate, laterally compressed body, and extremely powerful oar-tail. And finally there are also quite similar shapes among the amphibians, as e.g. *Amphiuma*, *Siren*, and also *Proteus*, which are distinguished by reduction of the limbs, an elongated trunk, and oar-tail.

That the extremities undergo a reduction in animals living principally in water, if they are not used as propulsive organs, is indeed easy to understand. For since the body completely or almost completely loses its weight in the water, the legs also have scarcely any burden to carry and due to the decreased use they must atrophy more or less strongly.

Yet it remains questionable whether a complete disappearance of the limbs can come about in this way. In any case, this has not yet been determined. But the question we are concerned with at the moment is precisely whether it is probable that the snakes developed from such forms that suffered a reduction of their extremities through life in the water. The case which is also thinkable, that this [reduction] had already occurred in terrestrial ancestors of the former [i.e. of snakes], will not be considered further here. Of special importance is the circumstance that in all the enumerated cases, where adaptation to aquatic life leads to an elongated body form and reduction of the limbs, yet another adaptation is always present, which is expressed in the formation of a lateral compression of the tail and possibly also of the trunk.

The development of an oar-tail, especially if it is as powerful as within the Dolichosauridae - that of *Dolichosaurus* itself, though, is not yet known - or in *Pleurosaurus*, and likewise of a stronger lateral compression of the trunk, are specialisations which, with reduction of the limbs at the same time, without question make locomotion on dry land more difficult, and surely do not allow development of the mobility and swiftness necessary for hunting prey. These adaptations to aquatic life are thus directly contrary, in their biological effects, to those by which the land snakes have become such mobile and quick animals. It may hence hardly seem probable, least of all that the land snakes are descended from the Dolichosauridae, or at least from those among them that we know completely enough to use in phylogenetic conclusions, as Boulenger assumed. Rather, we must imagine the precursors of snakes more legitimately as pure land forms, probably from the group of lacertilians, without adaptations to aquatic life.

But it now remains to consider whether perhaps the water snakes, or some of them, could have developed from dolichosaurids or similar forms. But to support this view would mean at the same time to assume a di- or polyphyletic origin of snakes. But in view of the extremely great uniformity of the whole order of snakes, one might only decide in favour of this under the forcible impression of unambiguous proof, which is now completely lacking.

Biological considerations lead us, on the other hand, to the view that **the water snakes have developed from land snakes**, but not the other way around. A highly specialised water snake would no longer be in a position to exist on land and to adapt to this environment. This specialisation is too one-sided for it, on the other hand there are many land snakes which, without further special adaptation, are perfectly capable of long stays in the water.

The different groups of living water snakes have obviously developed separately from land snakes, with which they also show in the structure of the skull and in the dentition much closer relationships than among each other. And in just the same way *Archaeophis* represents a highly specialised form which, probably independently, adapted to aquatic life from terrestrial precursors.

Nopcsa's second family Aigialosauridae, which together with Dolichosauridae formed the original group Dolichosauria encompassing them both, are lizards similar to the genus *Varanus*, only distinguished by stronger adaptation to aquatic life. This also applies, for example, to the feet, which according to Nopcsa, in the genus *Opetiosaurus* stand between the walking foot of the varanids and the paddle of the pythonomorphs in their organisation. The named author also makes it extremely probable that the pythonomorphs evolved from the Aigialosauridae. That the latter could not be regarded as the ancestors of snakes can be argued on essentially the same grounds as are presented below, from the structure of the extremities, against the descent of [snakes] from the pythonomorphs.

Let us now turn to the discussion of the supposed direct relationship of the snakes and pythonomorphs, held for probable by Cope and Kornhuber. Special cause for this, at this point, is given by the peculiar type of tooth that we have come to know in *Archaeophis*. Its formation of ridges recalls especially, to a certain degree, the form of the teeth in certain pythonomorphs. Namely, e.g. in *Platecarpus*, apart from two main ridges lying in the longitudinal direction of the jaw bone, there are also a number of weaker ones, which run down from the tip and produce a polygonal cross-section. It can now be asked whether, and to what extent, the external similarity of the teeth of *Archaeophis* and the corresponding pythonomorph can be seen as signs of a closer relationship between them. Let it firstly be pointed out in this regard that the formation of the ridges is by no means in perfect agreement, as in the teeth of *Archaeophis* they are very much sharper and also appear in different number and arrangement than in the pythonomorphs. But more important is the circumstance that in the latter the tooth crown sits on a deep base, that the replacement teeth form within this and that they fit into grooves, while in *Archaeophis* the the base is only very low, the replacement teeth form in folds of the mucosa and the teeth themselves stand in quite shallow, pit-like hollows, and thus are to be described as acrodont.

Thus, there are also very substantial differences present between the two tooth forms. Besides, incidentally, it is apparent that having multiple ridges can not be a very characteristic property of the teeth of pythonomorphs, for in many of their forms they have only two ridges. And also in the genus *Opetiosaurus* from the family Aigialosauridae, according to Baron Nopcsa to be regarded as ancestors of the pythonomorps, the otherwise perfectly pythonomorph-like teeth lack ridges. One must hence assume that in the pythonomorphs the multiple ridging of the tooth developed only as a special specialisation, so long as precursors with the same property have not been found. The tooth structure can thus not be used as evidence for a closer relationship of *Archaeophis*, or snakes in general, with the pythonomorphs.

Whether the development of five tooth ridges in *Archaeophis* also represents only a phenomenon of specialisation within a restricted group, or whether it was present in all old snakes, can not be decided either way in the total lack of completely preserved snakes from the Eocene or the Cretaceous.

As the tooth structure affords no grounds for determination of any phylogenetic relationship between ophidians and pythonomorphs, there is a need for a short consideration of the overall organisation of these two groups. The question arises, in which directions have they each developed. It is clear that quite different types of specialisation are present, which also represent adaptations to different living conditions.

The pythonomorphs are pronounced water animals. The fore- and hind limbs are transformed into perfect swimming paddles. A strengthening of the thorax has appeared, as e.g. in *Tylosaurus* 10 ventral ribs are attached to the sternum.

This number is worth mentioning because, according to Baron Nopcsa, there are 6 in *Carsosaurus* among the aigialosaurids, the precursors of the pythonomorphs, and in *Varanus* only 3, so that this author is certainly correct in assuming a direction of development towards an increased number of such ribs attached to the sternum. A further adaptation to aquatic life consists in the formation of a strongly laterally compressed oar-tail, which in *Clidastes* and *Tylosaurus*, as is clear from the shape of the spinous processes, even bore a tail fin.

The grounds for us to have to think that the development of snakes took place on the land but not in the water were already set forth in detail above. The same also speak against descent of the ophidians from the pythonomorphs. But still more against it speaks the consideration that one would be forced to assume the latter had first attained their peculiar type through gaining paddles and strengthening of the thorax, but then set off on a totally different direction of development, as now a reduction of the limbs and of the sternal rib atachments set in. This complete reversal [*Umschwung* = turnaround, volte-face] in the tendency of development may well be described as totally improbable, the more so as one must imagine it to have taken place in the water, as it had surely become impossible for the pythonomorphs to visit land due to their extreme adaptation to aquatic life. There could thus, apparently, have been no intervening alteration of lifestyle to cause such a profound reversal of developmental tendency. That remarkable differences, incidentally, also appear in the skull structure, as e.g. in regard to the formation of the quadrate, need not be further explained here. Even if, given the notorious incompleteness of the palaeontological record, no too great emphasis should be placed on the circumstance that the pythonomorphs first appear in the late Cretaceous, while the oldest snake vertebrae are already found in the middle Cretaceous, yet such important considerations arise against the descent of snakes from the former that only indisputable proofs could help that view to victory.

That the ridged form of the teeth perhaps also represents an adaptation to aquatic life, such as for a particular food, proof can hardly be provided, even if this view is perhaps the correct one. But the same may also apply to the pythonomorphs, in which the many-ridged tooth structure is absolutely not universally present. As long as we do not know definite precursors of the archaeophids and their tooth structure, which so far is not the case, it is not to be decided whether their tooth form is an inherited one, or independently acquired through adaptation.

Summary of most important results.

1. The skull shows typical snake characters, only the mandibular rami are relatively short and the quadrates oriented anteriorly.

2. The tooth form is totally different from all other known snakes and reptiles, in that they show five sharp edges. Their acrodont position, their presence on the maxillae, palatines, pterygoids and mandibles, as well as their replacement by replacement-teeth forming in the mucosa, are as in the recent forms.

3. On the procoelous vertebrae the post- and prezygapophyses are very weakly developed, also the articulation of zygosphene and zygantrum is indistinct. Moreover, the transverse processes are scarcely indicated. The trunk vertebrae bear a hypapophysis, the caudal vertebrae two haemapophyses. The number of vertebrae comes to about 565, of which about 111 belong to the tail. The total number of vertebrae is significantly higher than in any other known snake.

4. The ribs are very long, thin, very slightly curved and strongly directed posteriorly.

5. There is nothing present of the extremities, or the shoulder or pelvic girdles.

6. The scales are extraordinarily small and arranged in very numerous rows. Ventral shields were not developed.

7. The trunk was strongly laterally compressed, a ventral zone was no longer supported by the ribs.

8. *Archaeophis* represents a highly specialised water snake.

9. *Archaeophis proavus* Mass. and the second, much larger species *Archaeophis bolcensis* Mass., belong very probably to the same genus, possibly even to the same species.

10. No certain phylogenetic relationships to other fossils or to living snake genera can be recognised. On the basis of the tooth form a new family Archaeophidae is to be erected.

11. The snakes could not descend from the pythonomorphs. It is further improbable that they could be derived from the dolichosaurids and aigialosaurids. Probably they developed from an unknown terrestrial lizard, not adapted to aquatic life.