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ANOMALOPHIS BOLCENSIS (MASSALONGO), A NEW GENUS OF FOSSIL SNAKE FROM THE ITALIAN EOCENE

By WALTER AUFFENBERG

Department of Biology and Florida State Museum,
University of Florida

The genus *Archaeophis* as defined by Massalongo (1849) was based on two fossil specimens of presumed snakes originally in the collection of DI Canossa from the well known Middle Eocene teleost and plant beds of the Monte Bolca limestone near Verona, Italy.

One specimen was designated as the type of *Archaeophis proavus*. It was smaller than the second specimen and much more complete, including almost the entire skeleton as well as an impression of the skin. The larger specimen lacked a head, nor was there any indication of an impression of the skin. This specimen was made the type of his second new species, *Archaeophis bolcensis*. Both were considered to be primitive snakes. Massalongo thought that they were merely quite distantly related to the only fossil snakes known at that time (*Palaeophis* and *Palaeryx*). They were not compared with any Recent genera. On the basis of the round form of the vertebrae as well as the general shape of the tail, Massalongo believed that *Archaeophis* was a terrestrial genus.

In the following years the specimens became separated. The type of *A. proavus* was purchased by the Berlin Museum and the type of *A. bolcensis* was deposited in the Museum of Comparative Zoology, having been purchased by Louis Agassiz.

A recent study of the two species formerly attributed to *Archaeophis* shows that *A. bolcensis* differs radically from *A. proavus,* and necessitates erecting a new family and genus based on the characters exhibited by the type and only specimen of *bolcensis.*

In 1904, Janensch briefly described the skull, teeth, vertebrae and ribs of *Archaeophis proavus,* but in somewhat greater detail than had been previously done by Massalongo. It was also in this paper that Janensch first suggested that the genus may have been a highly specialized marine form. This idea was based on his interpretation of the shape of the tail and body which he thought were very compressed in life.

In 1906 he redescribed, in much more detail, the type of *Archaeophis proavus.* Various parts of the skeleton and particularly the skull had been further prepared, and all elements were examined with the aid of a binocular microscope. The description of the skull is far better than any previously given. Unfortunately, the skull capsule is badly crushed, so that the individual bones are very difficult, if not impossible to trace. The bones of the jaw apparatus are all fairly well preserved. Certain parts are missing, but in some cases the shape of the missing elements can be determined from stains or impressions appearing on the limestone slab on which the specimen is preserved. The head is unusually pointed for a snake, a fact of which Janensch was quite cognizant. The teeth are most non-snakelike in that in cross-sectional view they are definitely 5-sided. Janensch interpreted certain elements partially hidden by matrix as quadrates and squamosals. McDowell and Bogert (1954:67) suggest that the "quadrate" agrees fairly well with the branchial bones of an eel, but from what can be seen of them they are not considerably different from the same elements in Recent snakes. However, the major parts of the squamosals(?) are hidden by matrix, so that their exact shape, or method and place of articulation with the skull cannot be determined.

The vertebrae and ribs of *Archaeophis proavus* are very important, since only these elements can be compared with corresponding structures in *Archaeophis bolcensis.* Janensch points out that the exact form of each of these elements is very difficult to ascertain. This is due to several factors. The bone making up

the neural arch of each element is very thin, and thus most of the elements are badly broken. When the limestone block in which the specimen was imbedded was split some of the bone making up the individual vertebrae was accidently removed. Furthermore, the outer layer of bone has been lost in most of the vertebrae along the column, so that only the deeper part remains. This means that only the more general structure of the vertebrae can be determined in most parts of the column. Reasonably complete elements occur in only a few areas. For the most part these are regions which were originally completely covered by matrix until prepared at the Berlin Museum. Unfortunately, full preparation was not possible due to the fragile nature of the elements. No single vertebra could be profitably removed intact, so that anterior and posterior views of separate elements are not available. In addition, because of the overlapping nature of these vertebrae, the exact shape of either the neural arch, cotyle or condyle is not determinable. Janensch prepared a reconstruction of the side view of one of the middle thoracic elements based on several vertebrae in this area. His ventral view of a vertebra from the same part of the column is taken from only one prepared element (Fig. 1C). One of the vertebrae was split when the block was separated into two slabs, providing a fair cross section (Fig. 1 I).

The exact number of vertebrae is difficult to ascertain with any degree of certainty due to broken or missing segments. Massalongo had estimated this number as 507. Janensch believes his estimate of 565 is much closer. One hundred and eleven of these are caudal members. The entire length of the specimen is about 95.5 cm., of which the tail makes up about 10.5 cm.

The individual vertebrae show considerable variation in size and proportion along the length of the column. The more anterior members are small, and higher than long. The middle vertebrae are largest. The posterior vertebrae are smaller, and longer than high. All of the segments appear to be procoelous. The condyle is strongly oval, with the main axis in the horizontal plane. From the side the condyle is flattened at its posterior end, not rounded as it is in all fossil and modern snakes. However, this difference may be due to breakage. The cross section of a thoracic element illustrates the unusual thinness of the neural

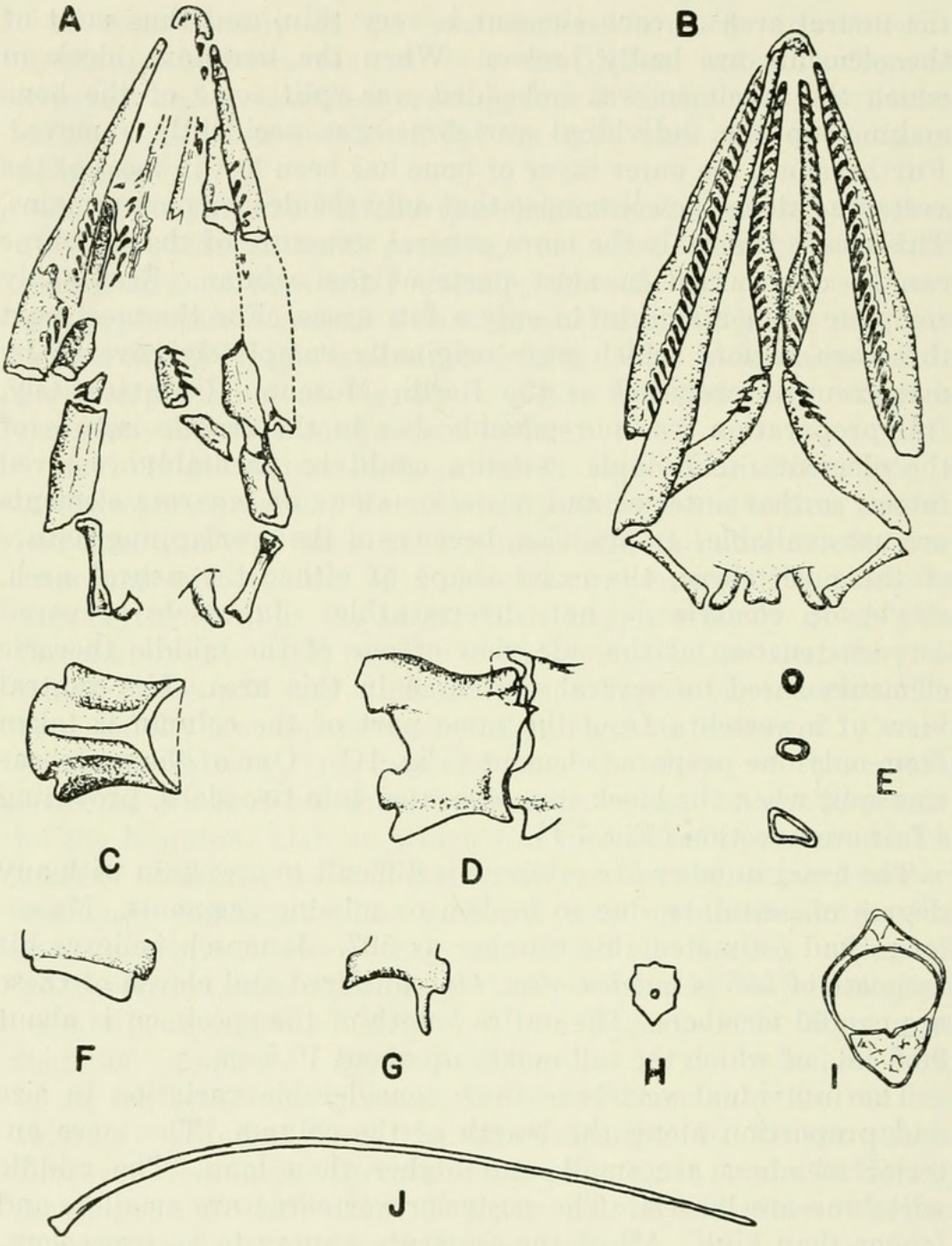

Fig. 1. Certain structural features of the type of *Archeophis proavus* Massalongo (*fide* Janensch, 1906). A, Skull, from below. B, Reconstruction of the jaw apparatus. C, Vertebra 78 seen from below. D, Vertebra 46, seen from the side. E, Cross sections of a single rib. F, Vertebral centrum and hypapophysis. G, Vertebral centrum and haemapophysis. H, Cross section of tooth. I, Cross section of vertebra. J, Rib from the middle of the body.

arch, even considering that the outer lamellae were accidently removed in splitting the rock. There is no well developed neural spine, but rather a small keel that begins near the anterior edge of the neural arch and continues posteriorly to near the posterior edge of the element. The neural canal is roughly pentagonal in shape when viewed in cross section. The centrum is seen to be subtriangular in cross-sectional view. This condition is not seen in any fossil or Recent snake, where the centra are always oval to round. The zygosphene is very small and its articular surfaces are little developed. The articular facets of the post- and prezygapophyses are horizontal, not vertical as McDowell and Bogert (1954) claim. This is obvious not only from Janensch's illustration, but is clearly stated in the text as well. The paradiapophysial articulations are single and rather small, located anterior to the middle of the vertebrae, and placed low on the centrum. Janensch states that several individual vertebral elements indicate that these small structures are not the result of erosion, but that they may have been topped by a cartilaginous surface of considerable extent in life. Whether or not they represent an entire, or partial, synapophysis or are even homologous to part of one is unknown. Accessory processes are apparently absent throughout the column, as they are in several families of fossil and Recent snakes. Well developed, laterally compressed hypapophyses are developed along the entire presacral portion of the vertebral column. From the side they vary from sigmoid-shaped structures in the anterior part of the column, to much lower, broad-based triangular structures posteriorly. A midventral keel runs anteriorly from the anterior edge of the base of the hypapophysis to near the anterior edge of the centrum. The posterior portion of the base of the hypapophysis does not come in contact with the base of the condyle. Paired haemapophyses are found on all of the caudal elements. They are long, spine-like structures, placed far back on the centrum and directed almost straight downwards. The ribs are quite long, bent posteriorly and considerably compressed laterally. There are no costal processes on any of the ribs.

These are the most important structural features of the vertebrae and the ribs, as described by Janensch. Many of the characters are not found in other snakes, such as the triangular

centrum in cross section, the very small articular processes, the poorly developed zygantrum and zygosphene, and the strongly oval condyle. The ribs are considerably longer, less curved, and more compressed than in any other fossil or Recent snakes known. For a complete description of these structures as well as those of the skull and skin the reader is referred to Janensch (1906).

On the basis of his study of the type of *Archaeophis proavus*, Janensch concluded that: (1) the type of *A. proavus* is a highly specialized marine snake; (2) the type of *A. bolcensis* belongs to the same genus, perhaps even to the same species as the type of *A. proavus*; and (3) *Archaeophis* represents a new family of snakes, the Archaeophidae, distinguished mainly on the shape of the teeth.

McDowell and Bogert (1954: 66-67) point out several remarkable features of the vertebral structure of *Archaeophis*. These are: (1) the smooth and unsculptured vertebrae; (2) the fact that the prezygapophysis is reduced to a small spine; (3) the plane of the articular surface of the postzygapophysis is vertical, not horizontal; and (4) there is no neural spine. To these authors the combination of characters seemed to suggest that *Archaeophis* was not a snake. They point out that some of the features of the genus are found in certain eels, and other characters are similar to those found in some snakes. They state that, "Looking at Janensch's figures, we are led to suspect that *Archaeophis* might not even be reptilian, for there is much to suggest (though not enough to prove) affinities with the teleost fishes, particularly some eel of the *Ophichthus*-like group." They go on to suggest that *Archaeophis* might best be placed as a vertebrate of unknown affinities. Some of the characters they list as remarkable (if *Archaeophis* is a snake) are certainly not very important, or very remarkable, such as the degree of smoothness and sculpturing of the vertebrae. As pointed out above, some of the outer lamellae of bone have been lost. Only general shape of the structures is really determinable. Much detail has been lost, and absence cannot be used as any sort of criterion, except as regards degree of mineralization or breakage. Furthermore, details of configuration of Recent snake vertebrae vary greatly from genus to genus. The absence of a well developed neural

spine is characteristic of several groups of Recent and fossil snakes. As pointed out previously, McDowell and Bogert misinterpreted Janensch's figure of the side view of the middle thoracic vertebra as well as his text discussion, since they stated that the articular surface of the postzygapophysis is vertical. Both the figure and the text clearly indicate that this surface is horizontal, as it is in all snakes. However, this in itself proves nothing, since a zygapophysial articular surface when present in fishes is sometimes horizontal.

McDowell and Bogert, as well as Janensch, assumed that the type of *Archaeophis bolcensis* was structurally very similar to the type of *A. proavus*. Massalongo stated that this was true, but his analysis of the characteristics of both species was rather superficial. Janensch examined *proavus* very closely, but failed to examine the type of *bolcensis*. McDowell and Bogert relied only on Janensch's description of *proavus* for the generic characters. The present study of the type of *A. bolcensis* has shown that this species is quite unlike *proavus* in many of its structural details. The two species are very different in a number of important features. I wish to thank Drs. E. E. Williams and A. S. Romer for permission to examine the type of *Archaeophis bolcensis*, and especially for allowing me to prepare it further.

The specimen in the Museum of Comparative Zoology is represented by sections of the anterior, middle and posterior parts of the vertebral column and their associated ribs. These were originally located on three limestone slabs (MCZ 1001, 1002 and 1003). One of the slabs was intentionally sawn in half and one became broken sometime in the past. The specimen is considerably larger than the type of *A. proavus*. There is no trace of the skull. A dark stain on the limestone matrix in several places may represent portions of the flesh, or skin, but no details of scalation, if it exists, can be made out. The middle and posterior parts of the specimen are resting on their dorsal sides, so that only the ventral surfaces of the vertebrae are visible. The anterior section rests on its ventral side. Unfortunately, throughout most of the column the vertebrae are crushed, or badly broken, on the exposed surface. However, most obvious at once is the fact that, broken as they may be, there are no hypapophyses on any of the middle or posterior vertebrae. On this

basis alone it is obvious that two genera are involved. As in *A. proavus* the ribs are all long, curved backwards only slightly, and lack costal processes.

To aid in uncovering certain details of structure of both the vertebrae and ribs, acetic acid had been applied to several areas along the vertebral column, in the past. This was a most unsatisfactory undertaking, since the loss of the encasing matrix caused ends of ribs and the dorsal or ventral surfaces of some of the vertebrae to disintegrate. Fortunately, dry preparation was still possible in several areas. Two vertebrae were completely freed from the matrix so that anterior and posterior views could be drawn and studied. The surfaces otherwise hidden were examined and the structures compared with those in fossil and Recent snakes. The isolated vertebrae are considerably cracked. Some processes had been broken off in the past, and a few slightly damaged in extricating the delicate elements. It was thus necessary to reconstruct, very slightly, the missing parts of the isolated middle thoracic element. The reconstructed portions were drawn from other vertebrae, in the immediate area, in which these particular processes were still complete. The quite reasonable complete reconstruction of at least the middle dorsal member allows a thorough comparison with *A. proavus* and with all fossil and Recent snakes. Most important, it proves beyond doubt that *Archaeophis bolcensis* is a snake, regardless of the taxonomic position of *A. proavus*.

Unlike *A. proavus*, the vertebrae of *A. bolcensis* possess well developed zygantral and zygosphenal articular surfaces. There is a well developed neural spine. The pre- and postzygapophysial articular surfaces are also well developed. The vertebrae are much more robust than are those of *A. proavus*. The paradiapophysial articulating surface is better developed than in *A. proavus*. The elements are well ossified throughout the column, and the outer laminae of bone are still present.

To facilitate future comparisons of *Archaeophis bolcensis* with other fossil or Recent snakes, a description of the partly reconstructed middle thoracic vertebra is given below.

Description of vertebra: — Centrum long, the sides converging posteriorly, a truncated triangle from below, provided with a

well developed, slightly oval cotyle anteriorly, and a well developed condyle posteriorly, which is only slightly separated from the basic portion of the centrum by a small constricted area. A haemal keel is present, gladiate to spatulate in shape, and slightly flattened ventrally. It extends from near the lip of the cotyle to just anterior to the condyle. The ventral surface of the centrum is slightly flattened on either side of the haemal keel. There is a faint subcentral ridge extending posteriorly from just behind the synapophysis, or the paradiapophysial articular facets on either side, to near the base of the condyle. The paradiapophysial articular facets are oval in shape, and located low on the centrum, well in front of the middle of the vertebra. From the side, the ventral surface of the centrum is reasonably straight, not concave, or convex, as it is in many snakes. The buttresses of the prezygapophyses are well developed. In anterior view they are seen to possess a sharp anterior edge. The buttress is closer to the median line ventrally than dorsally. Between the buttress and the projected lip of the cotyle there is a small scooped out area. Whether or not this small depression possessed a nutritive foramen is unknown. There is no extended accessory process below the prezygapophysial facet. The facet is slightly higher anteriorly and outwardly than posteriorly and medially. From above, the articulating surface is ovoid to sub-triangular. The articular surfaces of the postzygapophyses are developed on the laterally expanded posterior portion of the neural arch, as they are in all snakes. The facets are oval, the main axis being anteroposteriorly. The neural arch is fairly long and not greatly emarginate from above. The interzygapophysial ridges are fairly prominent, especially posteriorly. The neural spine is long at its base, extending from just above the base of the zygosphene to the anteriorly indented posterior edge of the neural arch. It is slightly thickened and truncated dorsally. The posterior edge is slightly lower than the anterior one. There are no overhanging edges at the top of the spine either anteriorly or posteriorly. From above, the dorsal edge of the spine is relatively thin, not overly thickened into a peg-like or oval-shaped structure, as in some primitive snakes. The zygosphene is well developed, robust, but small for the length of the centrum when compared to the Boidae. From above, the anterior edge of the zygosphene is

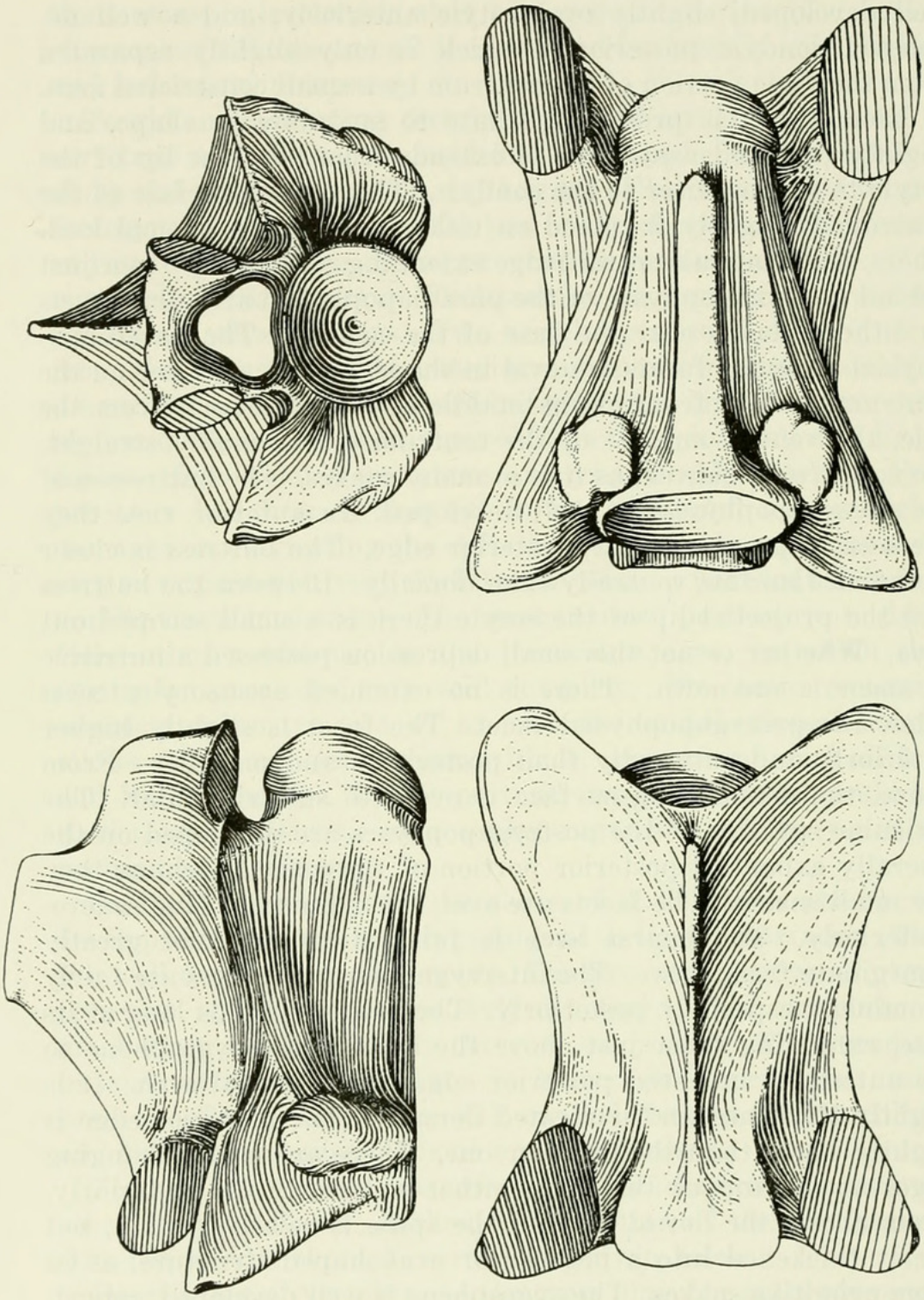

Fig. 2. Middle thoracic vertebra (slightly reconstructed), MCZ 1001, holotype, *Anomalophis bolcensis*.

almost straight, perhaps with a small median notch. From the front, the zygosphene is somewhat thickened dorsoventrally, the dorsal edge slightly convex, presumably with a small notch medially. The zygosphenal articular facets are oval, the anterior edge being at an angle of about 45 degrees when viewed from the front. The neural canal is fairly small, roughly triangular in shape. The medial edges of the prezygapophysial articular facets are even with the floor of the neural canal. It is impossible to determine the position and size of the zygantral foramina, if they are present at all. Whether or not a medial anapophysis occurs on the floor of the neural canal cannot be determined, since the canal is filled with matrix, which, if removed, would weaken the isolated fossil considerably.

The partially reconstructed middle thoracic vertebra is illustrated in Figure 2. Table 1 gives all of the pertinent measurements possible on the vertebra.

TABLE I

APPROXIMATE MEASUREMENTS (IN MM.) OF A SINGLE THORACIC VERTEBRA FROM THE TYPE OF *ARCHAEOPHIS BOLCENSIS*

Centrum length	11.0
Centrum width at its narrowest part	8.0
Pre-prezygapophysial width [1]	22.0
Post-prezygapophysial length [2]	16.0
Cotyle width	4.5
Cotyle height	4.0
Length of neural spine along dorsal edge	4.0
Height of neural spine along anterior edge	3.5
Zygantrum width at its widest part	5.5

A single vertebra was also removed from the anterior part of the column of the type of *A. bolcensis*. Unfortunately, the anterior elements are even more crushed than the middle and posterior ones. Unlike the middle thoracic region, the anterior

[1] The pre-prezygapophysial width is measured from the outer edge of one prezygapophysial facet to the outer edge of the opposite prezygapophysial facet.

[2] The post-prezygapophysial length is measured from the posterior edge of the postzygapophysial facet to the anterior edge of the prezygapophysial facet.

portion of the specimen is resting in a natural position, so that the ventral surface of each vertebra is imbedded in the matrix and thus is somewhat protected. The dorsal and lateral surfaces are almost completely crushed. By careful preparation of one

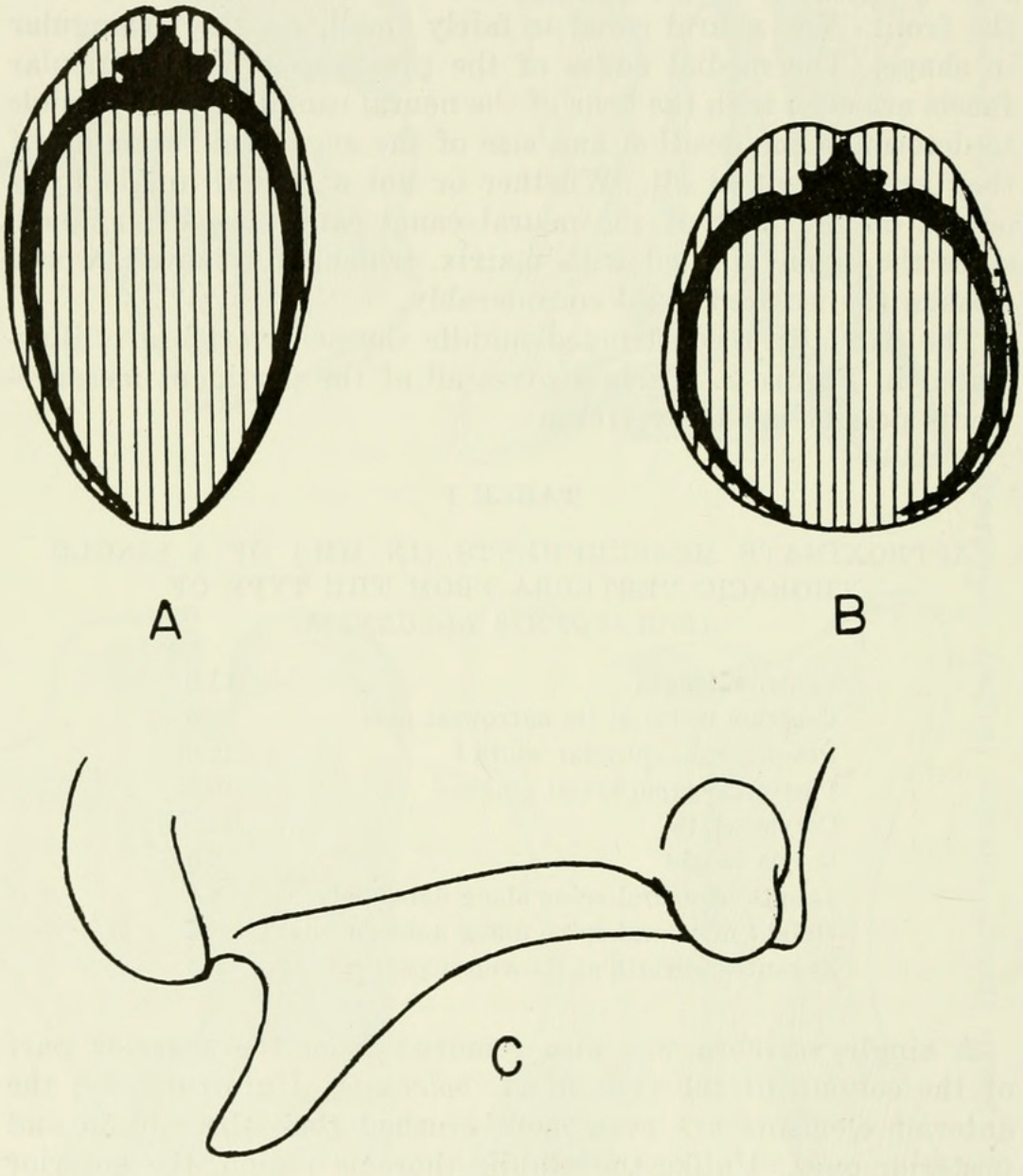

Fig. 3. Reconstruction of assumed cross section of the mid-body region in *Anomalophis bolcensis* (A), compared with that of a Recent *Constrictor constrictor* (B). The lower drawing (C) illustrates the general shape and position of the single hypapophysis present in the more anterior vertebrae of the type of *Anomalophis bolcensis*.

of these elements it was possible to remove it from the articulated position. The ventral surface of the centrum is provided with a well developed hypapophysis. It is only slightly compressed laterally. From the side it forms a very gentle sigmoid-shaped structure, directed more ventrally than posteriorly. Anteriorly, it is continued as a low midventral keel to the lip of the cotyle. The spine is located posteriorly on the centrum, the posterior edge beginning just anterior to the slight constriction near the base of the condyle (Fig. 3).

A well developed ridge extends from the posterior edge of each paradiapophysis to near the base of the condyle. These ridges converge only slightly posteriorly. The ventral surface of the centrum is quite flattened between the two ventrolateral subcentral ridges. The lateral borders of the centrum are almost parallel, but converge slightly posteriorly. No nutritive foramina are visible. Very little of the structure of the lateral or dorsal surfaces of the element are determinable. The prezygapophysial articular surfaces are quite evident. They are horizontal. From above, they are oval, with the long axis nearly parallel to the axis of the centrum, but diverging anteriorly.

The ribs vary considerably along the column in regards to their length, curvature, and degree of compression. Anteriorly, these elements are about 80 mm. long, only slightly curved, and very little compressed. They are quite attenuate. The middle thoracic members are somewhat more robust and more curved, particularly proximally. The entire length of a single rib in this area is about 90 mm. These members are proportionately more compressed proximally than are more anterior or more posterior ribs. Near the proximal end they are somewhat subtriangular in cross section. The more posterior ribs are about 110 mm. long, very filiform, little curved and hardly compressed at all along any part of their length. Views of the individual ribs and cross sections of them are given in Figure 4. The cross sections were obtained by taking out small broken sections of ribs in the various areas and then replacing them after examination. The proximal rib ends vary only slightly throughout the column from almost round to decidedly oval. The middle thoracic members are provided with a small indentation near the middle, presumably marking a very weakly developed costal process in these

elements. More anterior and posterior ribs lack any evidence of such a structure.

The shape of the rib, i.e., its length and degree of curvature, indicates that *Archaeophis bolcensis* possessed a body which was much more laterally compressed than any of the living snakes

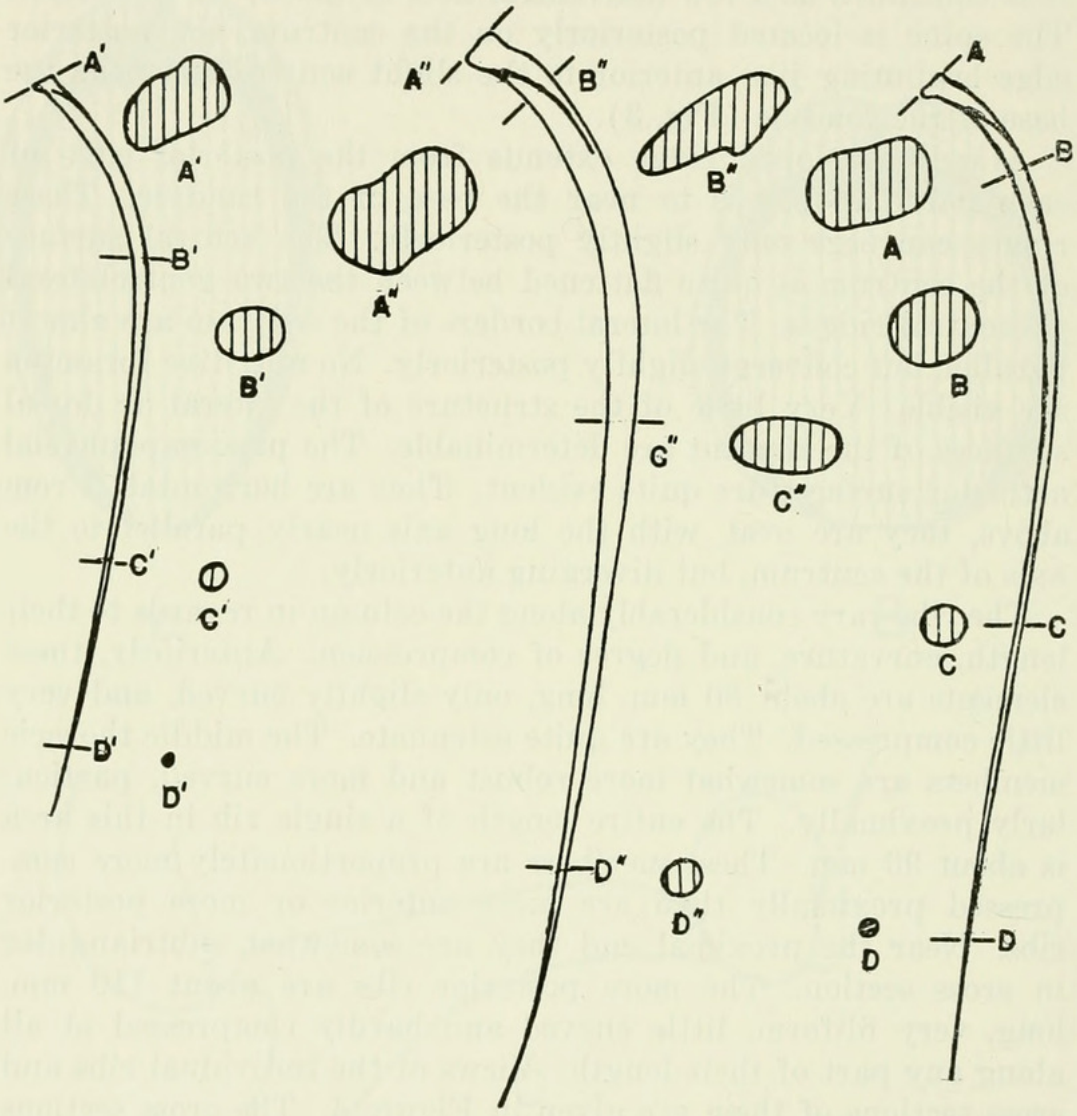

Fig. 4. Lateral and cross sectional views of the ribs from several regions along the body of the type of *Amomalophis bolcensis*. Left, anterior rib; middle, thoracic rib; right, posterior thoracic rib.

(Fig. 3). Its body shape is probably approached most closely by the posterior portions of some of the living hydrophids. Janensch's conclusion that this compression indicates that *Archaeophis* represents a highly modified marine form seems quite reasonable.

The type of *Archaeophis bolcensis* has been shown to differ in a number of structural features from that of *Archaeophis proavus*. The most important differences are: (1) the presence of a much better developed zygantrum, (2) the absence of hypapophyses throughout the middle and posterior portions of the vertebral column, (3) a condyle which is much more rounded, and (4) a well developed neural spine. *Archaeophis bolcensis* is unquestionably a snake. The type is to be referred to a genus other than that which includes the type of *A. proavus*. It has been suggested that the latter may be a fish (McDowell and Bogert, 1954). This idea was based on several characters already mentioned above. However, as these authors have pointed out, certain features of *A. proavus* are quite snakelike. The phyletic position of *A. proavus* is thus uncertain. Furthermore, this species is generically distinct from the type of *A. bolcensis*. The type of *Archaeophis* has been fixed as *proavus* (Kuhn, 1939). The species *bolcensis* is thus left without a generic name, for which I propose the following:

ANOMALOPHIS new genus

Diagnosis. A genus of Eocene snake, differing from all Recent and most fossil genera in lacking a costal process of the ribs. In the absence of this structure *Anomalophis* is approached by the Paleophidae.[1] It differs from members of this family in lacking well developed pterapophyses on the posterior part of the neural arch.

Genotype. Anomalophis bolcensis.

ANOMALOPHIS BOLCENSIS (Massalongo)

Diagnosis. Same as for the genus.

Holotype. MCZ 1001, 1002 and 1003.

Type Locality and Horizon. Near Verona, Italy; Monte Bolca limestone, Middle Eocene.

[1] Romer has recently (1956:563) provisionally placed the Paleophidae in the Lacertilia. The family was formerly considered to include only *Paleophis* and *Pterosphenus*, though he added *Simoliophis* and *Pachyophis*. The two latter genera may indeed be lizards, since their vertebrae are quite varanoid in general appearance. These two genera are placed in the Simoliophinae (Pachyophinae). However, *Paleophis* and *Pterosphenus* (Palaeophinae) are most certainly snakes, though perhaps somewhat aberrant. I propose that *Paleophis* and *Pterosphenus* be returned to the Suborder Ophidia (Serpentes), and that they constitute a distinct family distinguished largely on the basis of well developed pterapophyses and double hypapophyses in some of the vertebrae.

The combination of the differences, pointed out above, in both the vertebrae and ribs suggests that *Anomalophis* should be placed in a separate family of snakes, the Anomalophidae, containing only one genus at the present time, *Anomalophis*. The single specimen of the type species of the genus lacks a skull, but certain vertebral and rib characters are quite distinctive. The new familial characteristics are as follows: A single hypapophysis occurs in each of the more anterior vertebrae; in the middle and posterior vertebrae the hypapophysis is reduced to a low keel; centrum long; neural spine with a long base and not overly thickened; neural arch normal, without aberrant processes; no well developed accessory processes; ribs long, filiform, no costal processes, slightly compressed, with little curvature.

Cranial and pelvic girdle material of all of the earlier fossil snakes is sorely needed. Until this becomes available it seems best to defer a complete comparison of all of the later Mesozoic and early Cenozoic boid-like snakes (of which *Anomalophis* seems to be a member) until a later date.

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